



Victor F. Bugaev

ASIAN SOCKEYE SALMON

(freshwater period of life,
biological structure,
population dynamics)

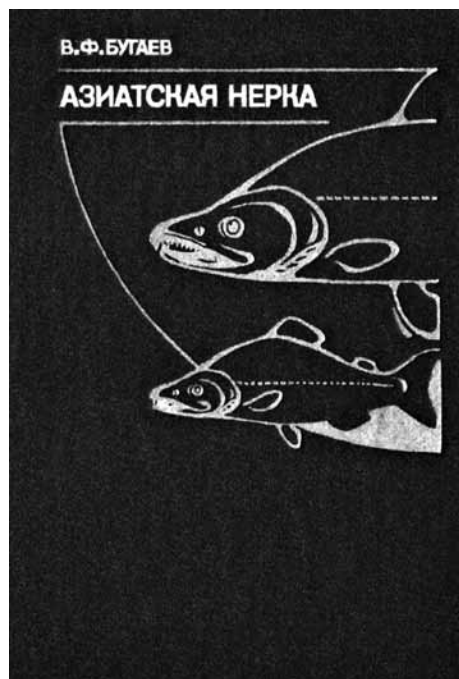
Kamchatka Research Institute of Fisheries & Oceanography
(KamchatNIRO)
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Victor F. Bugaev

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Edited by William E. Ricker and Richard J. Beamish



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Abstract

Key words: sockeye, age, length, weight, growth, scale structure, freshwater period, food competitors, infestation, food supply, population dynamics, fishing operations.

In Asia, the sockeye is the most abundant on the Kamchatka Peninsula in some years where approximately 90-95 % of all the Asian sockeye is harvested in the watersheds of the Kamchatka and Ozernaya rivers alone. This study is a summary of long-term observations on the Asian sockeye, and is based on the results of the author's 20 years of research. He examines the biological characteristics of 38 local sockeye populations (from Iturup Is. to Eastern Chukotka). Long-term data was used to analyze the interannual variability in the growth of juvenile sockeye of the Kamchatka and Ozernaya rivers. Questions concerning the structural analysis of the scales in juveniles and spawners of the sockeye are discussed in detail for the purpose of standardizing the age-determination procedure. Data on the feeding behaviour of juvenile sockeye in the watersheds of the Kamchatka and Ozernaya rivers are presented, and questions concerning the food competition of fish in the Kamchatka River watershed are discussed. The causes of fluctuations in the abundance of the sockeye in the Kamchatka and Ozernaya rivers are analyzed, and the latest methods of forecasting the abundance of these stocks and the fluctuations in the abundance of some secondary populations of Asian sockeye are examined. The author also looks at the future of natural and artificial reproduction of the species. The book also includes reference information.

This English version of book “Asian Sockeye Salmon” is intended for students, fishery biologists and scientists of the Pacific Rim countries, using the valuable resource – Salmon.

Tables – 165, Illustrations – 134, Bibliography – 612 + 55 titles.

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On front side of the cover: the spawning sockeye salmon in Azabach Lake (14 July 2010, Photo by Kentaro Morita (Hokkaido National Fisheries Research Institute, Japan).

On back side of the cover: the location of principal stocks of sockeye salmon in Asia (Bugaev, Kirichenko, 2008): 1 – Okhota R., 2 – Kukhtuy R., 3 – Ola R., 4 – Palana R. (Palaskoye L.), 5 – Tigil R., 6 – Khairyuzova R., 7 – Icha R., 8 – Oblukovina R., 9 – Krutogorova R., 10 – Vorovskaya R., 11 – Kol R., 12 – Kikhchik R., 13 – Utkha R., 14 – Bolshaya R. (Nachikinskoye L.), 15 – Opala R., 16 – Ozernaya R. (Kurul L.), 17 – Kambalnaya R. (Kambalnoye L.), 18 – Listvenichnaya R. (Listvenichnoye L.), 19 – Paratunka R. (Dalneye L., Blizhneye L.), 20 – Avacha R., 21 – Zhupanova R., 22 – Tikhaya R., 23 – Kronotskaya R. (Kronotskoye L.), 24 – Kamchatka R. (Azabash L., Dvukhyurtochnoye L., Nerpichye L.), 25 – Stolbovaya R., 26 – Khailyulya R., 27 – Rusakova R., 28 – Ivashka R., 29 – Dranka R., 30 – Karaga R., 31 – Tymlat R., 32 – Kichiga R., 33 – Vyvenka R., 34 – Avyavayam R., 35 – Kultushnaya R. (Ilir-Gythyn L.), 36 – Pakhacha R. (Potat-Gythyn L., Khai-Gythyn L.), 37 – Impuka R., 38 – Apuka R. (Vatyt-Gythyn L.), 39 – Ananapylgen R. (Anana Lagoon L.), 40 – Severnaya R., 41 – Tamanvayam R., 42 – Machevna R., 43 – Ilpiveem R., 44 – Ukalayat R., 45 – Khatyrka R., 46 – Meynypilgyn R. (Vaamochka L., Pekulneiskoye L.), 47 – Velkilveem R. (Kaipyngen L.), 48 – Orianda Lagoon, 49 – Amaam Lagoon, 50 – Tumanskaya R. (Mainitz L.), 51 – Seutakan R. (Seutakan L.), 52 – Achchen R. (Achchen L.), 53 – Sarannaya R. (Sarannoye L.), 54 – Gavanka R., 55 – Ladyginka R., 56 – Bettobu R., 57 – Zerkalnaya R., 58 – Sopochnaya R. (Sopochnoye L.), 59 – Urumpet R. (Krasivoye L.), 60 – Shikotzu R. (Shikotzu L.), 61 – Abira R.

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PREFACE TO ENGLISH VERSION

I am really happy today, as my book “Asian sockeye salmon” comes published in English. It is a translation of the monograph “Asian sockeye salmon (freshwater period of life, structure of local stocks, stock abundance dynamics)”, published in Moscow in 1995 by the publishing house “Kolos”, to be addressed to English speaking readers.

In Russia this book has been known extensively among salmon biologists, it often has been used to refer to, what can indicate of calling (popularity) of this data source for. In the other countries, say, in the USA, Canada or Japan, for today there are no fish biologists to read in Russian, and, alas, this is why till now the book unfortunately stayed off the English speaking community of fish biologists and out of the use which it deserves indeed.

In the mid of 1991 I started to write this book and told about that to several colleagues of mine abroad. Unexpectedly, in November I had received a telegram from Dick Beamish, Pacific Biological Station Nanaimo, where he wrote: “*I will help you book in English please let me know when you expect to have manuscript completed and the number of pages and figures*”. This telegram inspired my creative activity immediately, thus, in February of 1993 the book was finished to go to Canada for translation.

Canadian colleagues provided the translation into English through the Department of Fisheries and Oceans, Government of Canada. By autumn of 1994 the work was finished generally, the work (translation of the text, comments to the figures and citations) was done by H. De.

In May of 1995 I visited Canada, where in assistance with William Ricker and Dick Beamish I made some corrections in the version translated to clarify some moments pointed by William and Dick. Same time, Ed Elliot, a citizen of Nanaimo speaking Russian helped to translate the comments to the tables. Thus, the manuscript required making final technical preparations to be published by Canadian part.

In the course of the translation activity I succeeded in publication of my book in Russian in April of 1995 (last 50 samples having currently against 1000 samples at first), being supported by Mikhail Selifonov, who was a director of Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO) that time.

Meantime, the economic conditions in Canada changed, and the Pacific Biological Station unfortunately could not provide a sponsorship for publication to finish the project in 1996.

During several years the fate of the project was uncertain. The time stopped. Moreover, due to a delay, caused by personal life circumstances (getting sick heavily), I got able to renew the publication process activity about English version to publish it in Russia only in 2004.

It should be clarified also that Dick Beamish had not electronic version of the manuscript – it was taped, – and the taped manuscript required scanning at first and improving according to the remarks provided by Ricker in the original. All this job was accomplished in 2005 thanks to Victoria Plischenko from staff of KamchatNIRO.

From 2005 to 2010 I was captured strongly due to preparation several scientific and popular books on biology of sockeye salmon and other species for publishing, where I was one or one of authors: “The Fishes of Kamchatka River” (2007), “The Fish of Kamchatka River Watershed” (2007), “Rearing and Spawning Lakes for Asian Sockeye Salmon Stocks (2008), “Sockeye Salmon of the Ozernaya River” (2009), “Sockeye Salmon of the Kamchatka River” (2010), “The Flight Over the Sockeye Salmon Redd” (2010) and some others.

In view of a huge burden of permanent research work I had finished the English version of “Asian sockeye salmon” only in September of 2010. In the end of ends because of Ricker’s handwriting, which I hardly could or could not understand sometime, some comments he made were not included. I realized that further delay instead publishing the translated version as it is can make the book never published. No one can be immortal. So, I’m asking sincerely English speaking readers forgive me for some mistakes they might find in the text rather as a result of my poor English or misunderstanding, and no way because of the editorial comments by William Ricker.

I would like to express my sincere gratitude to all translators into English, including H. De, Ed Elliot and gone Zbignevev Kabata, who assisted in translation of some really complicated places of the manuscript.

My special deepest gratitude to William Ricker, a famous Canadian fish biologist and enthusiast of Science unfortunately gone now, who provided a huge editorial job to polish translated version, and also to Dick Beamish, excellent inspirer and editor, who’s supporting voice in the telegram was so important for me to go forward. Dick Beamish helped with the editing and arranged for the Canadian Government to translate the Russian into English.

No doubts that the publication of the book in Russia for English speaking researches of Pacific Salmon hardly could be without active support by S. G. Korostelev, current director of KamchatNIRO, and deputy director E. A. Shevlyakov, responsible for salmon researches. They helped to find necessary finances – a practical basis required to make the project accomplished.

I believe that the publication of the monograph “Asian sockeye salmon” in English would promote information exchange, better understanding between fish biologists of the Pacific Rim countries, using the valuable resource – Salmon.

*Dedicated to all past, present and future
researchers of the Sockeye salmon*

INTRODUCTION

The Pacific Ocean is inhabited by six species of Pacific salmon of the genus *Oncorhynchus*, namely the pink salmon *O. gorbuscha* (Walbaum), the chum salmon *O. keta* (Walbaum), the sockeye (red) salmon *O. nerka* (Walbaum), the coho salmon *O. kisutch* (Walbaum), the chinook salmon *O. tshawytscha* (Walbaum), and the masu salmon *O. masou* (Brevoort).

Pacific salmon are widely distributed off the Asian and American coasts in the North Pacific. The pink and chum salmon are the most common and abundant species on the Asian coast. The rest are relatively scarce. The opposite is observed on the American coast of the Pacific, i.e. the pink, sockeye, chinook and coho salmon are the most abundant. The masu is encountered only on the Asian coast.

Pacific salmon make up a comparatively small part of the total catch of fish; however, they provide one of the most popular and economically most profitable delicacies.

The sockeye is one of the most valuable species of Pacific salmon. The problem of preserving and rationally exploiting the biological reserves of the sockeye (and other species of Pacific salmon) has become one of international significance. The sockeye is one of the most researched species; it is the subject of more than 10,000 scientific publications. However, it should be said that not all the sockeye populations have been studied to the same extent. The largest number of publications to date is devoted to the largest or small model sockeye populations. Many of the secondary ones of local commercial significance have not been sufficiently studied to this day, which does not permit us to construct a unified model of the biology and population dynamics of the sockeye within its range. Another obstacle to this is that we still do not have a unified method and program by which to study this species, one which would combine and coordinate the efforts of scientists from different countries, though in the past 10-15 years, agreements to this effect have been reached and attempts made to coordinate the work between the scientists of Canada, USSR (Russia), USA and Japan. In addition to international efforts, there are national regional programs for research into Pacific salmon (including the sockeye), which have in some cases produced good results.

Under present-day conditions, when the anthropogenic effects on the environment and the direct impact of man on the fish population are causing and will continue to cause various and only partially predictable consequences, consistent evaluation of overall past research into the major commercial species of fish (in this case the sockeye) has become an increasingly urgent problem.

Specialized international conferences followed by the publication of participants' reports are extremely useful in the assessment of the overall level of research being conducted at a given time. A brilliant example of such a conference is the International Sockeye Symposium, Sockeye '85, held in Nanaimo (Canada) in 1985. The papers submitted by participants of this conference (including papers from the USSR) were published in the book "Sockeye Salmon (*Oncorhynchus nerka*) Population Biology and Future Management" (H. D. Smith, L. Margolis, C. C. Wood – ed., 1987).

Monographs written collectively or by one author are of great importance for a complete interpretation of the overall picture of the biology and population dynamics of fish species. R. E. Foerster's "The Sockeye Salmon (*Oncorhynchus nerka*)", published in Canada (1968), is a classic example of this type of monograph for the sockeye. In his book, the Canadian scientist summarizes his 40 years of research into the biology, reproduction and fishery of the sockeye, and attempts to bring together all that was known at that time about the life of this species at all the stages of its development.

Other, more specialized, monographs on the sockeye include the book "Studies of Alaska Red Salmon" (T. Koo – ed., 1962) and "Further Studies of Alaska Sockeye Salmon" (R. L. Burgner – ed., 1968), both published at Washington University in Seattle, USA. F. V. Krogus, Ye. M. Krokhin and V. V. Menshutkin's books "The Community of Pelagic Fishes of Lake Dalneye" (1969) and "The Pacific Salmon (Sockeye) in the Ecosystem of Lake Dalneye (Kamchatka)" (1987) should also be mentioned here. To this list we should also add I. B. Birman's book "The Marine Period of Life and Questions Concerning the Population Dynamics of the Stock of Pacific Salmon" (1985), many sections of which are devoted to the sockeye, as well as S. M. Konovalov's "Populational Biology of Pacific Salmon" (1980) which is devoted mainly to the sockeye of Azabach L. (Kamchatka R. watershed). The latter is, in our opinion, a very good example of an unsuccessful monograph due to gross errors in age determination.

Finally, a collective monograph entitled "Pacific Salmon Life Histories" (C. Groot, L. Margolis – ed., 1991) was recently published in Canada. It presents, in condensed form, the latest concepts on the biology of each of the species of Pacific sal-

mons. The section "Life History of the Sockeye (*Oncorhynchus nerka*)", written by R. Burgner, is practically all about the American sockeye.

However, the available generalizations on the biology of the sockeye do not make up for the lack of current information on the biological characteristics of the Asian sockeye.

At the present stage, due to the large number of publications and the high specialization of research, the appearance of personal monographs which would cover all the aspects of the sockeye's life cycle within its range is highly unlikely. In all probability, the future belongs to many-volumed collective works. In our own book, we limited ourselves strictly to the freshwater period of life, examining with a single subjective error the available archival material on the Asian sockeye, and using as a basis the results of our own research and those of our closest colleagues. We hope that this book, by creating a certain general picture of the biological characteristics of the Asian sockeye, will assist specialists in planning their research programs.

Generally speaking, besides presenting specific data on the biology of the Asian sockeye (of a reference nature), the purpose of this book was to present a specific approach to the study of its biology, illustrating its application with examples of real situations known to us. Without thrusting our point of view on anyone, we have presented our ideas concerning general questions directly related to the subject at hand. Our positions on these questions were formed over the 20 years that we have been studying the biology and ecology of sockeye populations, and were influenced considerably by people with whom I have communicated and worked.

I am deeply grateful to the staff of the Salmon Section of the Kamchatka branch of TINRO, with whom I have worked during expeditions and in laboratories, and with whom I have discussed the questions examined in this book, primarily B. B. Vronsky, L. Ye. Grachev, V. A. Dubynin; A. G. Ostroumov and M. M. Selifonov, as well as to the participants of joint expeditions and the staff of observation stations, V. N. Bazarkin, L. A. Bazarkina, T. L. Vvedenskaya, A. V. Maslov, L. V. Milovskaya, K. Yu. Nepomnyashchy, M. F. Selifonova, A. M. Tokranov and A. N. Khodko. I also wish to thank A. G. Kutsykh who executed the drawings for this book.

I am also grateful to the late I. B. Birman, I. I. Kurenkov and I. I. Lagunov, the oldest members of the Kamchatka branch of TINRO, who assisted me in every way possible and supported my endeavors.

I wish to express my profound respect for my colleagues R. Burgner, O. Mathiesen, D. Rogers (USA), G. Bilton, D. Brett, W. Ricker and the late R. Foerster (Canada) whose works on the sockeye of Alaska and British Columbia have had a great influence on me.

I always experience a special feeling of gratitude to my oldest friend, M. V. Mina, who works at the Laboratory of Post-natal Ontogenesis of the N. K. Kol'tsov Institute of Developmental Biology of the Russian Academy of Sciences (Moscow); it was during my personal contacts with him that my views emerged, and it was he who took upon himself the task of reading through and commenting on the contents of my manuscript.

Section 1. Distribution and life cycle of the sockeye

The sockeye breeds in rivers that fall into the Pacific Ocean, from the Southern California Klamath R. to the northern part of the Bering Sea in North America and from the northern part of Hokkaido to the northern part of the Bering Sea in Asia; it is not encountered in the rivers of the Sea of Japan watershed (Berg, 1946; Kaganovsky, 1960; Nikita, 1962; Hanamura, 1966; Foerster, 1968; Klovov, 1970; Forrester, 1987; Chereshev, 1990).

The range of the sockeye is noticeably narrower than that of the pink and chum salmons. The sockeye is second to these species in catches; in the eastern part of the range, it is second only to the pink salmon (Kuznetsov, 1937; Krogius, Krokhin, 1956; Levanidov et al., 1970; Forrester, 1987). According to Cleaver (1964), approximately 64 % of the North American sockeye catch came from the Naknek, Kvichak and Ugashik rivers, a number of other rivers of Bristol Bay and from the Frazer R. during 1955-1959. According to Taguchi (1956), the sockeye stocks of the Ozernaya and Kamchatka rivers alone made up 87 % of Japan's coastal take of this species.

The migration timing of sexually mature sockeye to the spawning grounds in different parts of the range varies from mid May up to the end of September (Kuznetsov, 1928; Pritchard, 1947; Semko, 1954; Krogius, Krokhin, 1956; Rousefell, 1958; Yegorova, 1977; Bugaev, 1987a). After entering the spawning waters, the adult fish can spend up to a month in rivers and from 1-2 to 3-4 months in lakes before they begin to spawn (Krogius, 1954; Krogius, Krokhin, 1956; Iyevleva, 1964; Foerster, 1968).

In some cases, seasonal races of the sockeye are clearly distinguished on the basis of the periods and areas of reproduction; there is usually an interval of 15-20 days between the spawning periods. For example, an early (spring) race and a late (summer) race are differentiated in the Asian sockeye; in some cases, the latter may be represented by several forms (Berg, 1948; Ostroumov, 1965; Smirnov, 1975). Some of the lake populations of sockeye do not have clearly defined seasonal races (Yegorova, 1970a; Konovalov, 1980), which is often due to the extremely low numbers of one of them. Seasonal races are sometimes distinguished in American sockeye populations as well, but the principal stocks still belong to the late form (Narver, 1968; Foerster, 1968; Burgner, 1991).

The spawning grounds of the sockeye are located in places where ground waters emerge in the shallows of rivers, near springs, in small spring-fed lakes, in the littoral zone of lakes (Krokhin, 1960).

The nests are usually built at depths varying from 30 cm to 2 m, less commonly 4-6 and even 30 m (Ricker, 1966; Os-

troumov, 1970). The velocity of the current does not exceed 10-20 cm/s at river spawning grounds, and is equal to zero at lake spawning grounds. For spawning, the sockeye prefers places where the ground can be loosened quite easily and there is a substantial admixture of sand and silt (Kuznetsov, 1928; Krogius, 1951; Burner, 1951; Semko, 1954; Krokhin, 1960; Foerster, 1968).

The spawning periods of the sockeye in various bodies of water is very closely related to the mean temperature of egg incubation, i.e. the higher the temperature, the later spawning occurs (Brannon, 1987). It is presumed that the clearly defined temperature differentiation of the separate groups at the spawning grounds is one of the factors responsible for the existence of the markedly different seasonal races of the sockeye in the watersheds of some rivers and lakes (Brannon, 1987; Burgner, 1991).

As established by Hanson and Smith (1967), the female selects and protects a small territory; she digs and then buries the nest. After spawning, the females remain at the nest until they die. The males of the sockeye are polygamous. In some cases, they also help build the nests (Hartman, Raleigh, 1964). The eggs are deposited in individual portions, and buried at a depth of 10-30 and even 40 cm; in the case of shifting ground, one redd consists of up to 4-5 individual nests of eggs (Kuznetsov, 1928; Semko, 1954; Mathisen, 1966a).

The embryonic and larval development of the sockeye lasts from 5 to 8 months (Smirnov, 1975).

The period of emergence of alevins from the ground is a lengthy one due to the differences in the spawning periods of the adult fish and the temperature conditions in the breeding areas. The earliest emergence of sockeye alevins from the redds is noted in January–February (Krogius, Krokhin, 1956) in the watershed of the Kamchatka R. (Krogius, Krokhin, 1956), and from the end of March up to September in Kuril L. (Selifonov, 1970a). In the waters of North America, the emergence of sockeye alevins from the ground begins in April and continues up to September (Burgner, 1964; Ricker, 1966; Foerster, 1968). Sexual differentiation occurs in the alevins prior to the disappearance of the yolk sac (Persov, 1968).

Beginning with the larval period, the sockeye lives in groups, but this is not always observed (Hoar, 1958). Its young begin to forage even with the yolk sac still intact (McCart, 1967). While at the spawning grounds, the young feed mainly on benthic organisms (Synkova, 1951; Semko, 1954; Rogers, 1968; Simonova, 1972a; Bugaev, Nikolaeva, 1989). In lakes, young fish several days old to 1-3 months old live in the littoral zone and feed on small crustaceans, chironomid larvae and flying insects; they later migrate to the pelagic zone where they feed on mostly zooplankton, flying insects and, as an exception, benthopelagic organisms (Krokhin, Krogius, 1956; McCart, 1967; Rogers, 1968; Burgner et al., 1969; Belousova, 1974; Grainoth et al., 1986; Vvedenskaya, 1991). During the winter, the young feed mainly on plankton (Markovtsev, 1972).

From the spring-fed breeding areas, the young of the sockeye migrate to the quiet areas near river banks or to lakes. If this migration to the foraging grounds happens to be downstream, it takes place during the night (Robertson, 1949; Semko, 1954; Simonova, 1974). However, if the foraging grounds lie upstream, the migration of sockeye alevins takes place during the day (Brannon, 1972). The upstream and downstream migration of young sockeye has been described in detail by McCart (1967). The upstream migration of sockeye fry to lakes has been noted for some breeding areas both in Asia, and in North America (Andrew, Green, 1960; McCart, 1967; Belousova, 1974; Konovalov, 1980; Bugaev, 1981a).

The length of the freshwater period in the young of different sockeye populations usually varies from one to four years (Foerster, 1968; Mosher, 1969, 1972; Bugaev, 1989; Bugaev, 1991a, 1992), but in the Asian sockeye we have encountered individuals with a freshwater period of even 5-6 years (Bugaev, 1991a, 1992). During the freshwater period of life, growth depends greatly on the foraging conditions which are indirectly dependent on the abundance of the year-classes. During the years when young fish are highly abundant, the growth rate drops significantly, and vice versa, which is due to the variability in feeding conditions, i.e. the depletion of food organisms (Foerster, 1944; Krogius, 1961; Johnson, 1965; Burgner, 1964; Mathisen, Kerns, 1964; Ward, Larkin, 1964; Meehan, 1966; Burgner et al., 1967; Burgner et al., 1969; Mathisen, 1969; Parr, Burgner, 1971; Goodlad et al., 1974; Bugaev, 1983a; Dubynin, 1986; Graynoth, 1987; Burgner, 1987; Kyle et al., 1988; Bugaev et al., 1989; Bugaev, 1989; Koenings, Kyle, 1991, etc.).

The interannual variability in the growth of the young affects both their survival in fresh waters (Koenings, Kyle, 1995), and their future survival at sea (Ricker, 1962; Koenings, Barket, 1987a; Koenings et al., 1993).

As they feed and grow in lakes, the young of the sockeye perform intricate vertical feeding migrations (Narver, 1970; Krogius, 1974; Eggers, 1978; Brett, 1983; Levy, 1987; Nikolaev, 1988a, 1990; Burgner, 1991).

During the freshwater period, the young of the sockeye compete for food not only with their own species, but with other species as well (Burgner et al., 1969; Ellis, 1974; Jaenicke et al., 1987; O'Neil, Nyatt, 1987), and they are also exposed to predators (Foerster, Ricker, 1941; Ricker, 1941; Burgner et al., 1969; Kokhmenko, 1970; Ruggerone, Rogers, 1984; McInture et al., 1988; Ruggerone, Rogers, 1992).

From spring-fed creeks* and rivers that are not connected with fairly large and deep lakes, the young of the sockeye can migrate downstream to the sea during the first year, even with the remains of the yolk sac still intact (Andreyeva, 1954; Krogius, Krokhin, 1956; Semko, 1954; Clemens, Wilby, 1961; Burgner, 1962; Ricker, 1966; Hartman et al., 1968; Mosher, 1972; Karpenko, 1979; Bugaev, Karpenko, 1983; Bugaev, 1984; Bugaev, 1987; Wood et al., 1987, 1987a; Birtwell et al., 1987; Murphy et al., 1988; Thedinga et al., 1988; Either et al., 1988; Bugaev, 1989; Heifetz et al., 1991; Bugaev, 1991a, 1992).

Sockeyes migrate to the sea mainly as one-year-olds, two-year-olds and, less commonly, three-year-olds, the age composition of the downstream migrants being specific for each breeding area (Foerster, 1968; Selifonov, 1970, 1975; Mocher,

*The word "klyuchi" is used here; in W. E. Ricker's "Russian-English dictionary for students of fisheries and aquatic biology" (1973), this word is translated as "a slow-flowing spring-fed creek, or abandoned river channel, sometimes with lake-like expanses (used particularly in Kamchatka where many of them are used by salmon for spawning).

1969, 1972; Ricker, Smith, 1975; Bill, 1984, 1986; Bue, 1984, 1986; Eggers, 1984; Hattanen, 1984; Bucher, 1986; Minard, Brandt, 1986; Frid, Yuen, 1986, 1987; Krogius et al., 1987; Burgner, 1987; Bugaev, 1989; Bugaev, 1991a, 1992, etc.).

The seaward migration of the young from each body of water occurs mostly during the same period, but the migration timing within the boundaries of the range may fluctuate from the end of March and up to September (Lagunov, 1939; Krogius, 1954; Clutter, Whitesel, 1956; Hartman et al., 1967; Bugaev, Karpenko, 1983; Bugaev, Bazarkin, 1987; Burgner, 1991). The young of older age groups are usually the first to migrate downstream (Clutter, Whitesel, 1956; Krogius, 1967a; Foerster, 1968; Selifonov, 1970; Bugaev, 1976; Bugaev, Bazarkin, 1987).

Dwarf (residual) and freshwater (kokanee) forms of the sockeye, which mature without migrating to the sea, develop in some bodies of water (Ricker, 1938, 1940; Smirnov, 1959; Ward, Larkin, 1964; Krokhin, Kurenkov, 1964; Kurohagi, 1965, 1966; Krokhin, 1967; Kurenkov, 1977, 1979; Gorshkov, Gorshkova, 1977; Ostroumov, 1977, 1979, 1985a; McDonald, Hume, 1984; Graynoth, 1987; Burgner, 1991).

The sea period in the life of the sockeye has been studied in less detail than the freshwater period. The downstream-migrant young sockeye stay close to the shores usually for a short period of time, and in autumn migrate to the open parts of the North Pacific (Konovalov, 1971). The young of different age groups spend the winter mainly in the zone from 168° E to 139° W long. (Research by Canada, 1966; French et al., 1966-1967); their wintering grounds extend to 57° N lat. (French, Mason, 1963-1964; Birman, 1967, 1985), and in the south to the 47th parallel in the eastern part of the range, and to the 42nd parallel in the western part of it (Tagushi, Kisikawa, 1954; Birman, 1958, 1967; Margolis et al., 1966; French et al., 1966-1967; Konovalov, 1971; Birman, 1985; Forrester, 1987; Burgner, 1991).

In summer, the young sockeye of Bristol Bay begin their foraging migration northward to the Aleutian region of the Pacific, along the Aleutian Isls. westward, entering the Bering Sea through all the straits; the Kamchatka sockeye migrates en masse to the Commander Isls. region, and the sockeye from the Pacific coast of North America migrates to the northern part of the Gulf of Alaska and Aleutian Isls. region (Birman, 1958, 1967; Hart, 1962, 1966; Kondo et al., 1965; Research by Canada, 1966; Konovalov, 1971; Birman, 1985; Forrester, 1987; Burgner, 1991). The foraging migrations of young sockeye are largely a repetition of the spawning migrations of sexually mature fish.

The food organisms at the foraging grounds of the sockeye at sea consist mainly of the prolific subarctic species of crustaceans, pteropods, and the young of pelagic, bathypelagic and bottom fishes. Its food spectrum comes the closest to that of the pink salmon (Andriyevskaya, 1958, 1966; Allen, Aron, 1958; Ito, 1967; LeBrasseur, 1966; Favorite, 1970).

After one winter at sea, a very small part of the fish migrates to the spawning grounds. After the second winter, the part that migrates to the spawning grounds increases significantly. Of the fish that have already spent three winters at sea, nearly all migrate to the spawning grounds, and only a small part remains for a fourth winter.

The survival, growth and migration timing of the sockeye during the sea period of life depend on the foraging conditions and the abundance of the sockeye in the ocean (Rogers, 1980; Burber, Walker, 1980; Burgner, 1980; Peterman, 1980; Birman, 1985; Burgner, 1991, etc.).

During the anadromous migration, the sexually mature fish enter the spawning waters with a different ratio of the various age groups (Fosket, Jenkinson, 1957; Krogius, 1958; Henry, 1961; Killick, Klemens, 1963; Mosher, 1972; Hanamura, 1966; Foerster, 1968; Krogius, 1970; Konovalov, 1980; Fried, Yuen, 1986, 1987; Burgner, 1987; Bugaev, 1987; Bugaev, 1989; Burgner, 1991; Rogers et al, 1991; Bugaev, 1991a, 1992, etc.).

The length of the freshwater period of the sockeye is definitely correlated with the length of its sea period, but this question has not yet been clarified, and requires further verification (Bilton, 1970a, 1971; Dirin, 1984; Rogers, 1984; Peterman, 1985; Bradford, Peterman, 1987; Bugaev, 1992, etc.).

The "homing instinct" is well-developed in the sockeye, i.e. the adult fish enter only the home river or tributary to spawn (Gilbert, 1916-1923; Barnaby, 1944; Krogius, 1958; Zaks, Sokolova, 1961; Cleaver, 1964; Hartman, Raleigh, 1964; Raleigh, 1967; Konovalov, 1971, 1980; Il'in et al., 1983; Quinn et al., 1987; Varnavsky, Varnavskaya, 1985; Burgner, 1991); however, this attachment of certain parts of a local population to particular breeding areas still requires conclusive proof (Yarzhombek, Klyashtorin, 1980). Yu. P. Altukhov's observation (1974) that the sex ratio at the spawning grounds of a local stock is variable, but approximates the natural ratio (1:1) for the entire population points indirectly to the influence of random factors during the distribution of spawners to the different breeding grounds. Marine investigations have also shown that the sockeye, like other salmons, forages in specific areas, which is an indication of its "attachment" to specific water masses in the ocean (Birman, 1964, 1967, 1985).

The population dynamics of the principal commercial stocks of the sockeye has been researched fairly well, and these stocks are currently being monitored by scientists (Kerns, 1961, 1966; Mathisen, 1971; Dahlberg, 1973; Smith, 1975; Ricker, Smith, 1975; Harris, Rogers, 1979; Straty, Janicke, 1980; Ricker, 1982; Cross et al., 1983; Cook, Guthrie, 1987; Gard et al., 1987; Henderson et al., 1987; Hyatt, Steep, 1987; Marshall et al., 1987; Minard, Meachem, 1987; Ricker, 1987; Quinn, Terhart, 1987; Blackbourn, 1987; Collie, Walters, 1987; Macdonald et al., 1987; Eggers, Rogers, 1987; Walters, Staley, 1987; West, Mason, 1987; Wood et al., 1987; Sproot, Kadowaki, 1987; Rogers, 1987; Williams, 1987; Woodey, 1987; Selifonov, 1988, 1988a; Bugaev, 1987a; Fried, Yuen, 1986, 1987; Eggers, 1989; Collie, Peterman, Walters, 1990; Rogers et al., 1991, etc).

In order to obtain more accurate information on the abundance of large local stocks of the sockeye, differentiation of the catches and estimates of the removal of sockeye from the sea are being carried out (Mocher, 1963; Selifonov, 1975; Fredin, Worlund, 1974; Cook, Lord, 1978; Harris, 1987, etc.).

Over the past few years, there has been a steady tendency to research minor sockeye stocks in an effort to increase the effectiveness of their exploitation (Meehan, 1966; Kurenkov, 1970; Eggers, 1980; Chereshev, 1981; Ivankov, 1984; Kurenkov, Kurenkov, 1988; McGregor, 1985; Bergander, 1985; McPherson, 1987; Williams, 1987; Eiler et al., 1988; Bugaev, 1989; Koenings et al., 1989; King, Tarbox, 1989; Heifetz et al., 1989; Clupach, Kyle, 1990; Kyle, Litshfield et al., 1990; Kyle, White et al., 1990; Shields, Kyle, 1990; White et al., 1990; Kyle, Honold, 1991; Bugaev, 1991a, 1992, etc.).

Catch statistics for Pacific salmon, including the sockeye, are being published (INPFC, 1979; Alaska Commercial..., 1989; Catches of Pacific Salmon..., 1979, etc.).

The natural fertilization of lakes by volcanic ash during the eruption of volcanoes can increase the abundance of sockeye stocks (Either, Rounsefel, 1957; Kurenkov, 1966; Kurenkov, 1975; Bugaev, 1986b; Bugaev, 1987a; Mathisen, Poe, 1987). This has initiated a new trend to increase the abundance of the sockeye stocks by artificial fertilization of their foraging grounds (Barracough, 1972; Manzer, 1976; Le Brassier et al., 1976; Rogers et al., 1982; Stockner, Shortreed, 1985; Kurenkov, Tarasov, 1986; Stockner, 1987; Kurenkov, Kurenkov, 1988; Selifonov, 1986, 1988; Problems of Fertilization..., 1988, etc.).

An attempt has been made to acclimatize the anadromous form of the sockeye in New Zealand by introducing fertilized eggs (ova) from British Columbia (Tompson, 1922). The eggs were collected from anadromous sockeye spawning in Shuswap L. (Frazer R. watershed) in September 1901, and it is possible that some of the eggs were taken from kokanee. The eggs were incubated and the alevins released into the tributaries of Ohau R. and Waitaki R. A stock of landlocked sockeye (kokanee?) formed in Ohau L. (Ayson, 1958), but a migratory anadromous form did not develop, probably because the downstream migrants which had grown at sea became disoriented in the southern part of the Pacific Ocean. At the present time, the highest abundance of landlocked sockeye is noted in Ohau L. and other lakes of the Waitaki R. watershed (Graynoth, 1987). In February-March, sexually mature fish begin their spawning migration to the Larch R. at the head of Ohau L., and to other breeding areas.

In 1964, due to the construction of a dam in the lower reaches of the Waitaki R., a lake (Benmore) formed in its watershed, and some of the young landlocked sockeye from Ohau L. migrated downstream to this lake to forage. With the appearance of Benmore L., two groups of landlocked sockeye with different spawning periods formed in the Waitaki R. watershed (Graynoth, 1987).

In Benmore L., young landlocked sockeye migrate from the alevin stage to the age of 3+, and they reach sexual maturity at the age of 2-5 years. In Ohau L., landlocked sockeye reach the adult stage also at the age of 2-5 (Graynoth, 1987).

Benmore L. landlocked sockeye migrate to Ohau L. to spawn, and they spawn somewhat earlier than other fishes that spawn in Ohau L., but do not migrate as juveniles to forage in Benmore L.. Interbreeding of these two forms is not observed. If these two forms emerged as a result of genetic differences, then it is unlikely that the genetic differences came about over a period of 12 years (since 1964). This indicates that genetic differences were not the main factors responsible for the differentiation in growth, age and biology (18-25 year-classes cryptogenetic) after the formation of Benmore L. where landlocked sockeye grow considerably better than in Ohau L. The result was a form with a higher growth rate and earlier spawning time, which migrates to Benmore L. to feed and grow, and a form characterized by a lower growth rate, which spends its entire life in Ohau L. and spawns later (Graynoth, 1987).

From 1964 to 1979, salmon could migrate freely between Ohau L. and Benmore L. located in the lower part of the Waitaki R. watershed. In 1980, due to the construction of a dam at the outfall of the river flowing out of Ohau L. and the construction of yet another dam in 1981 in the middle of Ohau L., which connected the latter with Benmore L., the spawning migration of landlocked sockeye upstream was blocked (Graynoth, 1987, 1988).

As the above review has shown, the biology of the New Zealand landlocked sockeye is, in miniature, highly reminiscent of the life cycle of the migratory anadromous sockeye of the North Pacific.

Section 2. Species structure in the sockeye

At the present time, evolutionists view the species as consisting of a multitude of populations (subunits) which play the role of "evolutionary units", combinations of individuals which participate in the process of evolution as something whole (Dobzhansky, 1950, 1955, 1970; Schwarts, 1967; Mire, 1968; Timofeyev-Ressovsky et al., 1973; Shaposhnikov, 1974; Mina, 1980).

According to T. Dobzhansky (1950, 1970), species fall into assemblages of "Mendelian populations" (Wright, 1931) of different hierarchy, i.e. subspecies, races, local populations of different ranks. A Mendelian population is a community of individuals of a sexually reproducing species in which mating occurs, individuals sharing a common gene pool (Dobzhansky, 1970); the evolutionary processes occurring in any part of it are capable of affecting the fate of the whole (Dobzhansky, 1955).

M. V. Mina (1980) wrote that the majority of authors later accepted the idea of populational hierarchy itself, but all efforts were, as a rule, directed at searching out that one "main" level in this hierarchy, and it was claimed that only groups of this level served as "evolutionary units" and that only these groups deserved to be called populations.

We share the point of view (Mina, 1980) that the hierarchy of Mendelian populations as defined by T. Dobzhansky (1950, 1955, 1970) suits the situations observed in nature to the fullest extent.

According to M. V. Mina (1980), a population can be defined as 1) a self-reproducing group, 2) a group of individuals

more likely to mate with any member of the same group than with individuals not belonging to this group, and 3) a group of individuals with genes that can become part of the genome of one individual in a number of generations.

The largest population unit is the species, and the smallest one is the group of individuals which at certain periods of its existence can be represented even by a family or a pair of spawners. Populations of the higher hierarchy are more stable over time and more isolated reproductively than the lower hierarchy.

The term “population” is primarily an evolutionary-genetic one. It is advisable to view a stock as a population or a group of populations which are exposed to the same fishing tactics or strategy (Kuznetsov, Mina, 1982).

Within its area of distribution, the sockeye is distributed intermittently, and is represented by local stocks (isolates), the existence of which is not being questioned by anyone at the present time (Foerster, 1968; Konovalov, 1971, 1980; Smirnov, 1975; Burgner, 1991).

Local stocks of sockeye may consist of well-defined seasonal races which are characterized by biotopic and temporal isolation; however, some do not have clearly defined seasonal races (Yegorova, 1970a; Konovalov, 1980).

At the present time, the question concerning the mutual hierarchy of a local stock and seasonal races in Pacific salmon remains unclear (Berg, 1948; Birman, 1952, 1981; Ostroumov, 1965; Ivankov, 1967; Roslyi, 1975; Smirnov, 1975; Konovalov, 1972, 1980; Gritsenko, 1981; Krogus, 1983). O. F. Gritsenko’s point of view (1981) appears to be the most realistic; he believes that the seasonal races of different species of Pacific salmon can have a different ecological-genetic nature and origin.

For the sockeye, we view the seasonal races as structural components of local stocks of varying complexity in much the same way as S. M. Konovalov does (1972, 1980). In our opinion, this is based on the fact that markedly different seasonal races of sockeye, due to the extreme scarcity of one of them, are not observed in all the primary stocks (Yegorova, 1970a; Konovalov, 1980) and practically come down to a single one in several stocks of a lower order (Ostroumov, 1975b; Bugaev, 1983c, 1986a), as well as on the fact that several forms of a late seasonal race are known to exist (Berg, 1948; Ostroumov, 1965; Smirnov, 1975). For example, because of its low numbers, an early seasonal race was only recently established in the sockeye of Ozernaya R. (Varnavskaya, 1988a).

The presence of a direct correlation between the area of the spawning grounds of each seasonal race and the abundance of these seasonal races in river watersheds corroborates the point of view that seasonal races in the sockeye are the components of local stocks (Section 6), as does the formation of seasonal races in the migratory anadromous sockeye acclimatized in New Zealand which developed into landlocked sockeye and formed seasonal races only after the construction of a dam and the formation of a lake in the river watershed 18-25 generations after acclimatization (Graynoth, 1987). There is a possibility that the seasonal races in the sockeye interbreed during extremely abundant years (Bugaev, 1986a).

As for the spatial subdivision of certain local stocks of the sockeye, we believe that this question requires an individual approach in each case, due to the fact that there are local stocks which are confined to a system of large rivers with local stocks that breed in tributaries of a second, third, etc. order (sub-stocks), in small separate rivers and large lakes (often with a system of sub-stocks).

In local sockeye stocks, S. M. Konovalov (1972, 1975, 1980) distinguishes “sub-isolates”, i.e. self-reproducing groups of separate breeding areas. Each seasonal race is characterized by its own specific subisolates. These subisolates are characterized by their own genetic, ecological, age and other structures which are correlated in a specific way (Konovalov, 1975, 1980).

Without rejecting the concepts of a subisolate being a population of a lower rank, a number of biologists (including us) do not share S. M. Konovalov’s interpretation of the structure of a subisolate (Konovalov, 1975, 1980), and believe that further research is necessary in this area (Yarzhombek, Klyashtorin, 1980; Mina, Gritsenko, 1981).

Section 3. Research history of the Asian sockeye

Detailed information on the history of research into the Asian sockeye has been presented by I. F. Pravdin (1940), I. I. Lagunov (1968) and Ye. M. Krokhin (1968). In our review, we have made use of some of the data provided by these authors, supplementing them with our own recent material.

The research on the Kamchatka region was begun much earlier than in other regions of the Far East. The earliest data on this peninsula and the fishes in its coastal waters appear in the book “Description of the Land of Kamchatka”, written by a participant of the 2nd Kamchatka Expedition, S. P. Krasheninnikov (1949), and published for the first time in 1755.

Scientific expeditions and individual explorers visited Kamchatka in the 19th century and at the beginning of the 20th. The most fruitful Kamchatka expedition was the one undertaken by the Russian Geographic Society (1908-1909) with the participation of V. L. Komarov, P. Yu. Schmidt, A. N. Derzhavin and others. The papers of the zoological section of this expedition contain data on the biology of the fishes and other aquatic animals of this peninsula.

In 1925, the Pacific Scientific Fisheries Station (TONS) was established in Vladivostok. In 1929, it became the Pacific Scientific Institute of Fisheries (TIRKh), today known as the Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO). Its scientists studied the commercial fishes of Primor’ye (Maritime Territory), Kamchatka and the north-western coast of the Bering Sea. For example, during the 1920s, I. F. Pravdin worked on the Bolshaya River, I. I. Kuznetsov on the Kamchatka R., A. G. Kaganovsky on the Anadyr R., I. A. Polutov on the Apuka R., etc. Some of the results of these

investigations were published in I. I. Kuznetsov's study "Some Observations on the Reproduction of Amur and Kamchatkan Salmon" (1928) and I. F. Pravdin's "A Review of Research on Far Eastern Salmon" (1940).

The study of the sockeye on the Kamchatka Peninsula is inseparably linked to the organizational history of scientific fishery research in this region.

Regular investigations of the commercial fishes of Kamchatka, primarily Pacific salmon, were begun in the summer of 1932, after a branch of TIRKh had been set up in the city of Petropavlovsk-Kamchatsky. A great deal of effort was put into the organization of this branch by M. A. Fortunatov, its first scientific adviser. The first scientists on staff were A. S. Baranenkova, V. B. Bool, D. G. Manizer, F. V. Krogus, Ye. M. Krokhin, V. I. Gribanov, K. I. Panin, I. A. Polutov, R. S. Semko, M. L. Alperovich, and others.

The primary and main goal set before the Kamchatka branch of TONS was to study the biology and breeding conditions of Kamchatka salmon, to determine the causes of the fluctuations in commercial stocks, and to develop a method of forecasting the magnitude of spawning migrations. Since the biology of salmon had been poorly researched, it became necessary from the very first years to launch expeditions to the areas where these fishes breed.

In August 1932, Ye. M. Krokhin, F. V. Krogus and A. S. Baranenkova visited Dalneye L. in the watershed of the Paratunka R., and collected material on the biology of the sockeye breeding in this lake. This work was continued in 1933 by A. S. Baranenkova, and in 1934-1935 by P. I. Orlova and V. Ye. Gorogodsky; from 1935 and up to the middle-end of the 1970s, the research on this lake was continued by F. V. Krogus and Ye. M. Krokhin.

In September-November 1932 and in the spring and autumn of 1933, Ye. M. Krokhin and F. V. Krogus conducted investigations on the sockeye of Kuril L. (Kurilskoye Lake). The results of these investigations are found in the monograph "Synopsis on Lake Kurilskoye and the Biology of the red salmon, *Oncorhynchus nerka* (Walb.), in Its Basin" (1937).

During the autumn of 1932 and spring of 1933, A. S. Baranenkova studied the sockeye of Nachikinskoye L. (watershed of the Bolshaya R.).

During the investigations on lakes Kurilskoye, Nachikinskoye and Dalneye, a visual assessment of the abundance of sockeye at the spawning grounds was carried out for the first time, the sizes of the breeding areas were determined and the latter charted, and the survival rate of the fish eggs was also determined.

In the summer of 1933, Ye. M. Krokhin and F. V. Krogus began joint investigations in the Bolshaya R. watershed where all the species of Pacific salmon breed. The results of these investigations were published in the book "Synopsis on the basin of the Bolshaya River and the Salmon Spawning Grounds Located There" (1937a).

In 1934, the research in the Bolshaya watershed was carried on by P. A. Dvinin, and from 1935 was continued by him and R. S. Semko who had conducted research in this area for many years. A number of biological facts on the sockeye of the Bolshaya R. are presented in R. S. Semko's extensive work "The Stocks of Western Kamchatka Salmon and Their Commercial Significance" (1954).

In the spring of 1935, Ye. M. Krokhin and M. L. Alperovich launched an expedition to Kronotskoye L. to study this lake and the freshwater form of sockeye (kokanee) found there in an effort to determine the possibility of turning this lake into a breeding place for a large population of anadromous salmon.

Due to the fact that expeditionary research does not make it possible to establish the causes of fluctuations in the natural reproduction of salmon and to characterize the dynamics of their abundance, the Kamchatka branch of TINRO eventually began to organize permanent research stations.

The first permanent station for observing the reproduction of the sockeye was set up in 1937 on Dalneye L. in the watershed of the Paratunka R., and that same year another one was set up at the Ust-Kamchatsk fish cannery to study the salmon in the watershed of the Kamchatka R. In 1940, a permanent observation station was established on Kuril L. at the outlet of the Ozernaya R. In 1941, a permanent observation station was set up at Karymaisky Klyuch [spring] in the watershed of the Bolshaya R.

The observation station on Dalneye L. (Paratunka Experimental Laboratory - PEL) operated successfully. Only several years after its organization, it produced the first quantitative forecast of sockeye abundance for this area. At the first stage (up to the end of the 1940s), the PEL developed a sockeye forecasting method (Krogus, Krokhin, 1948, 1956). This method, with some modifications, is still being used in a number of sockeye breeding areas (Krokhin, 1968).

Long-term data on the breeding conditions of the sockeye have shown that they are closely correlated with the hydrodynamic conditions in the lakes. It has been established that the degree of cooling of the latter prior to freeze-up determines the extent to which these conditions are favourable to the feeding and growing of the juveniles in the coming vegetative period (Krogus, Krokhin, 1948).

At the end of the 1940s, the abundance of the Eastern Kamchatka sockeye stocks began to diminish considerably. This ushered in the second stage of PEL operations. It became necessary to develop methods of restoring the abundance of the sockeye. In an effort to accomplish this, PEL conducted fish-rearing investigations, which included studying the food consumption of the sockeye (Krokhin, 1957). During the same period, a comparative study of sockeye breeding areas was carried out (Krokhin, 1960).

Analysis of long-term data on the phosphate regime of Dalneye L. has shown that dead spawned-out fish are an important element of the phosphate balance in lakes used for spawning and foraging (Krokhin, 1957a), and influences the population dynamics of the sockeye breeding in these lakes.

Questions concerning the periodic fluctuations in the ecosystem of Dalneye L. and their correlation with the rhythms of solar activity have also been discussed (Krokhin, Krogus, 1979).

The physiological condition of downstream-migrant sockeye was studied in relation to the foraging conditions of the juveniles in the lake (Yarzhombek, 1964; Akulin, 1966, 1968). The seasonal and diel rhythms of the downstream migration of juvenile sockeye from Dalneye L. were examined in detail (Krogus, 1954, 1967a). B. P. Kozhevnikov studied the diel vertical migrations of the zooplanktonic food organisms in Dalneye L. in relation to the vertical migrations of juvenile sockeye in the lake (Kozhevnikov, 1968).

When the Japanese renewed and stepped up their high seas salmon fishery, the depressed state of the sockeye intensified even more. This made it necessary to redefine the forecasting methods by recording the Japanese high seas catches, which could be achieved by identifying the sockeye of the Kamchatka stocks in the sea catches. Such a method was developed with the help of scale structure analysis (Krogus, 1958). This method was successfully used by F. V. Krogus for determining the removal of sockeye from a number of stocks of the Asian sockeye and for compiling forecasts of sockeye runs (Krogus, 1961). All of these data have been extensively used during annual Soviet–Japanese talks concerning fishing operations. Later, in cooperation with F. V. Krogus, S. M. Kononov (1966, 1971) developed a scale-parasitological method of identifying local sockeye stocks at sea (Krokhin, 1968).

As a result of many years of research, the scientists of PEL developed a model of the pelagic fish community of Dalneye L. (Krogus, Krokhin, Menshutkin, 1969).

M. Ya. Iyevleva studied gametogenesis in the juvenile sockeye of Dalneye (Iyevleva, 1970, 1970a), I.V. Tiller examined the feeding behavior of juvenile sockeye and the growth of the threespine stickleback (Tiller, 1972, 1978), and V.G. Markovtsev studied the feeding behavior and food relations of juvenile sockeye and the threespine stickleback (Markovtsev, 1972).

Long-term data were later used to examine and analyze the significance of the vertical migrations of juvenile sockeye in the energy balance of the sockeye of Dalneye L. (Krogus, 1974), and I. I. Kurenkov (1975a, 1975b, 1976) conducted a detailed study of the life cycles of the main food organisms consumed by juvenile sockeye in Dalneye L.

The results of the long-term investigations of F. V. Krogus and Ye. M. Krokhin in co-authorship with V. V. Menshutkin were published in the book “The Pacific Salmon (Sockeye) in the Ecosystem of Lake Dalneye (Kamchatka)” (1987).

The monitoring of the ecosystem of Dalneye L. has continued over the past years. The growth and feeding behaviour of underyearling sockeye are being examined in greater detail (Vvedenskaya, 1991, 1992; Pogodayev, 1991).

More detailed information on the work of the PEL from the time of its organization and up to the end of the 1960s is available in Ye. M. Krokhin’s paper (1968).

During 1937–1939, I. I. Lagunov and A. I. Synkova worked at the Ust-Kamchatsk observation station in the lower reaches of the Kamchatka R. where they studied lakes Nerpichye and Azabachye and the Yelovka R. (the largest tributary of the Kamchatka R.). During 1939–1944, investigations were continued by K. A. Lyamin and V. A. Rudakova who studied the breeding areas in the Tolbachik R. (a tributary of the Kamchatka R.). In 1940, I. I. Lagunov carried out the first summary of the research done on the sockeye of the Kamchatka R. watershed, penning his dissertation for the scientific degree of Candidate of Biological Sciences, “The Sockeye Salmon, *Oncorhynchus nerka* (Walb.) of the Kamchatka River”. The first data on the downstream migration of Kamchatka R. sockeye as underyearlings were presented by I. I. Lagunov (1939).

Beginning in 1948, the catches of sockeye and pink salmon in the Kamchatka Gulf diminished drastically. This prompted scientists to step up their research. In 1949, V. V. Azbelev and V. I. Sinyukova investigated the Kamchatka R. from its mouth to the village of Milkovo and Azabach L.

I. I. Kurenkov worked there from 1951, studying the breeding areas, the food supply and the foraging conditions of the juveniles in the spawning and foraging waters (Kurenkov, 1964, 1967, 1967a), as well as the interrelations of the juvenile sockeye with the carp released into the Kamchatka R. by I. I. Kuznetsov at the beginning of the 1930s. I. I. Kurenkov came to the conclusion that the carp, widely distributed in the river, was not a food competitor of the juveniles sockeye, and therefore could not have a negative effect on the abundance of the sockeye (Kurenkov, 1952). At the beginning of the 1960s, F. V. Krogus collected data and arrived at her first conclusions regarding the nonuniformity of the sockeye stock in the watershed of the Kamchatka R. (Krogus, 1968, 1970).

In 1940, on the proposal of the Kamchatka branch of TINRO (KoTINRO), the Far Eastern Administration of Fish Conservation organized an observation station on Kuril L. A worker of this administration, V. V. Azbelev, set up a weir near the outlet of the Ozernaya R. to count the adult sockeye spawning in the lake and its tributaries. In 1941, after this observation station was placed in the hands of KoTINRO, the research was supervised by V. I. Gribanov who, together with V. V. Azbelev, carried out assessments of the abundance of downstream-migrant juveniles, as well as regular observations on the structure of the stock, egg survival, the food supply of juvenile sockeye in the lake, and the hydrological conditions of the lake. All of these investigations are still in progress. The workers of the observation station presented their first forecast of the abundance of the Ozernaya R. sockeye for 1946. T. V. Yegorova began to work at the lake’s observation station from 1949, M. M. Selifonov from 1960, V. A. Dubynin from 1974, and A. V. Maslov from 1987.

The data collected at the Ozernaya observation station served as the basis for the later research into the biology of the Ozernaya sockeye. The causes of the fluctuations in the abundance of the Ozernaya sockeye were examined by F. V. Krogus and Ye. M. Krokhin (1956, 1956a), T. V. Yegorova et al. (1961), T. V. Yegorova (1964), M. M. Selifonov (1983, 1988), and Selifonov (1982); a method of forecasting spawning migrations was developed (Yegorova, 1966; Selifonov, 1987; Selifonov, 1988a), and embryonic development was studied (Yegorova, 1970). A number of authors devoted their investigations to studying the scales of the sockeye (Krogus, 1958; Mathisen, 1966; Selifonov, 1970; Bugaev, 1976; Selifonova, 1978;

Bugaev et al., 1989), the factors affecting the growth rate of the fish at sea (Mathisen, 1962; Krogius, 1965; Yegorova, 1968), and the growth of juveniles in fresh waters (Selifonov, 1970, 1974; Dubynin, 1986; Dubynin, Bugaev, 1988; Gorodovskaya, 1988; Bugaev, 1991; Bugaev, Dubynin, 1991). Questions concerning the distribution and estimation of the abundance of juvenile sockeye in Kuril L. were solved with the help of the hydroacoustic method (Nikolayev, 1983, 1986, 1988, 1988a, 1988b, 1990). The migrations and distribution of the sockeye at sea was studied (Birman, 1964; Konovalov, 1967, 1971; Birman, Konovalov, 1968), and the Ozernaya sockeye was separated from the sea catches and the effect of the Japanese high seas fishery on its abundance was analyzed (Krogius, 1961a; Menshutkin, 1967, 1969; Krogius, 1967; Menshutkin, Kislyakov, 1968; Selifonov, 1975, 1975a, 1978; Selifonov, 1987a, 1989). Genetic methods were used to prove the nonuniformity of the sockeye stock of Kuril L. (Varnavskaya, 1988a), which had once been rejected (Yegorova, 1970a), and the genetic conformities of age differentiation in the sockeye were examined (Varnavskaya, 1988).

Simultaneously with the ichthyological research being conducted on Kuril L., studies on the food supply of juvenile sockeye and the causes of its interannual variability were carried out (Akatova, 1937; Krokhin, Krogius, 1937; Nosova, 1968, 1970, 1972, 1972a, 1986, 1988; Milovskaya, 1986, 1988, 1991; Lepskaya, 1986, 1988).

The hydrochemical regime of the lake (Krokhin, Krogius, 1937; Stepanov, 1986; Ukolova, 1986, 1988, 1991), the trace-element composition of its waters (Stepanov, Faistova, 1986) and the hydrological conditions of the lake (Krokhin, Krogius, 1937; Nosova, 1968; Karyukhin et al., 1986) were also studied. The climatic conditions in the Kuril L. watershed were analyzed (Grantovskikh et al., 1986), and the geological structure of this region was examined (Solov'yova, Nasedkin, 1986). Questions concerning chemical control, brought on by the fertilization of Kuril Lake, were discussed as well (Galanitsky et al., 1986).

All of the above-mentioned investigations in the watershed of Kuril L. have enabled us to form a specific concept of the biology and population dynamics of the Ozernaya sockeye.

Information on the abundance of sexually mature salmon (including the sockeye) was gathered at the Karymaisky observation station of KoTINRO with the help of a fish-counting fence, and the effect of abiotic conditions on the survival of salmon eggs, alevins and juveniles was also studied. The results of these investigations were published in R. S. Semko's book (1954). The data collected at this station have never lost their importance.

Later, at that same Karymaisky observation station, N. V. Chebanov studied how the body length and age of the spawners influenced the viability of the offspring at the early stages of ontogenesis in the sockeye (Chebanov, 1984), and how the density of the brood stock influenced spawning success and the survival of the eggs and offspring of this species (Chebanov et al., 1983; Chebanov, 1991).

At the beginning of the 1950s, F. V. Krogius conducted an aerial survey of salmon in the breeding areas in order to determine the effectiveness of the ban on sockeye fishing in the watershed of the Kamchatka R. The experiment proved to be so successful that it was repeated for other spawning rivers of the Kamchatka Peninsula. Aerial photography of the spawning grounds was used to verify the results. A. G. Ostroumov has been conducting aerial surveys of salmon since 1957 (with K. Yu. Nepomnyashchy since, 1979). A. G. Ostroumov has worked out the method of aerial survey and data processing in detail, and describes it in a number of papers (Ostroumov, 1962, 1964a). The data obtained on the abundance of spawning salmon in breeding areas by means of aerial surveys are now the principal data used for judging the status of salmon stocks (Ostroumov, 1975a).

The cycle of investigations on the freshwater period of the sockeye and other species of salmon includes reconnaissance surveys of the lakes of the Kamchatka Peninsula, which were carried out in an effort to determine the abundance of the brood stocks and the abundance of the sockeye in the few local sockeye populations. Such surveys were carried out on Kronotskoye L. (Krokhin, Kurenkov, 1964), lakes Ilir-Gytkhyn and Potat-Gytkhyn in the Koryak highlands, Medvezhye L. and Avacha L. at the outfall of the Avacha R. (Krokhin, Kurenkov, 1967), Kambalnoye L. in the extreme southern part of the peninsula, Tolmachevskoye L. (in the watershed of the Bolshaya R.) and a number of other bodies of water. The most active participants of these expeditions were Ye. M. Krokhin (1965), I. I. Kurenkov, 1964, 1964a, 1967, 1967a, 1970, 1972, 1975c) and A. G. Ostroumov (1965, 1970a, 1970b, 1977, 1977a, 1979, 1982, 1982a, 1985, 1985a, etc.).

Stock-taking of the freshwater fauna of Kamchatka enabled I. I. Kurenkov to take the first step in establishing the correlation between the abundance of juvenile Pacific salmon (including juvenile sockeye) and their supply of food organisms. A study of the food spectra of the salmon and other representatives of the Kamchatkan ichthyocomplex enabled I. I. Kurenkov to solve a number of practical questions related to the acclimatization of new species of freshwater fish in Kamchatka. Among other things, the previously negative view of acclimatizing the wild goldfish (*Carassius auratus*) on the Kamchatka Peninsula was re-examined.

This view had been prompted by the diminishing numbers of the sockeye in the Kamchatka R. In the 1940s, the majority of specialists attributed this occurrence to food competition on the part of the wild goldfish which had been successfully acclimatized in the watershed of the peninsula's major river in 1930, and the acclimatization measure itself was referred to as a major mistake (Dryagin, 1954). Kurenkov's investigations showed that the food spectra of the wild goldfish and the young of the sockeye were almost entirely different, and that the biotopes of the two species also differed significantly (Kurenkov, 1952).

Analysis of the ecological cycles of planktonic crustaceans in the lakes of Kamchatka provided Kurenkov (1970a, 1972, 1975a, 1975b, 1976, 1978, 1978a) with data not only for determining the production of the principal food organisms, but also for recommending the biotechnology for certain piscicultural measures. Among other things, he showed that the ferti-

zation of the waters for the purpose of increasing the reproductive success of the sockeye had to be approached in different ways (Kurenkov, 1976, 1978). Grading to determine the suitability of waters when fertilizers are added to them should be determined by the factors which form the basis of the system used to classify lakes by depth (Kurenkov, 1976, 1978), i.e. primarily the species composition of the zooplankton and the structure of the latter's populations, which depend largely on the depth of the lake.

The numerous unsuccessful or inconsistent results from determining the fishery effect of lake fertilization on sockeye abundance are due mainly to the fact that the experimenters chose small and shallow lakes where the zooplankton (and to a large extent the benthos as well) undergoes winter diapause. Other differences in the production processes of small and deep lakes are also noted (Kurenkov, 1976, 1978).

On the other hand, the attempts at artificial fertilization and natural volcanic-ash fertilization of deep lakes have produced excellent results (Kurenkov, 1988; Kurenkov, 1975, 1988; Kurenkov, 1966; Bugaev, 1986; Bugaev, 1987a).

Kuril L. has produced and continues to produce more than 10,000 tons of sockeye during its better years. However, there is an even larger freshwater lake, Kronotskoye, on the Kamchatka Peninsula, and there are no anadromous sockeye in it, as the rapids in the river connecting the lake with the sea prevent them from entering the lake.

In 1952, Ye. M. Krokhin and I. I. Kurenkov surveyed the lake and drew up a plan for stocking it with the anadromous form of the sockeye (Krokhin, Kurenkov, 1964). However, the opponents of this project were doubtful that Kronotskoye L. would have a sufficient food supply for the young of the sockeye. Estimates based on the results of long-term investigations on Kronotskoye L. have shown that the annual production of crustaceans in this lake is about 40,000 tons. Therefore, Kronotskoye L. surpasses Kuril L. 2-fold in this respect, and the future stock is not threatened by a shortage of food (Kurenkov, 1978a). In recent years, L. V. Milovskaya has been studying the zooplankton of Kronotskoye L. (Milovskaya, 1983, 1983a).

Investigations on the sea period of the Pacific salmon (including the sockeye) got underway during the very first years of KoTINRO. They began in 1934, but they were limited to the coastal waters of Kamchatka and the Northern Kuriles, and were irregular. They were conducted by K. A. Lyamin (1949), R. S. Semko (1958), V. A. Rudakova, V. N. Tripolskaya, and others.

Regular sea investigations began in 1955 under the supervision of I. B. Birman (1958, 1960, 1964, 1967, 1967a, etc.). The other participants included L. D. Andriyevskaya (1958, 1966, 1968, 1970, 1975), L. Ye. Grachev (1968, 1971, 1971a), A. S. Nikolayev (1974, 1975, 1977), S. M. Konovalov (1966, 1967, 1971), etc. The results of long-term investigations on the sea period of salmonid fishes are presented in I. B. Birman's monograph "The Marine Period of Life and Questions Concerning the Population Dynamics of the Stock of Pacific Salmon" (1985).

From the beginning of the 1970s and up to the present, V. I. Karpenko has been on the Kamchatka Peninsula conducting investigations on the coastal period in the life of Pacific salmon there (including the sockeye) (Karpenko, 1979, 1982, 1993).

More detail on the history of research into the sockeye and other species of Pacific salmon on the Kamchatka Peninsula, from the time it began and up to the end of the 1960s, is provided by I. I. Lagunov (1968), some of whose data is mentioned above.

In 1959, the Azabachye observation station of KoTINRO was set up on Azabach L. in the lower reaches of the Kamchatka R., and in 1970 the "Raduga" ("Rainbow") biological station of the Institute of Marine Biology of the Far Eastern Branch of the USSR Academy of Sciences was established.

At the "Raduga" biological station, Yu. P. Altukhov (1974) studied the spatial distribution of gene frequencies in the sockeye stock of Azabach L.

In the watershed of this lake, researchers of the Institute of Marine Biology studied the population structure of the sockeye of Azabach L. by analyzing the structure of the scales, the degree of infestation by indicator parasites, as well as osteological, age and size-weight characteristics (Konovalov, Il'in, Shcherbinin, 1971; Konovalov, Shcherbinin, 1973; Romanov, 1977, 1978, 1983; Konovalov, 1980).

Later, V. Ye. Il'in, S. M. Konovalov and A. G. Shevlyakov (1983) determined the coefficients of sockeye migration between separate breeding areas by tagging spawners. V. A. Parensky (1988, 1988a) studied the behaviour of the sockeye in the breeding areas. M. Yu. Kovalyov (1988, 1989, 1990) studied the growth of juvenile sockeye, and V. I. Ostrovsky (1985, 1987, 1987a, 1988, 1988a) analyzed the age composition of the parents and offspring of the sockeye by year-classes and by the biological structure of sockeye subsolates during the reproductive period. T. Ye. Butorina and M. B. Shedko (1988) worked on developing a method of differentiating various groups of juvenile sockeye in the lake. L. V. Il'ina (1987) examined the long-term dynamics of the ecological and genetic characteristics of individual sockeye populations confined to various types of breeding areas.

M. K. Glubokovsky worked on questions concerning the evolutionary biology of the Salmonidae (Glubokovsky, Glubokovskaya, 1981; Glubokovsky, 1990).

At the Azabachye station of KoTINRO, S.P. Belousova (1968, 1970, 1972, 1974, 1975) studied the forage base and feeding characteristics of juvenile sockeye and their food competitors in the lake, L. V. Kokhmenko (1970, 1972) examined the effect of predators on the young of the sockeye, and N. S. Simonova (1972, 1972a, 1974, 1975) studied the feeding behaviour of underyearling sockeye and the reproductive success on the spawning grounds, as well as the population dynamics of the Kamchatka River sockeye (1978).

S. A. Gorshkov and G. V. Gorshkova studied the chromosome sets in the seasonal races of the Azabach L. sockeye (Gor-

shkova, Gorshkov, 1978, 1978a; Gorshkova, 1978, 1979), and also gathered information on the residual form of the sockeye (from anadromous spawners) in this lake (Gorshkova, Gorshkov, 1977). S. A. Gorshkov examined the osteology (Gorshkov, 1977, 1979) and egg survival in the sockeye (Gorshkov, 1976).

Later, V.F. Bugaev (1978, 1981, 1981a, 1982, 1988c) determined the population structure of the sockeye of the Kamchatka R. watershed, and showed that up to 50-70 % of all the juvenile sockeye of this river feeds and grows in Azabach L., migrating to it as underyearlings. Later investigations were devoted to the study of sockeye growth in the lake (Bugaev, 1983a, 1991; Bugaev, Bazarkin, 1987; Dubynin, Bugaev, 1988; Bugaev, Dubynin, 1991), and to questions concerning the population dynamics of the the Kamchatka R. and Azabach L. sockeye (Bugaev, 1986; Bugaev, 1987a). After an interval of close to 10 years (Kurenkov, 1972; Belousova, 1968, 1972), hydrological and hydrobiological investigations were resumed on the lake in 1981 by L. A. Bazarkina (1983, 1986, 1989). Hydroacoustic investigations were also conducted (Nikolayev, Bugaev, 1985; Nikolayev et al., 1989). V. N. Bazarkin (1988, 1990, 1990a) studied the hydrological regime of various types of breeding areas, and examined ways of increasing the effectiveness of forecasting the abundance of Kamchatka River sockeye (Bazarkin, 1987). K. Yu. Nepomnyashchy (1983) analyzed the morphophysiological indices of sockeye smolts in the Kamchatka R. watershed.

N. V. Varnavskaya has recently begun to study the spatial genetic differentiation of the sockeye populations of the Kamchatka Peninsula on a regular basis (Varnavskaya, 1983, 1984, 1984a, 1988a, 1990; Varnavskaya, Varnavsky, 1988; Varnavskaya et al., 1988; Varnavsky, Everett, 1994; Varnavsky et al., 1994).

V. S. Varnavsky has studied the physiological status of sockeye smolts in a natural environment, and under the conditions of accelerated growth in geo-thermal waters (Varnavsky, 1981, 1984; Varnavsky, Varnavskaya, 1982, 1984). This scientist, together with N. V. Varnavskaya (1985), analyzed the migration between intrapopulational groups in the sockeye of Nachikinskoye L. (Bolshaya R. watershed).

S. I. Kurenkov spent years- studying the problem of establishing an anadromous stock of sockeye on the basis of the kokanee stock of Kronotskoye L. (Kurenkov, 1972, 1977, 1979); however, due to the fact that Kronotskoye L. is located on the territory of the Kronotsky Reserve where all hunting and fishing is prohibited (Naumenko et al., 1986), the subject was dropped and the idea trashed.

At the present time, S. I. Kurenkov is studying the kokanee and residual form of the sockeye on the Kamchatka Peninsula (Kurenkov, 1983), experimental fertilization of lakes (Kurenkov, Kurenkov, 1988), and the propagation of kokanee in Kamchatkan lakes (Kurenkov, 1985). The kokanee from lakes Kronotskoye and Karymskoye has been acclimatized in Nikko L. in Japan (Iwata et al., 1991).

Very few investigations on the sockeye are conducted outside the Kamchatka Peninsula, mostly because of its low abundance in other places. Here we can mention I. A. Chernyshev's studies in the eastern part of the Chukchi Peninsula (1981, 1982), S. I. Kurenkov's study on Bering Is. (1970), V. N. Ivankov's research on Iturup Is. (1968, 1984), O. A. Nikulin's investigations on the continental coast of the Sea of Okhotsk (1970, 1975), and V. F. Bugaev's work on the Asian sockeye in general (1991a, 1992).

Section 4. Material and methods

The basic material for this study consisted of juvenile and adult sockeye caught by the author himself and co-workers of the Kamchatka branch of TINRO and Kamchatrybvod (Kamchatka Fishery Management) during 1972-1991, as well as the very first records of biological analyses carried out on sexually mature sockeye earlier.

An additional source of information included specimens of scales from the brood stock of the Azabach L. sockeye for 1972 through 1979 from the Institute of Marine Biology of the Far Eastern Branch of the USSR Academy of Sciences (Vladivostok), as well as the results of biological analyses and samples of scales from sockeye spawners of the Urumpet, Sopochnaya, Okhota, Kukhtuy and Achchen rivers, which had been kindly made available to the author by associates of the Sakhalin and Magadan branches of TINRO and the Institute of Biological Problems of the North (Far Eastern Branch of the USSR Academy of Sciences) in Magadan, the Pacific Biological Station in Nanaimo (Canada), and the Alaska Department of Fish and Game in Anchorage.

Our biological characteristics of the Asian sockeye within the study area (fig. 1) are based on the results of a biological analysis of about 5000 specimens of sockeye spawners (28,000 with the Kamchatka and Ozernaya rivers taken into account). This material covers practically all the major local stocks of the sockeye in Asia.

From 1975 to 1980, about 5000 juveniles and 6000 adults of the sockeye were used to determine the biological characteristics of local sub-stocks in the Kamchatka R. watershed, and to develop the criteria for their differentiation. During this period, 29 local stocks were analyzed in the Kamchatka R. watershed (fig. 2), and juvenile specimens were collected in 23 areas of the watershed (fig. 3). For annual correction of the method used to identify local stocks and groups of the sockeye in the Kamchatka R. watershed, we subjected 2500 sockeye spawners from some parts of the river watershed (primarily from Azabach L.) to biological analysis for the years 1981 through 1991. In addition to this, the author and his KoTINRO associates carried out a biological analysis of about 11,000 specimens of sexually mature sockeye throughout the whole period of the spawning migration in order to estimate the removal by the USSR (Russian) fishery and to determine the biological indices of the Kamchatka R. sockeye for the period 1978-1991.

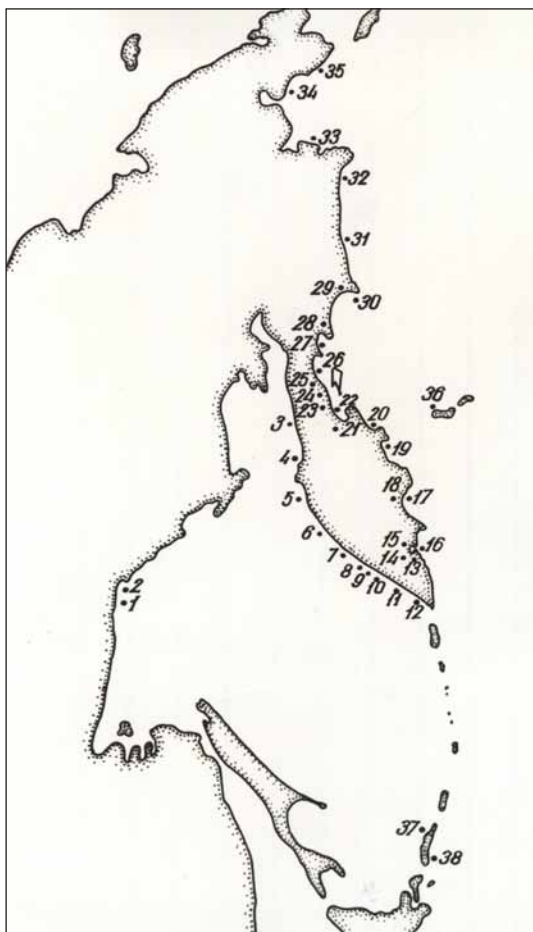


Fig. 1. Principal areas of reproduction, places of congregation of the brood stock and mature individuals of the Asian sockeye.

1 – Okhota R., 2 – Kukhtuy R., 3 – Palana R., 4 – Tigil R., 5 – Khairyuzova R., 6 – Icha R., 7 – Krutogorova R., 8 – Vorovskaya R., 9 – Kikhchik R., 10 – Utkha R., 11 – Bolshaya R., 12 – Ozernaya R. (Kuril L.), 13 – Dalneye L. (Paratunka R. watershed), 14 – Blizhneye L. (Paratunka R. watershed), 15 – Avacha R., 16 – Listvenichnaya R., 17 – Tikhaya R., 18 – Kronotskaya R. (Kronotskoye L.), 19 – Kamchatka R., 20 – Stolbovaya R., 21 – Malamvayam R., 22 – Khailyulya R., 23 – Ivashka R., 24 – Karaga R., 25 – Tymlat R., 26 – Kichiga R., 27 – Avyavayam R., 28 – Kultushnaya R., 29 – Apuka R., 30 – Ananapylgen R., 31 – Ukalayat R., 32 – Meynypilgyn R., 33 – Tumanskaya R., 34 – Seutakan R. (Seutakan L.), 35 – Achchen R. (Achchen L.), 36 – Sarannaya R. (Sarannoye L.), 37 – Sopochnaya R. (Sopochnoye L.), 38 – Urumpet R. (Krasivoye L.).

In the watershed of the Ozernaya R., biological analysis of sockeye spawners was carried out by staff members of the Ozernaya observation station of KoTINRO, located at the outfall of the Ozernaya R. Here, 500-600 sexually mature sockeye were caught annually during the spawning migration. In this study, we used material from 1970-1991, including about 12,000 sockeye specimens which characterized the main biological indices of the Ozernaya sockeye (data processed by M. M. Selifonov and M. F. Selifonova).

For many years now, V. A. Dubynin and I have been studying the biological characteristics of sockeye smolts that migrate from Azabach L. and Kuril L. (figs. 4 and 5). I collected and processed 1235 sockeye smolts from Azabach L. during 1978-1991, and V. A. Dubynin 6573 specimens from Kuril L. during 1975-1991. At the same time, trawling for juvenile sockeye was carried out in these lakes during the same periods. As a result, a total of 6100 young sockeye of different ages was collected in Azabach L., and 4200 in Kuril L. Figs. 4 and 5 show the trawling areas in these lakes.

Except for the specimens from the Kamchatka and Ozernaya rivers, the mature sockeye within the study area (fig. 1) were caught with 60-65 mm mesh gill nets made of monofilament, and in some cases with a drag seine.

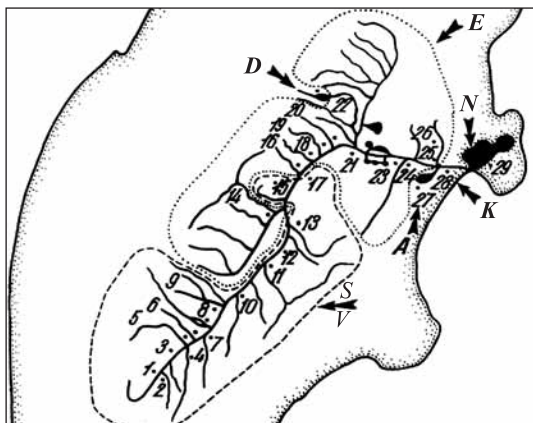


Fig. 2. Second-order local stocks and groups of second-order local stocks of the sockeye in the Kamchatka R. watershed.

1 – Kamchatka R. near the village of Pushchino, 2 – Kashkan R., 3 – Kamchatka R. near the village of Sharomy, 4 – Kavycha R., 5 – Andrianovka R., 6 – Zhupanka R., 7 – Vakhvina (Valagina) R., 8 – Kirganik R., 9 – Kimitina R., 10 – Kitilgina R., 11 – Shapina R., 12 – “Nikolka R.” springs, 13 – Tolbachik R., 14 – Bystraya-Kozyrevka R., 15 – Shekhlnun R., 16 – Kreruk R., 17 – “Lake Ushkovskoye” springs, 18 – Kryuki R., 19 – Polovinnaya R., 20 – Belaya R., 21 – Yelovka R., 22 – Dvukhyurtochnoye L., 23 – Bolshaya Khapitsa R., 24 – Malaya Khapitsa R., 25 – Raduga R., 26 – Nizovtsevo L. (Raduga River watershed), 27 – Azabach L., 28 – Kursin L., 29 – Soldatskaya R. (Nerpichye L. watershed).

At the Ust-Kamchatsk fish cannery, samples were usually taken once every five days (50 specimens from sea trap nets and 50 specimens from the catches of river drift nets) throughout the spawning migration. The sockeye spawners of the Ozernaya R. were caught before the counting fence, usually with a trap net. In all the cases mentioned, smolts were selected for biological analysis.

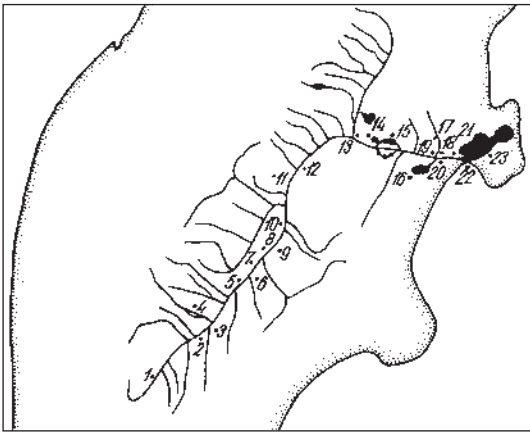


Fig. 3. Places of congregation of young sockeye and threespine stickleback in the Kamchatka R. watershed.

1 – branches of the Kamchatka R. near the village of Pushchino, 2 – old river channel of Kamchatka R. below the village of Milkovo, 3 – old channel of Kamchatka R. below the village of Vakhvina R., 4 – limnokrenes of the Kokhanok R. (tributary of Kirganik R.), 5 – oxbow lake of Kamchatka R. above the village of Tayezhnyi, 6 – nameless oxbow lake of Kamchatka R. above the village of Dolinovka, 7 – “Dedova Yurta” oxbow lake on Kamchatka R., 8 – old side channel and inlet of Kamchatka R. in the vicinity of the Shapina R., 9 – “Nikolka R.” springs, 10 – oxbow lake “Lake Kulpik” on the Kamchatka R., 11 – limnokrenes of the Shekhlun R., 12 – “Lake Ushkovskoye” springs, 13 – Yelovka R., 14 – Kurazhechnoye L., 15 – Kobylkino L., 16 – Azabach L. and its side channel, 17 – Nizovtsevo L. and its side channel (Raduga R. watershed), 18 – Krasikovskoye R. (Raduga R. watershed), 19 – oxbow lake of the Raduga R., 20 – Kursin L., 21 – side channel connecting Melkoye L. with “Pekalka” side channel of the Kamchatka R., 22 – mouth of the Kamchatka R., 23 – Soldatskaya R. (Nerpichye L. watershed).

A in the watershed of the Kamchatka R., sockeye spawners were caught in the breeding areas and during migration along spawning tributaries with 60-65 mm mesh gill nets made of monofilament. As a rule, the fish here had already undergone significant reproductive changes.

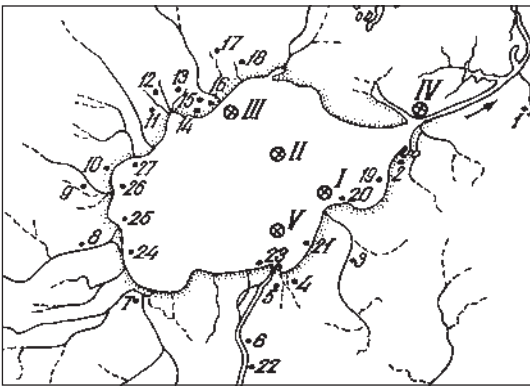


Fig. 4. Distribution of spawning grounds of the sockeye in the Azabach L. watershed (Konovalov, 1980) and places where research material was gathered on this lake.

Spawning grounds of the early (spring) seasonal race of the sockeye: 1 – Oleshkina chasha, 2 – Ozerko, 3 – Lotnaya R., 4 – Rybovodnyi klyuch-1, 5 – Rybovodnyi klyuch-2, 6 – Bushuyeva R., 7 – Lamutka R., 8 – Kultuchnaya R., 9 – Arichkin klyuch, 10 – Bezymyannaya chasha, 11 – Timofeyevskaya chasha-3, 12 – Timofeyevskaya chasha-2, 13 – Timofeyevskaya chasha-1, 14 – Zavodskaya chasha-3, 15 – Zavodskaya chasha-2, 16 – Zavodskaya chasha-1, 17 – Ponomarka R., 18 – Atkhol klyuch (chasha);
 Spawning grounds of the late (summer) seasonal race of the sockeye: 19 – Zemlyanka-Lotnaya, 20 – Lotnaya-Zemlyanka, 21 – Rybovodnaya-Lotnaya, 22 – Bushuyka, 23 – Bushuyka-Lamutka R., 24 – Lamutka-Kultuchnaya, 25 – Kultuchnaya, 26 – Kultuchnaya-Arishkin, 27 – Snovidovskaya-Arishkin.
 1 – station No. 1, II – station No. 2, III – station No. 3, IV – station No. 4 (outfall of Azabach side channel), V – hydrobiological station No. 5.

In the Kamchatka R. watershed, juveniles of the sockeye and threespine stickleback were caught with a beach seine for fry (length 10 m, mesh 6 mm).

Special mention should be made of the method for catching downstream-migrant underyearling sockeye at the mouth of the Kamchatka R., which was carried out during the daylight hours (15.00-18.00 hours) in the tidal zone on a spit separating the Vtorozavodskaya side channel from the waters of the Kamchatka Gulf. Depending on the size of the catch, the seine was cast 5-7 or 10-12 times. Usually, after 2-3 casts, the seining series was repeated 15-20 minutes later. The largest catches of underyearling sockeye were obtained when the high tide was equal to 50-70 % of the maximum level.

In the waters of Azabach L., the young of the sockeye and other fishes were caught with a pair trawl for fry (aperture 1.0-1.3 m, length 3.5 m) in the surface layer of water, from two boats of the “Progress” type with 20-30 h.p. motors, after the sun had set. One haul of a trawl lasted from 3 to 9 minutes, depending on the catch. Experience has shown that with a haul lasting more than 5-7 minutes, juvenile sockeye lose their scales en masse, and such specimens are not as valuable. The goal being to get a sufficient number of specimens in a sample, 2-3 hauls of a trawl were carried out at each station in some cases.

In the waters of Kuril L., trawling was carried out in a similar manner, but the hauls here usually lasted longer, 5-15 minutes, due to the leaner catches of juvenile sockeye in comparison with Azabach L. The trawl had an aperture of 1.9-2.6 m (when fishing) and a length of 4.5 m.

In sexually mature sockeye grouped according to sex, we measured the fork (Schmidt’s) length (in the Kamchatka R. watershed also the distance from the edge of the gill cover to the fork in the tail), body weight and gonad weight. As a rule, absolute fecundity was determined in the females. Fork length, body weight and sex were recorded for juvenile sockeye. The age of all the fish was determined by the scales. In the watershed of the Kamchatka R., body size was used to determine the duration of the sea period of some individuals.

A great deal of attention has been devoted in this book to the study of the scale structure of sexually mature and juvenile sockeye, i.e. in Pacific salmon, it serves as the basis for clarifying certain questions concerning the biology of populations and the development of population differentiation criteria (Gilbert, 1916-1923; Taguchi, 1948; Krogius, 1958; Henry, 1961; Koo, 1962; Mosher, 1963; Anas, 1963; Konovalov, 1966, 1971, 1972, 1980; Mason, 1964-1966; Mathisen, 1966; Savvaitova, 1968; Narver, 1968; Bilton, Smith, 1969; Anas, Murai, 1969; Krogius, 1970; Selifonov, 1970; Bilton, 1970, 1974; Messinger, Bilton, 1974; Bugaev, 1976, 1978, 1978a; Selifonova, 1978; Bugaev, 1986a; Nikolayeva, 1988; Cook, Lord, 1978; Krasnowski, Bethe, 1978; Myers et al., 1987; Myers, Rogers, 1988, and many others).

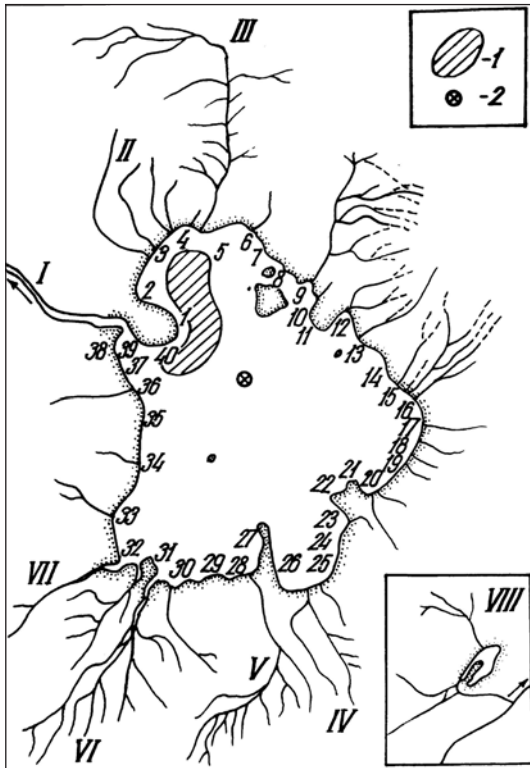


Fig. 5. Distribution of spawning grounds in the Kuril L. watershed (Ostroumov, 1970) and places where research material was gathered on this lake.

I – outfall of the Ozernaya R., II – rivers of Severnaya Bay, III – Vychenkiya R., IV – Gavryushka R., V – Kirushutk R., VI – Khakytsin R., VII – Etamynk R., VIII – Etamynk L.

1-8 – Severnaya Bay, 9-11 – Zapadnaya Teplaya Bay, 12 – Vostochnaya Teplaya Bay, 13-14 – shores between Vostochnaya Teplaya and Oladochnaya bays, 15-21 – Oladochnaya Bay, 22 – northeast of Cape Glinyanyi, 23-26 – bay east of Cape Tugumynk, 27 –32 – southern shore (around the mouths of the Etamynk, Khakytsin and Kirushutk rivers), 33-40 – western shore (from the mouth of the Etamynk R. to Cape Pulomynk).

In the upper right-hand corner: 1 – area of trawling for young sockeye, 2 – central hydrological-hydrobiological station.

Due to the fact that most of the scales from Asian sockeye spawners (fig. 1) were collected above the lateral line under the dorsal fin (Pravdin, 1966), we also used this method of scale sampling to get the essential material from the young and sexually mature fish. The exception was the sockeye of Kuril L. where all the scales of juvenile and adult fish were taken above the lateral line between the dorsal and adipose fins (Clutter, Whitesel, 1956), as well as the sockeye scale samples from fishes of Azabach L. and the sockeye of Iturup Is., the Achchen R. and Bering Is. (for 1990-1991), provided by the Institute of Marine Biology. Farther on in this book, the characteristics of the scales collected by Clutter and Whitesel's method (1956) are presented as if they had been collected by Pravdin's method (1966) in the cases where this is called for.

In order to determine the influence of the scale-collecting method on the results, we prepared specimens of scales (taken from sockeye spawners of the Kamchatka R. watershed) collected by the two methods from the same fish, i.e. 79 fish from Ushkovskoye L. in 1976 and 37 in 1978, 58 fish from the Raduga R. in 1976 and 40 in 1978, 41 fish from Dvukhyurtochnoye L. in 1975, and 36 fish from Azabach L. in 1976.

In the scales collected (fig. 6), we counted the number of sclerites in the first (second) and marginal zones of the freshwater part of the scale, as well as the number of wide and adjacent sclerites from the first year at sea. The radiuses of these structural elements were also measured.

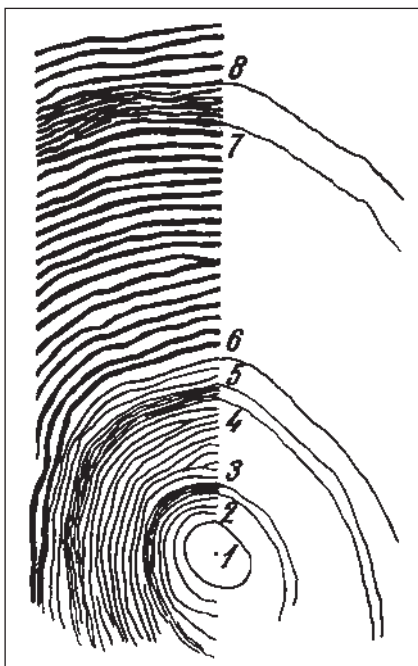


Fig. 6. Sockeye scales with two zones of adjacent sclerites (ZAS) in the freshwater part of the scales (drawing from a photograph).

1-3 – first growth zone, 3-5 – second growth zone, 5-6 – marginal zone of freshwater part of scales, 6-8 – zone of first year at sea, 2-3 – first ZAS, 4-5 – second ZAS, 7-8 – first sea ZAS;

1-3 – radius of first ZAS, 1-5 – radius of second ZAS, 1-7 – radius of wide sclerites of first year at sea.

We found that, when we counted the number of sclerites on scales taken from two different places, it was possible to utilize the data without any recalculation (for all growth zones except the first). Comparative analysis by means of Student's t-test showed insignificant differences in all the cases. In the first growth zone, there were more sclerites in the scales between the dorsal and adipose fins than in the scales under the dorsal fin; the radiuses of all the scale zones were also larger in the first case. Comparative analysis by means of the t-test showed that the existing differences were statistically reliable with $P < 0.01$.

The correlation of the values obtained for the number of sclerites in scales collected by these two methods can be expressed by an equation of regression of the particular values of "x" and "Y", where "x" – the parameter of scales collected by Clutter and Whitesel's method (Clutter, Whitesel, 1956), and "Y" – the parameter of scales collected by I. F. Pravdin's method (Pravdin, 1966) in the same fish. For translation of the values denoting the number of sclerites in the first growth zone, the regression equation takes the form of $Y = 0.956x - 0.406$ ($r = 0.960$; $P < 0.001$). For translation of the radiuses of the first and second zones of adjacent sclerites, as well as the radius of the wide sclerites from the first year at sea, the regression equation is $Y = 0.951x - 2.554$ ($r = 0.999$; $P < 0.001$). The differences in the number of sclerites in the first growth zone are due to the fact that the scales under the dorsal fin are initiated somewhat later than those between the dorsal and adipose fins. The differences in the radiuses are due partly to the larger overall number of sclerites on the scales between the dorsal and adipose fins, but basically to the fact that the distance between the sclerites forming on these scales is greater than in the ones forming under the dorsal fin.

The scales of juvenile sockeye were usually examined with 150-fold magnification, and that of spawners with x100 magnification. In some cases, the scales of juveniles were magnified 100-fold. When the data on the distance between sclerites in juvenile and adult scales were used together, we recalculated the scale characteristics of the juveniles, the values of which were brought to x100 magnification in the drawings (in text). Measurement of the distance between sclerites on a projection of the scales was carried out to within 0.5 mm.

The scales selected for analysis were of a regular shape with the most clearly defined zones of adjacent sclerites (ZAS) and the maximum number of sclerites in the first growth zone or on the scales (in underyearling). The sclerites were counted and the different zones of the scales measured along the anterior–posterior axis in the zone demarcated by lines diverging by not more than 20° from the axis (Clutter, Whitesel, 1956). The number of adjacent sclerites forming the ZAS, were counted by means of the diagram shown in fig. 7 (Bugaev, 1978). Other authors have used a similar principle of counting sclerites in chum and sockeye scales (Tanaka et al., 1969; Bilton, 1970). The scales of juveniles were measured in a similar manner, but it was the total number of sclerites in the existing zones that was counted, without subdividing them into zones of wide and adjacent sclerites.

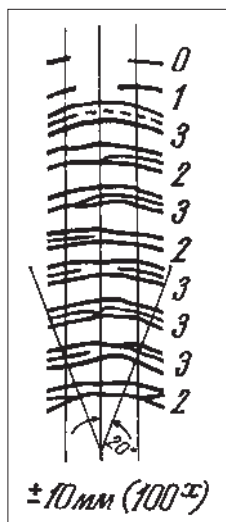


Fig. 7. Criteria for determining the number of sclerites in the zones of adjacent sclerites (ZAS).

In some fish, it was sometimes difficult to distinguish the adjacent sclerites in the zones of scale growth because the distance between them was almost the same, though growth zones are generally observed on the scales. In such cases, we shall be referring to "an indistinct ZAS". When the data was processed statistically, the number of sclerites in an indistinct ZAS was equated to "0" (Bugaev, 1978). The photographs of scales in Section 8 of the book (fig. 35.1, 42.3) depict examples of scales with an indistinct ZAS.

The mean distance between sclerites was determined by the formula $R - r/n - 1$, where "R" – the radius of the scale or growth zone, "r" – the radius of the first sclerite (of the central area), and "n" – the total number of sclerites.

For a more objective assessment, not all of the scale was used to compare the mean distance between sclerites in spawners and juvenile fish, due to the fact that, in some cases, it is the distance between the first year's sclerites that is being examined (in an effort to obtain more accurate information about the biology of the freshwater period of juvenile sockeye from the Kamchatka R. watershed). It was noted that the first 3-4 sclerites on their scales were usually somewhat more widely spaced in comparison with the ones that followed. Therefore, we excluded the scales of underyearlings without supplementary ZAS if they had fewer than 5 sclerites, as well as the scales of juveniles and spawners if they had fewer than 5 sclerites in the first zone of growth. These cases are mentioned in the text; in all other cases, scales with fewer sclerites were used.

Our study on the scale structure of the sockeye of the Kamchatka R. was augmented by investigations on the infestation of the young and the adult fish by the indicator parasite *Diphyllbothrium* sp., i.e. it was shown that the comprehensive scale-parasitological method produced the best results when studying the biology of the sockeye and differentiating its local stocks (Konovalov, 1971, 1980). Of all the indicator parasites, *Diphyllbothrium* sp. is the most convenient to use, due to the fact that its cysts are easily detected and its plerocercoids can be counted accurately. Furthermore, this prolific parasite infests the sockeye at the pleurocercoid stage, and therefore survives for a long time. It is this simplicity of studying fish infestation by plerocercoids and the high effectiveness of the research method (Margolis, 1963, 1965; Margolis et al., 1966; Konovalov, Konovalova, 1969; Konovalov, 1971, 1972, 1974, 1980; Kurenkov, 1977, 1979) that has prompted us to apply this highly recommended method in our own research.

Sockeye spawners were examined for pleurocercoid infection in fresh form, and juveniles in formalinized material (fixed in 8-10 % formalin). About 6000 spawners and 8300 juveniles of the sockeye from the Kamchatka R. and about 3000 adult fish from the catches of the USSR (Russia) were examined for pleurocercoid infection.

To analyze the feeding behavior of underyearling individuals in the Kamchatka R. estuary, we dissected 105 stomachs. The contents of the latter were processed by the quantitative-gravimetric method with calculation of partial and total indices of fullness, as well as the frequency of occurrence of food organisms in the bolus (Handbook..., 1961; Methodological Guide..., 1974).

The material on the feeding behavior of 501 underyearling sockeye for the whole of the Kamchatka R. watershed was processed by the quantitative-gravimetric method in accordance with the recommendations of the Handbook... (1961) and Methodological Guide... (1974). A total indices of fullness were determined individually, while the weight percentage of the food components was determined by the group method (the stomach contents from 20-25 fish were usually combined in a single sample).

Analysis of the stomach contents of fish from trawl catches carried out in the Azabach L. watershed during the summer-autumn of 1980-1990 provided the main data for our study of the food relationships of the fish in this watershed. L. V. Kokhmenko's data (archives of KoTINRO) on the June-September feeding behavior of certain species of fish in the littoral zone of Azabach L. (in the areas around the Lotnaya, Bushuyeva, Lamutka, Snovidovskaya and Ponomarskaya rivers) and the Azabach side channel for 1970, as well as our material on Timofeyevsky Bay for 1987-1988, was used as additional material. Samples collected with a trawl in the centre of the lake at station No. 2 (fig. 4) as darkness set in are discussed in this particular section. Fish were caught in the littoral zone of the lake during the day (12.00-15.00 hours) with a drag seine for fry. Altogether, 162 stomachs of juvenile sockeye, 884 of the freshwater form of the threespine stickleback, 106 of the migratory anadromous form of the latter, 57 of the ninespine stickleback, and 99 of the pond smelt were examined in an effort to characterize the food relationships of the fish species found in the Azabach L. watershed.

To illustrate the feeding habits of juvenile sockeye in the pelagic zone of Kuril L., we examined the stomach contents of 258 underyearlings and yearlings of this species. The young fish were caught after sunset with a pair trawl in the vicinity of Severnaya Bay (fig. 5).

The following parameters characterizing the feeding behavior of fish in lakes Azabach and Kuril are viewed as the standard ones in this book: frequency of occurrence (%), number of organisms per stomach, index of consumption ($\frac{\%}{1000}$), weight of organisms per stomach (%). The "reconstructed" weights of the food organisms are used. All calculations are based on the total number of fish in the sample (Handbook..., 1961; Methodological Guide..., 1974).

More than 4900 specimens of the anadromous and freshwater forms of the threespine stickleback from 14 areas of the Kamchatka R. watershed were caught and analyzed during 1985-1988.

Hydrobiological samples characterizing the abundance of *Cyclops scutifer* and *Daphnia galeata* (formerly identified as *D. longispina hyalina* – Kurenkov, 1972, and *D. cuculata* – Belousova, 1974) were taken in the Azabach L. watershed during 1979-1990 at the No. 5 standard station located in the deepest part of Azabach L. (fig. 4). The temperature of the water was measured from 1981 through 1991 at the same station at the 0, 5, 10, 15, 20, 25 and 30 m levels during the ice-free period. Samples of the plankton were taken with a Juday net (gauze No. 70, diameter of aperture 18 cm) every ten days, and were processed by the standard method (Bazarkina, 1989). The average monthly values of zooplankton abundance and water temperature were used. The hydrobiological samples were processed by L. A. Bazarkina.

The data on water temperature in Kuril L. at the 10, 20, 30... m levels and hydrobiological samples characterizing the abundance of *Cyclops scutifer* and *Daphnia longiremis* were taken by staff members of the Ozernaya observations station of KoTINRO at the central station (Fig. 5) where, from the beginning of the 1950s and up to the present time, standard samples of the zooplankton and water temperatures are taken every month (Nosova, 1972, 1986, 1988; Milovskaya, 1986, 1988, 1991, latest data). Zooplankton samples were taken with a Juday net (gauze No. 70, diameter of aperture 11.2 cm) twice a month, and processed by the standard method.

When referring to the abundance of *Cyclops scutifer* in our analysis of the effect of the latter on the growth of juvenile sockeye (Section 8.7), we have in mind the total abundance of copepodites of all the stages with the exception of nauplii. Unfortunately, we have no data on the abundance of zooplankton and water temperatures for certain years, which makes the information on scale structure incomplete.

Standard methods were used for statistical processing of the data (Lakin, 1990; Urbakh, 1975).

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Section 5. Anadromous migration

The anadromous migration of the Asian sockeye (during major fishing operations) in different regions has common features and significant differences at the same time, since this species forms two seasonal races based on the timing of its migration and spawning, i.e. early (spring) sockeye and late (summer) sockeye. The abundance ratio of the early and late sockeye can fluctuate considerably in a number of populations. This is probably determined by the fact that these groups cannot be differentiated by the timing of migration and spawning in all the stocks of the Asian sockeye. Furthermore, we also observe yearly fluctuations in the migration timing of some sockeye populations and seasonal races.

The periods of the spawning migration can be determined on the basis of the statistical data on salmon catches of the coastal and river fishery, the catches of control nets, as well as on the basis of escapement data. Each of these methods has its own advantages and shortcomings. For example, the catch statistics do not tell us exactly when the run begins and ends, but they do provide objective data on the timing of mass migration. On the other hand, the catches of control nets indicate more accurately the beginning and end of a run, but the periods of mass migration are determined more subjectively, since from some point in time the catch may depend on how frequently we remove the fish from the net (Gritsenko et al., 1987).

The spawning migration of the sockeye in the Okhota R. begins in June, and ends at the beginning of August. As a rule, the first fish fill up the upper spawning grounds and large tributaries first. The main part of the sockeye stock enters the Uyeginsky lakes (middle part of the Okhota R. watershed) at the end of July–beginning of August; the fish continue their run in large groups up to the end of September. Some make their way into lakes up to the first days of October, when all the tributaries are filled with spawning coho salmon (Nikulin, 1975). During certain years, due to low water levels in the rivers flowing out of the lakes, the sockeye of the Okhota R. watershed has difficulty migrating to the spawning grounds; in some places, waterfalls and other barriers obstruct their migration (Nikulin, 1975).

In the watershed of the Bolshaya R., the sockeye begins its run at the end of the second–beginning of the third ten-day period of May, and, after a certain interval, up to the middle of August. According to R. S. Semko (1954), the early sockeye begins its run on May 25th, mass migration takes place from June 1st to June 5th, and it ends on June 15th; the late sockeye begins its run on July 23rd, migrates en masse from July 26th to August 10th, and completes its run on August 15th.

T. V. Yegorova (1970, 1970a, 1977) notes that the sockeye of the Ozernaya R. begins its run at the end of May, migrates en masse during the second half of August, and completes its run at the end of September–beginning of October.

In Dalneye L. (watershed of the Paratunka R.), the early sockeye migrates from May up to the end of June, and the late sockeye from mid July up to the end of August (Krogus, Krokhin, 1956; Krogus, 1983).

A. I. Smirnov (1975) notes that the migration of the sockeye in the Kamchatka R. estuary begins at the end of May and lasts for more than three months; the main run of the early form of the sockeye takes place in June, while the run of the late form lasts up to the end of August. According to our own data, the migration of the sockeye in the Kamchatka R. ends at the beginning–middle of August.

Based on the data of Kamchatrybvod and KoTINRO expeditions, the first sockeyes in the Stolbovaya, Khailyulya, Avyavayam and Apuka rivers begin to appear in fixed gill nets during the first ten days of June. Fishery statistics indicate that, in the rivers of northeastern Kamchatka, migration begins at the start of the second ten days of June, mass migration takes place during the first ten days of July, and the run is completed at the end of the second–beginning of the third ten-day period of August.

For the eastern part of the Chukchi Peninsula, I. A. Chereshev (1981) notes that the sockeye begins to enter the lagoon of the Seutakan R. at the beginning of June, and the run ends in the middle or at the end of August; in 1975, the sockeye began to enter Achchen L. from the sea at the beginning of July (after washout of the bridge between the brackish Achchen lagoon and the sea), but the run there was completed at the end of August–middle of September.

Based on the data of commercial landings for 1982 through 1991, fishing for sockeye in Sarannoye L. (Bering Is.) begins on May 20–25th, and ends mostly at the end of July, less commonly on August 3rd–6th. Similar migration timing for the sockeye of Sarannoye L. was also noted by S. I. Kurenkov (1970).

The spawning migration of the sockeye from the sea into Krasivoye L. (Iturup Is.) lasts for about a month. According to V. N. Ivankov (1984), the migration in 1966–1967 began during the first days of July, and ended at the beginning of August. The mass migration of salmon was noted in the middle of July, a month later than in the Slavnaya R. (Iturup Is.) where the migration of salmon occurred in June.

Let us take a more detailed look at the dynamics of the spawning migration of the sockeye of the Kamchatka and Ozer-naya rivers.

Tables 1 and 2 depict the dynamics of the sockeye catches in the Kamchatka R., with river drift nets in the river and with trap nets in the Kamchatka Gulf. A comparison shows that sometimes weight catches are obtained first with trap nets at sea, and later with nets in the river.

Table 1. Sockeye river gill net catch dynamics, Kamchatka R., %

Month	Date	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May	21-25	–	–	–	–	+	–	+	–	–	–	–	–
	26-31	2.4	+	–	0.2	2.1	–	0,1	–	1,4	–	0.1	0.1
June	1-5	13.1	3.3	9.1	2.9	3.2	0.9	+	8.4	6.3	0.2	11.4	0.1
	6-10	28.0	13.6	9.9	3.8	47.6	3.4	8.6	17.4	22.7	0.6	17.0	3.9
	11-15	34.1	62.2	22.7	14.3	15.4	27.6	57.8	18.3	20.4	12.9	20.8	26.7
	16-20	8.8	9.9	9.0	26.2	9.6	29.9	14.2	16.0	23.1	38.7	19.8	37.4
	21-25	7.3	8.9	12.5	6.4	5.2	16.0	4.1	16.5	2.1	25.1	14.0	11.0
	26-30	2.6	1.2	26.7	12.5	7.7	5.7	4.9	11.2	5.0	5.4	5.2	8.6
	26-30	2.6	1.2	26.7	12.5	7.7	5.7	4.9	11.2	5.0	5.4	5.2	8.6
July	1-5	1.9	0.3	8.8	20.4	5.7	3.4	4.3	3.5	4.3	3.6	6.7	5.2
	6-10	0.3	0.1	1.0	6.9	3.2	1.8	0.7	0.4	4.3	0.6	2.9	2.3
	11-15	0.3	0.2	–	0.2	0.3	0.8	+	+	1.3	–	2.1	3.2
	16-20	0.6	0.1	+	1.2	–	4.3	3.2	1.5	3.2	6.9	–	1.0
	21-25	0.4	0.2	+	3.4	–	3.1	0.9	3.9	3.6	4.0	–	–
	26-31	0.2	+	0.1	1.6	–	2.5	0.7	1.7	2.3	1.8	–	–
August	1-5	–	–	0.1	–	–	0.6	0.5	0.6	–	0.2	–	–
	6-10	–	–	+	–	–	–	–	0.3	–	–	–	0.5
	11-15	–	–	0.1	–	–	–	–	0.3	–	–	–	–
	16-20	–	–	–	–	–	–	–	–	–	–	–	–
	21-25	–	–	–	–	–	–	–	–	–	–	–	–
Total		100	100	100	100	100	100	100	100	100	100	100	100

Note. The sign “+” averages less than 0.1 %.

Analysis of the sockeye runs to the Kamchatka R. estuary on the basis of the maximum catches with trap nets set up at various distances from the mouth of the Kamchatka R. and the catches from the “Ust-Kamchatsk” fishing grounds shows (fig. 8) that the dates of the maximum trap net catches and the catches at the fishing grounds do not coincide. The earliest maximum catches are observed on the “Ust-Kamchatsk” fishing grounds and in trap net No. 258 which is closest to the mouth of the river, as well as in the group of trap nets (Nos. 254-251) set up 12-18 km from the mouth. This means that the sexually mature fish approach the Kamchatka R. in two, almost simultaneous groups; one heads directly towards the mouth of the river and enters the river, while the other approaches it slightly farther from the south.

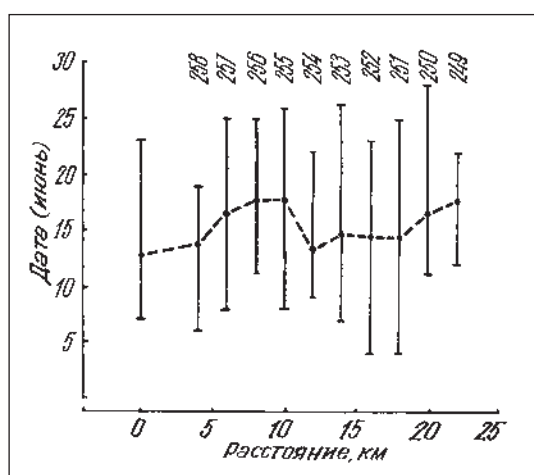


Fig. 8. Period of maximum sockeye salmon catches taken from marine trap nets and the Ust-Kamchatsk fishing ground.

Y-axis – days in June (dates); X-axis – distance from the mouth of the Kamchatka R., km.

Figures indicate numbers of trap nets; “0” marks the Ust-Kamchatsk fishing ground.

This, at first glance unexpected, structure of approach to the mouth of the river can be explained by the fact that the Kamchatka R. is historically known for its blocked delta which consists of sandy-pebbly spits running perpendicularly to the prevailing current of the river. The river once flowed along the coastline for a distance of about several km, and only then fell into the Kamchatka Gulf. Later, under the effect of an ever-increasing affluent, the river broke through the spit at the base and formed a new mouth from which a new spit gradually developed (Kurenkov, 1967a, 1970).

Table 2. Sockeye marine trap net catch dynamics, Kamchatka Gulf, %

Month	Дата	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May	21-25	+	-	-	0.1	-	-	-	-	-	-	-	-
	26-31	2.4	-	+	0.1	0.3	-	-	-	-	-	-	-
June	1-5	7.3	0.8	4.8	6.4	0.3	0.8	0.5	3.2	2.4	-	-	-
	6-10	5.9	12.4	4.6	11.1	42.3	5.7	20.0	15.3	13.3	2.3	0.4	2.7
	11-15	30.2	18.8	10.5	49.5	14.3	40.8	27.5	21.7	15.9	28.7	14.7	35.6
	16-20	21.4	31.8	6.4	6.2	9.1	7.4	18.1	10.8	20.7	26.0	16.4	6.7
	21-25	22.0	22.8	40.8	5.2	4.1	11.3	6.6	13.2	8.4	6.3	-	-
	26-30	6.7	5.0	20.0	10.4	4.9	0.8	12.7	3.5	11.3	11.4	9.0	-
July	1-5	1.7	5.8	4.8	4.2	6.6	3.5	4.6	1.9	9.3	9.0	10.5	21.4
	6-10	0.9	1.2	2.1	3.7	1.9	8.1	0.3	4.7	7.8	6.1	8.9	3.7
	11-15	0.2	1.1	2.6	1.5	0.2	5.5	3.3	4.0	2.9	-	13.3	15.7
	16-20	1.3	0.3	-	0.8	1.7	7.0	3.1	13.2	5.3	4.4	14.5	5.6
	21-25	-	-	1.4	0.5	6.5	6.5	1.7	5.0	2.5	3.4	8.5	2.2
	26-31	+	-	1.3	0.3	6.1	2.3	1.0	2.5	0.2	2.3	3.8	4.9
August	1-5	-	-	0.4	-	1.5	0.3	0.1	0.1	+	-	+	0.3
	6-10	-	-	0.3	-	-	-	-	0.5	-	0.1	-	1.2
	11-15	-	-	-	-	-	-	-	0.4	-	-	-	-
	16-20	-	-	-	-	-	-	0.2	-	-	-	-	-
	21-25	-	-	-	-	-	-	0.3	-	-	-	-	-
Total		100	100	100	100	100	100	100	100	100	100	100	100

Note. The sign “+” averages less than 0.1 %.

For the sake of convenience, the inhabitants of Ust-Kamchatsk periodically dug through the mouth of the Kamchatka R. near their village, and because of this the water in Nerpichye L. periodically became salty when the mouth was situated next to the village, and freshened up when the mouth of the river was located of several kilometres farther south. The mouth of the Kamchatka R. was last dug in 1943, and has since been maintained in this condition (Kurenkov, 1967a, 1970).

Taking the above into consideration, one can assume that the second group of fish (fig. 8) approaches the “old” mouth of the Kamchatka R., which points to a certain hereditary stability of this character.

As a whole, based on the catches from all the sea trap nets (for 5-day periods), we can distinguish several types of runs in the sockeye of the Kamchatka R., when the maximum catches are observed during different periods, or are not observed at all (fig. 9).

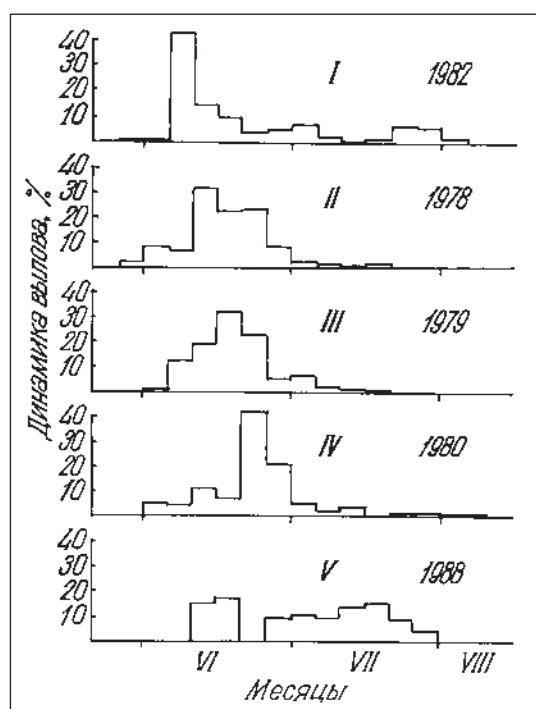


Fig. 9. Dynamics of removals of Kamchatka R. sockeye by means of trap nets (in five-day periods). Y-axis – dynamics of removals, %; X-axis – months. I – maximum catches on June 6-10, II – maximum catches on June 11-15, III – maximum catches on June 16-20, IV – maximum catches on June 21-25, V – uniform catches (trap nets not used on June 21-25).

The beginning of the sockeye fishing season on the Kamchatka R. (at least 100 tons of sockeye caught from the start to the end of the 1st, 2nd or 3rd ten-day period of June) depends on the abundance of the sockeye runs to the mouth of the Kamchatka R. (fig. 10), i.e. the larger the run, the sooner the sockeye begins to enter the Kamchatka R., but this applies only to specific levels of abundance.

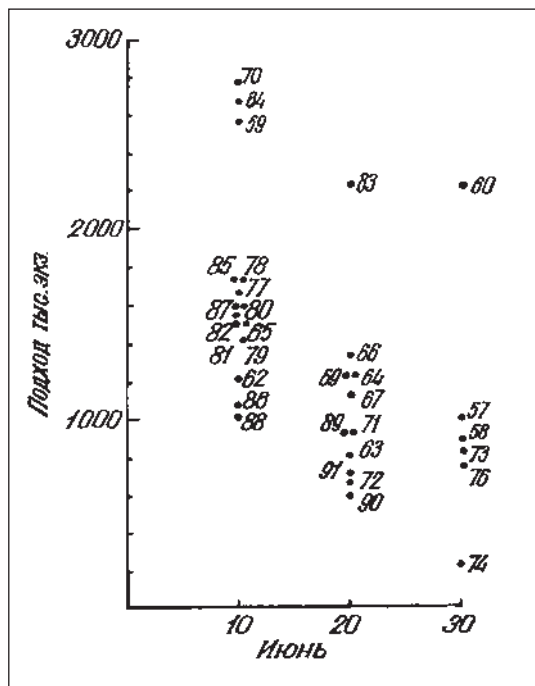


Fig. 10. Beginning of large-scale sockeye fishing (in ten-day periods), depending on the abundance of the spawning run to the mouth of the Kamchatka R. Y-axis – abundance of sockeye run, thou. fish; X-axis – 10-day period of June.

We have also noted that, during the cold years, the sockeye enters the Kamchatka R. usually slightly later than in the warmer years, but this is not always consistent. By and large, the mass migration of the sockeye in the Kamchatka R., from the seasonal aspect, coincides with an increase in the level and temperature of the water in the Kamchatka R., but does not manifest any clear correlation with these factors or with the force and direction of the wind and air temperature. Furthermore, the dates on which the sockeye enters the Kamchatka R. definitely depend on the ratio of the abundance of local second-order stocks (sub-stocks) and their groups in the total sockeye stock of the Kamchatka R. Investigations have shown (Bugaev, 1987; Bugaev, 1987a) that some local second order stocks and their groups of the sockeye in the Kamchatka R. watershed, which differ in the biology of their freshwater period, display specific dynamics of the spawning migration (Bugaev, 1987; Bugaev, 1987a).

Therefore, the above data indicate that the dynamics of the spawning migration of the sockeye in the Kamchatka R. is affected by a set of factors, the combined effect of which determines the general dynamics of the migration.

On the basis of the escapement through a counting fence at the outlet of the Ozernaya R. and the catches at the mouth of the river, T. V. Yegorova (1977) analyzed the spawning migration of the Ozernaya sockeye in detail, and found that, compared with the spawning migration of the Asian sockeye to other spawning grounds, it lasted the longest.

The spawning migration usually begins during the last days of May, and is completed at the end of October–beginning of November. Mass migration (1000 fish or more per day) takes place from the middle of July up to the beginning of September, the main part of the run occurring from the end of July up to the middle of August. The number of migrants increases drastically from the middle of the second ten-day period of July up to the beginning of August, and gradually decreases from the beginning of August up to the beginning of September. The total duration of the spawning migration of Ozernaya sockeye (based on long-term data) is 5.0-5.5 months; mass migration lasts 1.5-2 months, and the main part of the run lasts 10-22 days (Yegorova, 1977).

The beginning of the mass migration coincides with the period of maximum flooding in the river and lake, and the main part of the run coincides with the drop in water level and the increase in water temperature.

The change in the run of the sockeye through a counting fence at the outlet of the Ozernaya R. reflects to some extent the nature of its entrance into the mouth of the Ozernaya R. 2-4 days later (river about 60 km long). The timing of the mass run and the main part of the run of this sockeye stock fluctuates from year to year, due to the number of sockeye arriving at the mouth of the Ozernaya R., the hydrological conditions and, presumably, the existence of separate local groups within the stock (Yegorova, 1977).

Analysis of the escapement of sexually mature sockeye through the counting fence at the outlet of the Ozernaya R. has shown that an early and intensive beginning of mass migration is observed mostly during the years with a greater abundance of the total brood stock (about 6,000,000-9,000,000 sockeye) and the part entering the river to spawn (2,000,000-4,200,000). The most prolonged mass entrance of sockeye is usually noted during the same years. The main part of the run is particularly well-defined and prolonged. During the years of average abundance (2,700,000-5,500,000), the mass run does not usually be-

gin early, but only after July 15th. The main part of the run is brief. During the years of low abundance (400,000-2,500,000), the mass run is the lightest and the latest. The main part of the run is either not observed at all, or is very weakly defined (Yegorova, 1977). Sometimes, if the weather prior to the mass run is warm with not much wind and with little precipitation, which results in a significant temperature gradient at the mouth of the river and in the pro-estuarine region of the sea, the mass run and the main part of the run of the Ozernaya sockeye move to earlier dates (Yegorova, 1977).

During our work at the Ust-Kamchatsk fish cannery in 1978 through 1983, the sex ratio in the sockeye during the spawning migration varied. For instance, in the early sockeye, males dominated (60-70 %) in the trap net catches before the mass run to the river. their numbers dropped to 55 % during the mass run, and then females prevailed in the catches (55-60 %) after the peak of migration. In the late sockeye, due to its low abundance and the migration of a part of the fish with the early form, this was not as noticeable as in the latter. However, the overall pattern of the sex ratio during the spawning migration (males predominating at the beginning of the run and females at the end of it) was similar to that of the early form.

Analysis of the sex ratio on the basis of drift net catches in the Kamchatka R. is insignificant, for it depends largely on the characteristics of the nets used, and does not lend itself to objective consideration in the case of biostatistical material from the Ust-Kamchatsk fish cannery.

In the sockeye of the Ozernaya R., males prevail at the onset and at the peak of the run, and females at the end of it. On the whole, the sex ratio approximates 1:1, though males prevail somewhat more frequently (Yegorova, 1977).

As indicated by this review of the timing of anadromous migration in the Asian sockeye, the dynamics of its spawning migration may depend on a number of factors, i.e. abundance, hydrometeorological conditions, population structure, and a number of others. In each specific case, as demonstrated in the sockeye of the Kamchatka and Ozernaya rivers, the spawning migration of the sockeye can have its own characteristics, the study of which is of prognostic value.

Section 6. Characteristics of the breeding grounds and spawning periods

Not all the spawning grounds of the Asian sockeye in the area of our investigations have been studied to the same extent (fig. 1). This problem has been dealt with to the greatest extent in the centre of its breeding area, on the Kamchatka Peninsula.

Sockeye spawning grounds which are located in areas of ground water discharge have been thoroughly characterized by Ye. M. Krokhin (1960, 1965), A. G. Ostroumov (1965, 1977a, 1970, 1970a, 1970b, 1972, 1975, 1982, 1982a, 1984, 1985, 1989) and a number of other researchers (Kuznetsov, 1928; Smirnov, 1975; Yarzhombek, Klyashtorin, 1980; Leman, 1988; Bazarkin, 1988, 1990, 1990a).

According to the results of Ostroumov's long-term aerial and terrestrial surveys (1975, 1975a, 1985), 50-70 % of the sockeye in the Kamchatka Region (Kamchatka Peninsula and Koryak Highlands) spawn in lakes, and 50-30 % in rivers.

The sockeye, the reproductive success of which is determined by the presence of lakes, spawns in 220 lakes of the most diverse origin. These spawning lakes are found at all altitudes, from 0-4 to 913 m above sea level. However, the absolute majority of the lakes is located at altitudes from 3-6 to 300-350 m above sea level, and only 8 are found at altitudes above 500 m (Bezmyannoye at 913 m, Avacha at 828 m, Vorovskoye at 570 m, etc.). Most of the spawning lakes are located in river watersheds on the eastern coast of the Kamchatka Peninsula. They are scarce in Western Kamchatka. Here they are concentrated mainly in the southwestern river watersheds from the Bolshaya R. to the Kambalnaya R. inclusively, and are not found at all in the watersheds of many of the large Western Kamchatka rivers. Most of the spawning lakes have a water plane surface of 1-10 km², fewer of them from 10 to 20 km², and only several lakes appear large in comparison, namely Nerpichye (552 km²), Kuril (77.1 km²), Azabach (63.9 km²), Palanskoye (28 km²) and Potat-Gytkhyn (27 km²). In addition to these, Kronotskoye L. with an area of 245 km² is located on the peninsula; it is inhabited by kokanee (a freshwater form of the sockeye), for rapids make it inaccessible to the anadromous sockeye (Ostroumov, 1985).

The lakes can be classified into the following four groups based on how they are used by the spawners (Ostroumov, 1985):

1. All the salmon spawn in the lakes. as there are no suitable places for spawning in the tributaries;
2. Almost all the salmon spawn in the lake's tributaries (rivers and spring-fed creeks);
3. A large part of the salmon spawn in the lake, and a smaller part in its tributaries and at the head of the river flowing out of it;
4. The greater part of the salmon spawn in the tributaries, and a smaller part in the lake itself.

The first group includes lava-dam lakes (e.g. Bezmyannoye), crater lakes (maar in the watershed of the Opala R.), lagoon-liman lakes (Lebedinoye), and floodplain oxbow lakes (Ushkovskoye). The second group includes lava-dam lakes (Palanskoye), and lagoon-liman lakes (Nerpichye). The third group includes glacial lakes (Potat-Gytkhyn, Khai-Gytkhyn, Ilir-Gytkhyn), glacial-fjord lakes (Listvenichnoye, Nalychevo), caldera lakes (Kurilskoye), and crater lakes (Kambal'noye). The fourth group includes glacial lakes (Nachikinskoye, Dvukhyurtochnoye), and lagoon-liman lakes (Azabachye, Storozh).

As a rule, only the early and late forms of the sockeye, as well as kokanee, spawn in all of these types of Kamchatkan lakes (Ostroumov, 1977, 1979, 1983). Only in certain floodplain and glacial lakes with intensive groundwater feeding do the chum and coho salmon, less commonly the pink salmon, spawn alongside the sockeye (Ostroumov, 1985).

Of the numerous tributaries that fall into these lakes, not all by far are used for spawning. In the majority of lakes, with

Table 3. Average ratio between brood stock size of some early and late runs of Asian sockeye based on aerial observations in 1981-1990 (A. G. Ostroumov, personal communication), %

Watershed	Early run	Late run
Palana R.	0.6	99.4
Tigil R.	3.0 (0.9-6.9)	97.0 (93.1-95.1)
Khairyuzova R.	9.0	91.0
Icha R.	1.6	98.4
Krutogorova R.	0.8	99.2
Vorovskaya R.	13.3 (6.3-26.8)	86.7 (73.1-93.7)
Kikhchik R.	0.9	99.1
Utka R.	0.3	99.7
Bolshaya R.*	55.1 (10.2-89.3)	44.9 (89.8-10.7)
Ozernaya R. (Kuril L.)	1.9	98.1
Listvenichnaya R.	0.0	100.0
Avacha R.	0.4	99.6
Tikhaya R.**	0.0	100.0
Kamchatka R.	84.1 (72.7-93.1)	15.9 (27.3-6.9)
Stolbovaya R.	83.1 (69.2-96.7)	16.9 (30.8-3.3)
Malamvayam R.	No data	No data
Khailyulya R.	0.5	99.5
Ivashka R.	0.3	99.7
Karaga R.	0.2	99.8
Tymlat R.	0.1	99.9
Kichiga R.	0.9	99.1
Avyavayam R.	1.1	98.9
Kultushnaya R.	0.0	100.0
Apuka R.	2.0	98.0
Ananapylgen R.	0.0	100.0
Ukalayat R.	1.5	98.5

Note. The range of fluctuation in brood stock size of seasonal sockeye runs, 1981-1990, is given in brackets. *In the past (1930's-1940's) the ratio between the early and late sockeye runs in the Bolshaya R. was different, 25-30 % and 70-75 % respectively. **There is no complete certainty of an absolute absence of an early sockeye run in the Tikhaya R. In recent years individual fish have been seen, while in the past, dozens (perhaps hundreds) were observed. Late run sockeye have been seen in dozens and hundreds.

the exception of certain lagoon-liman lakes, the most important spawning tributary is the effluent of the river which flows out of the lake. It is usually called the Verkhnyaya (Upper) R., and falls into the lake farthest from the source of the river that arises in it. For the most part, "the Verkhnyaya R." has a length of 15-20 km, and only some are 35-45 km long. In the lakes that formed where sea inlets had once existed, it is not always possible to spot an analogue of the Verkhnyaya R. (Ostroumov, 1985).

All lake tributaries can be classified into the following four main groups based on the distribution of salmon (Ostroumov, 1985):

1. Spawning throughout the entire length of the tributary (Vereshchagina, Ryborazvodnaya in the watershed of Nerpichye L.; Taburetka in the watershed of Nachikinskoye L.);

2. Spawning in the lower and middle reaches (Poperechnaya in the watershed of Stolbovoye L.; Verkhnyaya in the watershed of Dvukhyurtochnoye L.; Babya and Pryamaya in the watershed of Nachikinskoye L.);

3. Spawning in the middle and upper reaches (1st-3rd Olkhovyie, Khalnitsa and Tarkhovaya in the watershed of Nerpichye L.);

4. Spawning in the middle reaches (Verkhnyaya Palana in the watershed of Palanskoye L.).

5. About one-half of all the sockeye breeding in the lake watersheds of the Kamchatka Region spawns in lake tributaries. Of the total number of sockeye that enter the tributaries of lakes, 60-90 % spawn in tributaries of the first order. Of all the sockeye that spawn in all the tributaries of the second order, third order, etc., 75-95 % do so in second-order tributaries. It appears that the sockeye strives to spawn primarily in rivers and spring-fed creeks that fall into lakes. Lacustrine spawning grounds dominate only in the cases where there are no tributaries or places suitable for spawning, or if these are too small (Ostroumov, 1985).

According to the estimates of A. G. Ostroumov (1985), up to 7,000,000-8,000,000 sockeye spawned in the river watersheds of the Kamchatka Region in the 1940s-1970s. Lakes alone accounted for 10-12 % of the total number of sockeye which entered spawning waters on the eastern coast, 36-40 % on the western coast, and 22-28 % for all the bodies of water in the Kamchatka Region. The spawning grounds found in lakes and their tributaries are of particular importance on the western coast of the peninsula (75-91 %). If we take into account the sockeye spawning grounds in all the bodies of water found in the Kamchatka Region, the lakes and their tributaries will account for up to 50-70 % of all the sockeye. The spawning significance of the various types of lakes on both coasts differs. On the eastern coast, the most significant is the large group of

lagoon-liman lakes, followed by glacial, floodplain, lava-dam, dammed and caldera lakes. On the western coast, the dominant one is the caldera Kuril L., followed by lava-dam, glacial, crater and tectonic lakes.

Examining the river spawning grounds of the sockeye within the Kamchatka Region, A. G. Ostroumov (1975) classifies them as follows:

1. Main river-beds 500-1000 km long, e.g. the Kamchatka R. There are no spawning grounds in the lower and middle reaches of the main bed of this river. In the main bed of the upper reaches, sockeye spawning grounds are encountered in some small areas from the village of Milkovo up to points 12-15 km away from the outfall of the Ozernaya Kamchatka R. and up to the outfall of Pravaya Kamchatka R. The largest number of sockeye spawns between Kenuzhen L. and the interfluvium of the Ozernaya and Pravaya Kamchatka rivers. On the stretch between the interfluvium of these rivers and the village of Milkovo, the sockeye spawns close to either bank, and above the outlets of these rivers often occupies the entire width of the bed, due to the shallowness of the water, depth and ground uniformity (gravelly-pebbly-sandy), and the presence of ground waters which are discharged at the point where the Kamchatka R. emerges from the mountains.

2. Main river-beds 100-500 km long.

The sockeye spawns in the central part of the bed, and close to the banks in small areas of the middle and upper reaches of the river.

The Ozernaya R. (eastern) is an example of such a river. In its middle reaches, sockeye redds are distributed over the entire bottom, or along the banks. The pair of fish often have not more than 3 m² of breeding area. The ground in these places is pebbly-gravelly-sandy, and the depth does not usually exceed 1 m (more commonly 0.4-0.7 m).

3. Main river-beds up to 100 km in length.

The sockeye rarely spawns in main channel in the lower reaches of these rivers, and not in large numbers. In the middle and upper reaches, it spawns in the central part of the river-bed and close to the banks.

The Kanurivayam R. is an example of such a river (Karaginsky district, length of river 60 km). Moderately meandering, its river bed is often relatively straight for several hundreds of metres (with a width of up to 10 m and more). The bottom is comparatively flat, and the depth measures 0.5-0.8 m. The lower spawning grounds consist of completely dug up areas, whereas spawning in the upper reaches is not as frequent.

Vast spawning grounds are encountered in the uppermost part of the Ozernaya R. which flows out of Kuril L. The breeding area located along the right bank joins with the lake. In some places, particularly at the top close to its outfall, the whole width of the river is occupied by fish. The depth in the central part of the slightly meandering bed does not exceed 1 m, and it is 2-3 times smaller near the banks; the flow velocity does not exceed 0.9 m/s (usually less according to M. M. Selifonov). The ground is gravelly, coarse-sandy and pebbly-sandy. The spawning grounds are located on an area measuring about 6 km in length and 20-100 m in width (Ostroumov, 1970).

4. Main river-beds of tributaries of the first, second, etc. orders.

In the river watersheds of the Kamchatka Region, the largest number of sockeye usually breeds in first- and second-order tributaries. Tributaries of the third order are many times less important, but some of them are not inferior to the first two. Few sockeye enter tributaries of the fourth order, and several times fewer yet enter tributaries of the fifth order. An insignificant number of sockeye enters sixth-order tributaries. For the most part, rivers from the third order on are not utilized by the sockeye at all (Ostroumov, 1975).

In first- and second-order tributaries that flow into rivers, spawning grounds may be situated anywhere from the mouth to the upper reaches inclusively, somewhat more frequently in the middle and upper reaches of the rivers. The breeding areas usually alternate with vast areas of river that are not occupied by fish. Sometimes, the spawning grounds, alternating with very short "empty" areas, occupy together with the latter several hundreds of metres or several kilometres of the river-bed; for many kilometres after that, individual spawners are encountered, and then again the concentration of fish increases drastically and remains high for several hundreds of metres or several kilometres. For the most part, spawning sock-eye salmon do not form very dense concentrations; a pair of fish usually occupies 8-4 m² of breeding area, but in some parts only 2-3 m² or less.

In wide high-water tributaries where the water is deeper now off one bank of the river, now off the other, areas with tens, hundreds and even thousands of spawners are usually scattered in the middle of the river-bed or along the banks, hardly ever occupying the entire river-bed from bank to bank. In narrow low-water tributaries with fairly uniform depths across the river-bed, spawning is common from one bank to the other for stretches varying in length (Ostroumov, 1975)

In small moderately and highly meandering streams, the distribution of salmon spawning grounds, particularly those of the sockeye, depends on the flow velocity and water depth to a greater extent than in slightly meandering streams. In all the cases, the main spawning grounds are located between the meanders. With small and almost uniform depths throughout the river-bed, the sockeye spawns in both the inside and outside of the bends; if the water is relatively deep, the sockeye spawns only in the inside.

Some tributaries of Kamchatkan rivers spring from typical lakes or lake-like bodies resembling limnokrenes, frequently located quite high in the mountains. From the outfall and for several hundreds of metres or several kilometres, the depths in the channel of this type of tributary are usually uniform, not more than 50-80 cm, the ground is loose and pebbly-sandy, and the flow is moderate, sometimes quite slow. The river-bed may be wide, slightly or moderately meandering, usually without side channels, and sometimes the riverhead is shaped like a funnel with the mouth facing the lake. Sometimes, a small part of the bed at the riverhead itself is a narrow channel which is later replaced by fairly wide reaches without distinct bounda-

ries. Such reaches and channels serve as spawning grounds for hundreds, less commonly thousands of sockeye (Ostroumov, 1975).

Sockeye spawning grounds in the tributaries of rivers flowing into rivers can be found in the following different parts of these tributaries (Ostroumov, 1975):

Sockeye spawn over the entire length of a tributary, as in the case of the Andrianovka R. (length 92 km, falls into the Kamchatka R. 590 km from its mouth).

Sockeye spawn in the lower and middle reaches of a tributary, as in the case of the Bystraya R. (length 154 km, falls into the Kozyrevka R. 5 km from its mouth, which in turn falls into the Kamchatka R. 299 km from its mouth).

Sockeye spawn in the middle and upper reaches of rivers, as in the case of the tributaries of the Bystraya-Kozyrevka and Dvukhyurtochnaya rivers (length 112 km; interflowing with the Kirevna R., it falls into the Kamchatka R. 144 km from its mouth).

Sockeye spawn in the upper reaches of rivers, as in the case of the Kuzanok R. (length 59 km, falls into the Golygina R. 50 km from its mouth) and the headwater of the river flowing out of Golyginskoye L.

In the valleys of most of the spawning rivers of the Kamchatka Region, there are numerous spring-fed creeks or abandoned river channels [klyuchi] which comprise over 25,000,000 m² or 9 % of the total spawning area used by all the species of salmon in this region (Ostroumov, 1975).

As a result of a long-term extensive study on the rivers and lakes of the Kamchatka Region, A.G. Ostroumov (1982) developed the following classification of the spring-fed bodies of water encountered in nature:

1) klyuchi-kur'i [Russ. klyuch – slow-flowing spring-fed creek. or abandoned river channel. sometimes with lake-like expanses; kur'ya – a long and narrow river inlet with standing water, formerly an oxbow, but later detached from the river at its upper end. or a portion of a river which has turned into a small lake surrounded by bars];

2) long meandering spring-fed creeks of uniform width (derivatives of branches of rivers, rheokrenes);

3) spring-fed creeks with a straight bed, comparatively slightly entrenched in fundamental lands (of the type found in the lower parts of the Vetlovaya R. in the watershed of Stolbovoye L.);

4) long spring-fed creeks with wide reaches (vaguely delineated kurchazhiny) [Russ. Far East – depressions in a body of water where migratory fish stay] that come one after another over a distance of hundred of metres to several kilometres;

5) long meandering spring-fed creeks with wide reaches and lake-like expansions of the main bed (kurchazhiny); separate kurchazhiny connected with a river by narrow channels;

6) spring-fed lakes (limnokrenes of the "Ushkovskoye L." type, Koratkanok and Shekhun in the the Kamchatka R. watershed);

7) spring-fed creeks with bowl-shaped lakelets at the springhead, comparatively deeply entrenched in the original banks (like the "Pod Taburettoi" creek in the watershed of Nachikinskoye L.);

8) long meandering wide spring-fed creeks with lake-like expanses, forming a multitude of kurchazhiny, directly at the outfalls (e.g. Nikolka R. and Svetlyi creek in the Kamchatka R. watershed);

9) spring-fed creeks with spherical, bowl-shaped expanses at the outfall, very deeply entrenched in the original banks formed by spurs of a mountain ridge (e.g. the Atkhl and Timofeyevsky creeks in the watershed of Azabach L.);

10) spherical or paddle-shaped spring-fed bodies of water formed from the separated parts of a lake (e.g. Kruglyi or Medvezhiy creek in the watershed of Nachikinskoye L.).

A fairly distinct boundary extends along the rivers of the western coast (Saichik, Sopochnaya) and the eastern coast of the Kamchatka Peninsula (Pakloayam, Kichiga), separating the more southern areas, where all the types of spring-fed bodies of water are encountered, from the northern areas where the absolute number of spring-fed bodies of water is quite low and the latter are not characterized by a diversity of types (Ostroumov, 1982).

Spring-fed bodies of the 2nd, 4th and 5th types, the most numerous in the Kamchatka Oblast, are found everywhere from the mouths of rivers to their upper reaches, up to altitudes of 800-1000 m. However, most of them are found in the watersheds of both fairly large rivers, and small rivers, at altitudes of 0 to 350-400 m and 0 to 50-100 m respectively, i.e. the majority of them are concentrated in the middle and lower parts of rivers (Ostroumov, 1982).

Sockeye spawn in all types of spring-fed bodies of water, chum and coho in the majority of types, and pink salmon spawn only in certain types of spring-fed waters. In spring-fed bodies of waters of the same type, the sockeye, chum and coho salmon spawn alternately, and the spawning periods of the sockeye and chum often coincide completely or partially. The run timing of the sockeye, chum and pink salmon also coincides, but the pink salmon usually spawns away from the breeding areas of the sockeye, chum and coho salmon (Ostroumov, 1982).

The length of the spring-fed bodies of water varies from 0.1-0.3 to 20-25 km, and the width from 0.5 to 200 and even 700 m. The area of the water plane does not differ much from the area of the bottom, and 70-90 % of the latter is suitable for spawning in the majority of spring-fed bodies of water. In the most numerous and widely distributed spring-fed bodies of water, the spawning area does not usually exceed 10,000-12,000 m², but in some it can reach 30,000-50,000 and even 100,000-200,000 m² (Ostroumov, 1982).

As we have mentioned earlier, the formation of seasonal races is a characteristic feature of the sockeye. Table 3 gives the abundance ratio of the spawned-out adults of some stocks of the early and late seasonal races of the Asian sockeye. As we can see from the table, the early seasonal race of the sockeye predominates in the Bolshaya, Kamchatka and Stolbovaya rivers, and is encountered in very small numbers in the other bodies of water.

The areas of the spawning grounds of the early and late seasonal races of the sockeye in some parts of the Kamchatka Region are given in table 4.

Table 4. Ratio of spawning areas for early and late sockeye runs in the watersheds of some Asian rivers (A. G. Ostroumov, KoTINRO archives), %

Watershed	Early run	Late run	Total spawning area, hectares
Icha R.	1.2	98.8	25.60
Krutogorova R.	5.0	95.0	10.65
Vorovskaya R.	12.6	87.4	11.38
Kikhchik R.	11.6	88.4	10.99
Bolshaya R.	30.9 *	69.1	115.71
Kamchatka R.	80.3	19.7	1674.80
Stolbovaya R.	85.5	14.5	34.23
Khailyulya R.	9.7	90.3	28.90
Ivashka R.	5.1	94.9	23.28
Karaga R.	4.0	96.0	19.87
Kichiga R.	15.5	84.5	0.97
Avyavayam R.	11.7	88.3	3.86
Kultushnaya R.	0.0	100	27.29
Apuka R.	7.1	92.9	42.53
Ananapylgen R.	0.0	100	67.57

*Nachikinskoye L. sockeye

The early and late seasonal races of the sockeye do not form their own specific “spawning pattern”. In both races, the configuration of the spawning grounds depends only on the morphology of the lake watershed, the type of ground and other environmental factors, as well as on the number of spawners (Ostroumov, 1989).

Analysis of the relationship between the ratio of the breeding areas of the early seasonal race of the sockeye and its proportion to the total numbers of the sockeye in the rivers has shown that it is a direct and statistically reliable relationship (fig. 11). This permits us to assume that the existence and correlation of the seasonal races of the sockeye in rivers is determined primarily by the presence of suitable spawning grounds which probably have different mean temperatures of egg incubation (Brannon, 1987). In our opinion, the data of fig. 11 attest to the fact that the seasonal races in the sockeye should be regarded as structural components of local stocks, as surmised earlier (Konovalov, 1980; Bugaev, 1983c, 1986a).

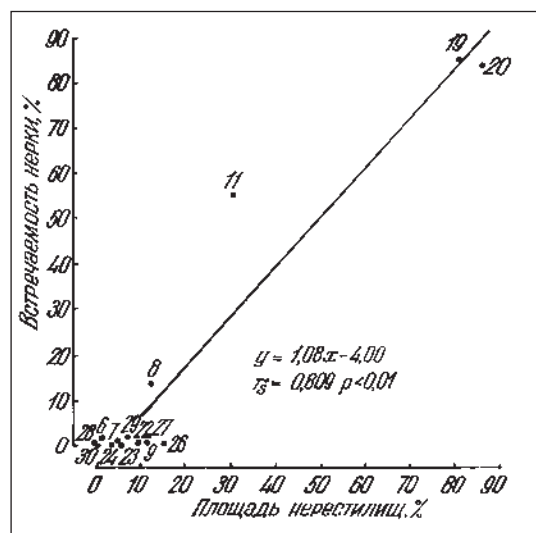


Fig. 11. Correlation between the size of the spawning grounds and the numbers of the early (spring) seasonal race of the sockeye on the Kamchatka Peninsula (calculations based on data A. G. Ostroumov – tables 3-4). Y-axis – occurrence of individuals of the early seasonal race (of the total numbers of the early and late seasonal races of the sockeye, %); X-axis – area of spawning grounds of the early seasonal race (of the total area of spawning grounds of the early and late seasonal races of the sockeye). Areas marked as in fig. 1.

The ratios of the various types of sockeye breeding areas in the Kuril L. watershed were examined in detail by A. G. Ostroumov (1970) (see table 5 and fig. 5). Somewhat later, the types of spawning grounds were also characterized in detail for the sockeye of Azabach L. (Ostroumov, 1972) (see table 6 and fig. 4). Data on the types of sockeye spawning grounds in the Kamchatka R. watershed were published recently (Bugaev, Ostroumov, 1989) (see table 7 and fig. 2).

With many other features in common, the spawning periods of the Asian sockeye can differ significantly in some populations. Furthermore, we also note some interannual differences which are determined by climatic and hydrological conditions. Here are some examples.

The spawning of the sockeye in Uyeginskoye L. (Okhota R. watershed) begins at the end of July, and peaks in August. Late-running sockeye spawn in September and at the beginning of October. The sockeye spawns in the littoral zone of the lake, near the shores, close to the mouths of small tributaries near the outfall from the lake, in small inlets with groundwater

Table 5. Distribution of sockeye spawning areas in the Kuril L. watershed (Ostroumov, 1970)

Spawning area	Length, m	Width, m	Area, thou. of m ²
Riverine spawning beds			
Soorse of Ozernaya R.	6000	20-100	120-150
Severnaya-1 R.	2500	2-3	5-7
Severnaya-2 R.	1500	2-3	3-4
Vychenkiya R.	4000	2-4	8-16
Gavryushka R.	3000	2-4	6-12
Kirushutk R.	4000-5000	2-4	8-20
Khakytsin R.	6000-8000	2-6	20-30
Etamynk R.	3000	3-10	20
River total (average)	31500	–	225
Spring-creek spawning beds			
Kirushutk R.	–	–	2
Khakytsin R.	–	–	18
Etamynk R.	–	–	4
Stream between the mouths of Khakytsin & Etamynk rivers	–	–	6
Spring-creek total	–	–	30
Lacustrine spawning beds			
North Bay (1-8)	5900	–	184-284
Warm Western Bay(9-11)	700	–	2.9-3.2
Warm Eastern Bay (12)	150	–	0.45-0.75
Shore between Warm and cold Oladochnaya Bays (13-14)	700	–	2.1-3.5
Oladochnaya Bay (15-21)	3900	–	75-110
N.-E. of point Glynianyi (22)	600	–	12-18
Bay E. of point Tugumynk (23-26)	5750	–	150-178
South coast (27-32)	5350	–	112-171
Etamynk L.	2000	2-4	4-8
West coast (33-40)	6100	–	66-126
Lake total (average)	31150	–	755
Watershed total, Kuril L. (average)	63000	–	1010

Note. See fig. 5

Table 6. Distribution of sockeye spawning grounds in the Azabach L. watershed (Ostroumov, 1972)

Spawning areas	Area, thou. of m ²	Spawning areas	Area, thou. of m ²
<u>Lacustrine</u>		<u>Spring-stream</u>	
Between mouths of Azabachya & Lotnaya rivers	5-10	Lotnaya R. watershed	0.2-0.3
Between Lotnaya & Bushyeva rivers	10-15	Rybovodnyie 1 & 2	2
Between Bushuyeva R. & point on South. shore of lake	1.5-2	Bushyeva R. watershed	15-20
Between Lamutka & Snovidikha rivers	100-125	Lamutka R. watershed	2-3
Alone both shores of the mouth of Snovidikha R.	15-20	Ostrovnyaya R. watershed	0.5-1
To S.-W. & N.-E. of mouth Ponomarskaya R.	12-16	Two unnamed streams, lake shore	2.8-3
		Two unnamed streams, lake shore	1
Lake total (average)	165	Orishkin	2-4
		Bulunka	0.5
		Snovidikhin	4-5
		Bolotnye 1 & 2	0.5-1
		Timofeevskiy	2.8-3
		Unnamed streams	1.5-2
		Ponomarskaya R. watershed	1.5-2.5
		Atkhl	1.5-2.5
		Unnamed stream entering from right into	0.5-1
		Azabachya R., 5 km from its source	
Rivers total (average)	235	Spring-stream total (average)	45
Total for Azabach L. (average) – 445 thou. of m ²			

Note. See fig. 4

discharges. The spawning grounds occupy parts of the littoral zone that are usually away from the edge of the water, with depths from 0.5 to 5 m. At the end of October, the sockeye spawns under the ice (Nikulin, 1975).

Table 7. Ratio of the area of various types of spawning grounds of second order sockeye stocks and their groups in the Kamchatka R. watershed (Bugaev, Ostroumov, 1989), %

Stock, group, seasonal race	River		Spring-stream		Location lake		Total	
	Vertical	Horizon	Vertical	Horizon	Vertical	Horizon	Vertical	Horizon
“S” (early)	32	78	58	21.93	1.2	0.07	35	100
“V” (late)	56	58	60	38	16	4	52	100
“E” (early)	63(93)	92	25 (60)	6	61 (61.5)	2	58 (90)	100
“E” (late)	34 (79)	64	19 (48)	21	32 (38)	15	29 (61)	100
“A” (early)	3 (4)	72	3 (7)	13	20.3 (21)	15	3 (4.6)	100
“A” (late)	4 (8)	28	0.5 (1.5)	3	36 (43)	69	7 (14.5)	100
“D” (early)	1 (1)	89	0.1 (0.3)	3	2.7 (2.7)	8	0.7 (1)	100
“D” (late)	0.2 (0.5)	32	0.1 (0.2)	6	2 (2)	62	0.4 (0.8)	100
“K” (early)	–(–)	–	0.3 (0.7)	69	0.8 (0.8)	31	0.1 (0.1)	100
“K” (late)	–(–)	–	0.5 (1.3)	24	4 (5)	76	0.6 (1.3)	100
“N” (early)	1 (2)	31	3.6 (32)	59	14 (14)	10	3.2 (4.3)	100
“N” (late)	5.8 (12.5)	27	19.9 (49)	60	10 (12)	13	11 (22.4)	100
All atocks and groups:								
early	100	85	100	13	100	2	100	100
late	100	54	100	33	100	13	100	100

Note. Indices per taming to “E”, “A”, “D” and K are given for the early (top line) and late (lower line) seasonal rases. In brackets is given the portion in % (vertically) for “E”, “A”, “D”, “K” and “N”; “N” is just the area of spawning grounds for Nerpichye L. sockeye stocks (group “N” spawning area is included with that of group “E”).

In Asia, the spawning of the sockeye lasts the longest in the Kuril L. watershed. It begins at the end of July–beginning of August, and continues up to the end of January–beginning of February, with mass spawning occurring from September up to November (Yegorova, 1970). According to N. V. Varnavskaya (1988a), the sockeye here begins to spawn even in mid July or at the beginning of the month.

The spawning periods of the sockeye at the different spawning grounds of Kuril L. vary (Yegorova, 1968). The spawning grounds are occupied from north to south. The first spawners appear at the nests of the northern part of the lake and in the Severnaya R. (Vychenkiya) at the end of July. Here, spawning ends in the second half of November. At the beginning or in the middle of August, sockeye begin to spawn in the Ozernaya R., in the southern part of the lake and in the Etamynk R. which falls into the lake from the west. In these areas, spawning continues up to the end of January. The latest spawning (from the end of September up to February) is noted in the spring-fed creeks of the Sredniy Khakytsin R. which falls into Kuril L. from the south, and in Etamynk L. (Yegorova, 1977).

The results of the tagging carried out by M. F. Selifonova (1978a) have shown that the sockeye of the Ozernaya R. does not display a clear correlation between the time at which the spawners pass through the counting fence and their place of spawning in the Kuril L. watershed. Sockeye with different run timing can spawn in the same breeding area (except in the rivers of the northern and eastern parts of the lake), just as spawners with the same run timing can disperse to breeding areas of different types (river, lake, mixed) where mass spawning begins at different times and lasts for different periods of time.

At the majority of the sockeye spawning grounds in the Kuril L. watershed, the depth does not exceed 1-2 m (usually 0.5-1.0 m). Only in Severnaya Bay is there a vast spawning ground where, in the southern part of it, sockeye spawn at a depth of 4-6 m almost every year (Ostroumov, 1970).

The run timing of the adult fish of some second-order stocks of the sockeye of the Kamchatka R. watershed is given in table 8.

According to A. G. Ostroumov (1972), the spawning of the early sockeye in Azabach L. (Kamchatka R.) begins at the end of June–beginning of July both in the littoral zone of the lake, and in its tributaries simultaneously. The most intensive spawning is observed at the beginning of the second half of July. Spawning ends at the beginning of August. The late sockeye spawn from about the middle of the first 10-day period of August and up to the middle of September. Mass spawning takes place in the second half of August. According to our observations, spawning in the littoral zone of Azabach L. sometimes ends at the beginning–in the middle of October. During some low-water years, some of the early sockeye cannot enter certain spring-fed creeks (Bannyi spring near the KoTINRO station), and spawns in the littoral zone of the lake. During the warm years, spawning of the early form ends several days earlier than in the cold years (no data available for the late form of the sockeye).

According to the data of I. I. Kuznetsov (1928) and A. G. Ostroumov (1975b), spawning of the early sockeye in the watershed of the “Ushkovskoye L.” limnokrene (Kamchatka R.) takes place throughout the last ten days of July and the first days of August (this form is scarce here), and spawning of the late form takes place at the beginning or in the middle of August, and usually ends on 15-30 October (during certain years, at the beginning or in the middle of November).

Spawning of the sockeye in Seutakan L. (Eastern Chukchi Peninsula) occurs from the first ten days of August, and in

Achchen L. (in 1975) at the beginning of the second 10-day period of August; mass spawning in both lakes was observed in the middle of August. Spawning ends at the end of September–beginning of October. Spawning of some of the residual males and females in Achchen L. was recorded in October (Chereshnev, 1981).

Table 8. *Spawning times of sockeye in the Kamchatka R. watershed on the basis of aerial observation in 1981-1990 (Ostroumov, 1972; A. G. Ostroumov, personal communication)*

Watershed	Early sockeye		
	Beginning	Main spawn	End
Kamchatka R. from sources to Milkovo village	23.06.-10.07	15.07-05.08	05.08-25.08
Rivers: Kirganik, Kimitina, Tsapina, Nikolka, Tolbachik, Kreruk	23.06-15.07 23.06-15.07	10.07-03.08 10.07-03.08	01.08-15.08 01.08-15.08
Ushkovskoye L.	01.07-08.07	10.07-03.08	01.08-15.08
Yelovka R.	01.07	10.07-31.07	25.07-05.08
Azabach L.	25.06-5.07	20.07-03.08	05.08-10.08
Nerpichye L. watershed (Soldatskaya, Kultushnaya, Olkhovye rivers)	01.07-08.07 01.07-10.07	16.07-18.07 15.07-05.08	01.08-05.08 01.08-15.08
Watershed	Late sockeye		
	Beginning	Main spawn	End
Kamchatka R. from sources to Milkovo village	15.07-10.08	10.08-05.09	05.09-30.09
Rivers: Kirganik, Kimitina, Tsapina, Nikolka, Tolbachik, Kreruk	15.07-31.07 15.07-31.07	05.08-25.08 05.08-25.08	05.09-30.09 05.09-30.09
Ushkovskoye L.	05.08-15.08	20.08-30.09	15.10-23.11
Yelovka R.	01.08-10.08	10.08-03.09	05.09-30.09
Azabach L.	05.08-06.08	16.08-30.08	15.09*
Nerpichye L. watershed Soldatskaya, Kultushnaya, Olkhovye rivers)	12.07-24.07 12.07-24.07	05.08-05.09 05.08-05.09	01.09-30.09 01.09-30.09

Note. The arabach is a special variant of the late type of sockeye in the upper and mid sections of the Kamchatka R. watershed, isolated by A. G. Ostroumov (1965, 1970, 1970a), spawning from early July to late September. Mass spawning of arabach occurs mainly from 25-31.07 to 01-10.09. By our classification (Bugaev, 1986a) arabach belongs in group "V" (fig.2). *We have observed the littoral spawning of sockeye in some years in Azabach L. up to 01-25 October. In warm years sockeye spawn usually a few days earlier, and late in cold years.

The spawning grounds of the sockeye in Achchen L. are located in the coastal zone of the lake's northeastern shore. Spawning takes place at depths of 1-4 m. In the areas of the spawning grounds, rivers and creeks do not reach the lake, but filter through the coastal alluvium, and emerge in the littoral zone of the lake in the form of springs, and this is where the sockeye reproduces. In Seutakan L., breeding grounds are found in the northwestern part of the lake at a depth of 1-2 m, probably near the mouths of large streams and creeks flowing into Seutakan L. and in the channel flowing out of Seutakan L. (Chereshnev, 1981).

According to the data of Ye. K. Suvorov (1911) and S. I. Kurenkov (1970), spawning of the sockeye in Sarannoye L. (Bering Is.) begins during the third 10-day period of July, peaks at the end of August or in September, and ends in November or at the beginning of December. It is presumed that two seasonal races of the sockeye, the early and late, inhabit the lake (S. Kurenkov, 1970).

The spawning grounds of the sockeye in the Sarannoye L. watershed are classified by S. I. Kurenkov (1979) into lacustrine ones located in the littoral zone of the lake, and fluvial ones located in spring-fed creeks that flow into the lake. The first are the dominant ones both in area, and in the number of sockeye that spawn in them.

The spawning periods of the Asian sockeye in areas other than those listed above are given in table 9.

The spawning behaviour and the spawning process of the sockeye have been described in a number of publications (Kuznetsov, 1928; Semko, 1954; Yegorova, 1970; Simonova, 1972, 1974, 1975; Smirnov, 1975; Parnsky, 1988, 1988a; Chebanov, 1991).

The embryonic-larval development of the sockeye prior to the emergence of alevins from the ground lasts from 5 to 8 months, and of all the species of Pacific salmon, the sockeye has the longest period of embryonic development. The latter has been described in detail for some of the Asian sockeye populations in A. I. Smirnov's monograph (1975) and in T. V. Yegorova's paper (1970).

Based on data from the 1930s, the mean mortality of the eggs at the Uyeginskoye L. spawning grounds was equal to 33 % with the average density of deposition equal to 3128 eggs per sq. metre (Nikulin, 1975).

During 1946-1965, the survival rate of the eggs of the Ozernaya sockeye varied from 62.2 to 94.1 % (mean 76.4 %). This is a high survival rate, which is not encountered (Foerster, 1968) in other bodies of water on the Asian and American coasts (Selifonov, 1975). We have not found that the survival rate of the eggs during their development depends on abiotic factors

Table 9. Spawning times of some early and late Asian sockeye brood stocks from aerial observations in 1981-1990 (A. G. Ostroumov, personal communication)

Watershed	Early sockeye			Late sockeye		
	Beginning	Main spawn	End	Beginning	Main spawn	End
Palana R.	05-15.07	15-31.07	05.08	20-25.07	05.08-05.09	01-31.10
Tigil R.	05-10.07	10-31.07	05.08	25.07	05.08-05.09	15-25.09
Khairyzoza R.	25.06-10.07	10.07-03.08	05-10.08	05-15.08	15.08-05.09	15.09-10.10
Rivers: Icha,	01-15.07	15.07-10.08	05-25.08	26.07-25.08	15.08-20.09	03.09-31.10
Krutogorova,	01-15.07	15.07-10.08	05-25.08	26.07-25.08	15.08-20.09	03.09-31.10
Vorovskaya, Kikhchik,	01-15.07	15.07-10.08	05-25.08	26.07-25.08	15.08-20.09	03.09-31.10
Utka, Bolshaya	01-15.07	15.07-10.08	05-25.08	26.07-25.08	15.08-20.09	03.09-31.10
Ozernaya R.	No data	05-15.07*	No data	30-31.07**	01.09-30.11	01-15.02
Avacha R.	10-20.06	01-31.07	01-10.08	05-15.08	20.08-15.09	30.09-31.10
Listvenichnaya R.	No data	No data	No data	05-15.08	20.08-25.09	05-31.10
Kamchatka R.	01-05.07	20.07-05.08	05-15.08	05-15.08	20.08-20.09	15.09-23.11
Stolbovaya R.	05-18.07	20-31.07	15-20.08	15.-20.08	25.08-15.09	01-15.10
Malamvayam,	15-30.06	01-31.07	01-05.08	01-05.08	15.08-15.10	01-31.10
Khailyulya, Tymlat,	15-30.06	01-31.07	01-05.08	01-05.08	15.08-15.10	01-31.10
Ivashka, Karaga,	15-30.06	01-31.07	01-05.08	01-05.08	15.08-15.10	01-31.10
Kichiga rivers	15-30.06	01-31.07	01-05.08	01-05.08	15.08-15.10	01-31.10
Aviavayam,	No data	01-31.07	01-03.08	01-05.08	10-25.08	05-30.09
Kultushnaya,	No data	No data	No data	10-20.07	05-25.08	15-30.09
Apuka,	01-07.07	5-25.07	01-03.08	25.07-05.08	05-31.08	No data
Ananapylgen,	No data	No data	No data	05-10.07	25.07-20.08	31.08-30.09
Ukalayat	No data	No data	No data	No data	25.08	No data

Note. Sockeye spawning times of various seasonal raises in the Kuril L. watershed require refinement. *Early sockeye spawning from N. V. Varnavskaya (1988a). **Late sockeye spawning from Yegorova, 1970 (in our opinion, it is possible that the start of the late spawning run, in this case, impacts on the end of the early run). Spawning begins earlier in warm years and later in cold years.

such as silting, freezing, the presence or absence of freeze-up on the lake, or water temperature. However, a direct relationship is noted between the total quantity of eggs from spawned-out females and the abundance of hatched alevins (Selifonov, 1975; Selifonov, 1987).

Egg mortality at the spawning grounds of Dalneye L. mean 50 % (range from 20 to 80 %), (Krogus, Krokhin, 1956).

The density of the sockeye brood stock at the spawning grounds appears to have a similar influence on the productivity of the year-classes both during the spawning period, and during egg incubation; the smallest egg and embryo losses are noted with a low density of the brood stock, and the highest losses with a high density. With a high density of the brood stock, the lowest egg losses during spawning and egg incubation are observed in small sockeye, and relatively high losses in medium-sized and large female spawners (Chebanov, 1984, 1991).

Section 7. Foraging waters

One of the main factors that determine the distribution of sockeye on the Kamchatka Peninsula and in Asia as a whole is the presence of lakes that can serve as foraging grounds for the young prior to the seaward migration. It is the presence of Azabach L. in the Kamchatka R. watershed and Kuril L. in the Ozernaya R. watershed that is responsible for the high abundance of these sockeye stocks.

According to A. G. Ostroumov (1985), the sockeye of the Kamchatka Peninsula reproduce and forage in more than 220 lakes. Unfortunately, these are mostly small lakes, and the abundance of the sockeye populations inhabiting them is not high.

Physicogeographical characteristics of lakes

The principal foraging waters of the sockeye in Kamchatka are the cold-water ones with a well-developed temperature stratification. The exceptions are Nerpichye L. in the lower reaches of the Kamchatka R. and Sarannoye L. (Bering Is.), which are both homothermic (Kurenkov, 1967a). In the case of the first lake, this is due to a small depth, and in the case of Sarannoye L. to strong winds against which the lake is unprotected (S. Kurenkov, 1970).

Table 10 contains general morphometric data on some of the lakes in which sockeye feed, grow and spawn. We have no information on the other lakes mentioned in this report.

Table 10. Morphometric and hydrological characteristics of some spawner-foraging sockeye lakes in Asia

Watershed	Area, km ²	Volume, km ³	Maximum depth, m	Mean depth, m	Watershed area, km ²	Water exchange index	Litoral area (0-5 m), %	Mean summer water transparency, m	Altitude above sea level, m	Notes
Uyeginskoye L. (Okhota R.)	2.50	0.040	28.0	16.0	–	–	–	–	400.0	Nikulin, 1970, 1975
Palanskoye L. (Palana R.)	28.35	0.568	28.0	14.8	623.0	0.76	16.3	–	276.0	Nikolayev, Siniakov, 1990*
Nachikinskoye L. (Bolshaya R.)	7.14	0.111	36.5	15.6	202.0	2.70	27.6	4.1	346.0	Nikolayev, Nikolayeva, 1991
Tolmachevskoye L. (Bolshaya R.)	11.20	0.088	26.0	7.9	–	–	45.5	–	–	Krokhin, Kurenkov, 1967*
Kuril (Kurilskoye) L. (Ozernaya R.)	77.05	15.040	316.0	195.2	392.0	0.19	1.0	10.0	104.0	Nikolayev, Nikolayeva, 1991
Kluchevoye L. (Ksudach volcano)	5.39	0.327	96.0	60.6	36.6	–	1.0	–	416.8	Kurenkov, Nikolayev, Siniakov, 1991*
Listvenichnoye L. (Listvenichnaya R.)	2.20	0.036	28.0	16.2	66.0	–	–	–	–	Kurenkov, Kurenkov, 1988
Medvezhie L. (Avacha R.)	1.35	0.040	41.4	29.9	44.6	3.50	7.3	3.8	913.0	Nikolayev, Nikolayeva, 1991
Avachinskoye L. (Avacha R.)	1.75	0.048	39.0	27.6	–	–	–	–	828.0	Krokhin, Kurenkov, 1967
Blizhneye L. (Paratunka R.)	2.59	0.047	37.8	18.3	19.6	0.51	23.9	2.5	19.0	Nikolayev, Nikolayeva, 1991
Dalneye L. (Paratunka R.)	1.36	0.043	60.0	31.5	–	–	15.1	–	17.9	Krogus et al., 1987
Khalaktyrskoye L.	2.10	0.008	12.0	4.0	–	–	–	–	–	Kurenkov, 1978
Karymskoye L. (Karymskaya R.)	12.00	–	80.0	–	–	–	–	–	624.0	Kurenkov, 1985
Kronotskoye L. (Kronotskaya R.)	242.00	12.390	128.0	51.2	2300.00	–	–	–	370.0	Kurenkov, 1978a
Dvukhyurtochnoye L. (Kamchatka R.)	9.61	0.195	28.5	20.3	214.0	2.2	7.2	5.0	271.0	Nikolayev, Nikolayeva, 1991
Azabach (Azabachye) L. (Kamchatka R.)	56.45	1.027	36.8	18.2	486.0	0.56	16.5	3.0	6.0	Nikolayev, Nikolayeva, 1991
Nerpichye L. (Kamchatka R.)	552.0	–	11.0	4.5	2550.0	–	–	–	–	Kurenkov, 1967a; Ostroumov, 1985
Kultushnoye L. (Nerpichye L.)	76.94	0.492	11.4	6.4	355.5	0.19	30.4	0.4	0.4	Nikolayev, Nikolayeva, 1991
Iilir-Gythyn (Kultushnaya R.)	7.97	0.239	65.0	30.0	90.00	–	–	–	95.0	Krokhin, 1964*
Potat-Gytkhyn L. (Pakhacha R.)	28.10	1.079	98.0	38.4	170.0	–	–	–	156.0	Krokhin, Kurenkov, 1965*
Sarannoe L. (Sarannaya R.)	31.10	0.435	31.0	14.0	–	–	–	–	–	Kurenkov, 1970
Krasivoye L. (Urumpet R.)	5.26	–	47.0	37.8	27.2	–	–	–	82.1	Zhulkov, Ivanov, Krysin, 1990**
Sopochnoye L. (Sopochnaya R.)	2.4	–	21.5	9.0	–	–	–	–	–	Ivankov, 1984

*Archive data KoTINRO. **Archive data SakhtINRO.

The lakes of Kamchatka are characterized by a high level of oxygen saturation throughout the year. The hydrochemical characteristics of some Kamchatkan lakes are presented in a number of scientific papers (Krokhin, Krogus, 1937; Kurenkov, 1970; Krokhin, 1972; Stepanov, 1986; Kurenkov, 1989; Ukolova, 1988, 1991, etc.).

The seasonal patterns of the vertical distribution of temperature in some of the lakes of Kamchatka are shown in figs. 12-19 and tables 1-13 (see Appendix), in order of decreasing lake depth.

Hydrobiological characteristics of lakes

The faunal complexes of the pelagic ecosystems of Kamchatkan lakes and the ecological characteristics of the species included in them are quite diverse. However, the majority of the lowland lakes can be subdivided with a certain degree of approximation into two main groups in this respect. The criterion of this subdivision is the depth of the lake (Kurenkov, 1978).

The pelagic ecosystems of the first group, i.e. small lakes with a depth of up to 13-18 m, are characterized by species of crustaceans which drop out of the plankton as the temperature falls in autumn, and spend the winter in diapause on the bottom of the lake. This circumstance greatly alters the foraging conditions for the young of the sockeye which are active plankton-eaters both in summer, and in winter.

In the pelagic ecosystems of the second group, the deep lakes of Kamchatka, the crustaceans are represented mainly by the eupelagic forms which do not drop out of the plankton in winter, but only decline in numbers and fall back in their development. In the very deep lakes, some of them can form ecological groups (cohorts) which have different types of life cycles (Kurenkov, 1975b)

If the depth of a lake exceeds 13-18 m, then *Cyclops scutifer* and *Daphnia longiremis* usually predominate in it. Such lakes are the most suitable for the foraging of young sockeye (Kurenkov, 1978).

Cyclops scutifer is widely distributed in the lakes of Kamchatka, and is an important food organism for local pelagic fishes. The population structures of this species can vary significantly in different lakes. In the majority of lakes, it is represented by monpopulations, and the crustaceans reproduce in the summer months. In large and deep lakes (Kuril, Kronotskoye, certain alpine lakes), the populations consist of two ecological groups (cohorts), the members of which have a two-year cycle, the individuals of one cohort reproducing during the even-numbered years and those of the second cohort during the odd-numbered years. It appears that Dalneye L. has a very complex structure of the *Cyclops scutifer* population; it consists of three cohorts (Kurenkov, 1975b, 1976).

Daphnia longiremis is widely distributed in many of the Kamchatkan lakes (Kurenkov, 1975a, 1976). Within the study area, this species is encountered on the Chukchi Peninsula, in the vicinity of Provideniya Bay (Achchen L.), and in the lakes of the Koryak highlands (Iilr-Gytkhyn, Potat-Gytkhyn). On the peninsula itself, it is noted in numerous lakes, both in comparatively small ones (Avachinskoye, Medvezhye, Dvukhyurtochnoye, Nachikinskoye, Kambalnoye and many others), and in the largest ones (Kronotskoye, Kurilskoye) (Kurenkov, 1975a, 1976). It is encountered in the lakes of the Kurile Isls, and Hokkaido, where it was found in the hypolimnion of the deep crater Akan L. (Kurohagi, 1962). The most recent studies (L. A. Bazarkina, personal communication) have shown that Azabach L. is home to *Daphnia galeata*, not *Daphnia longispina hyalina* (Kurenkov, 1972) or *Daphnia longiremis* (Belousova, 1974) as believed earlier.

We shall now examine the most important and the most researched foraging waters of the Asian sockeye (in declining order of their mean depth).

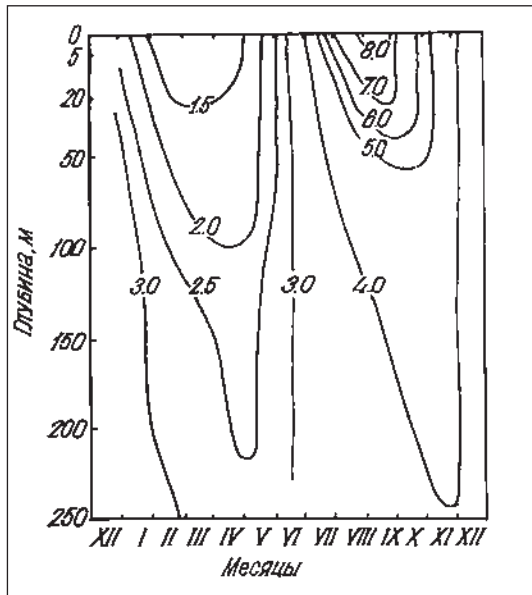


Fig. 12. Seasonal pattern of the vertical distribution of water temperature in Kuril L. (Nosova, 1968). Y-axis – depth of lake, m; X-axis – month.

Kuril Lake

Ye. V. Lepskaya (1988) groups the phytoplankton of Kuril L. into “food” phytoplankton (*Melosira italica*, *Stephanodiscus astrae*, *Cyclotella* sp.) and “nonfood” phytoplankton to which large solitary diatoms (Bacillariophyta) and the non-diatomaceous component of the phytoplankton were assigned (Monakov et al., 1972).

In the phytoplankton of Kuril L., *Melosira italica* dominates throughout the year, constituting up to 70 % of the abundance and biomass of the food phytoplankton (Nosova, 1986; Lepskaya, 1988). *Stephanodiscus astrae* and *Cyclotella* sp. belong to the subdominants. During certain years, *Synedra acus* appears in the plankton in masses at the end of summer. Solitary colonies of *Fragilaria* and representatives of the genera *Navioula*, *Cymbella*, *Amphora*, *Gomphonema*, *Ceratoneis*, *Diatoma*, *Sinedra*, *Achoanth* and *Nitzschia* are also encountered. The non-food phytoplankton attains a high level of abundance during certain periods, and is represented by small forms, which means that its contribution to the phytoplankton biomass is insignificant (Lepskaya, 1988).

The vertical distribution of phytoplankton abundance and biomass is non-uniform, and does not depend on the tempera-

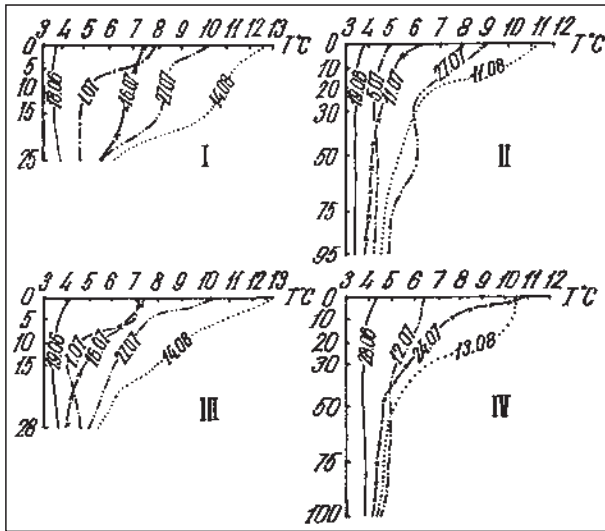


Fig. 13. Vertical distribution of water temperature in Kronotskoye L. (Kurenkov, 1979). Y-axis – depth of lake, m; X-axis – month.

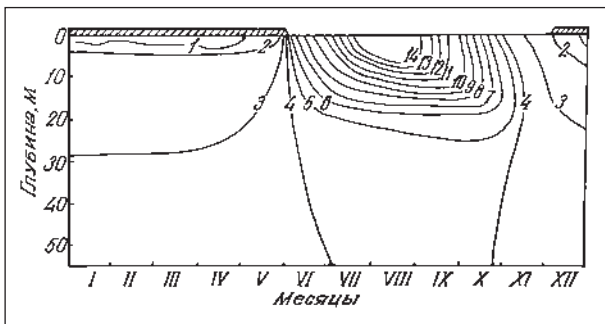


Fig. 14. Seasonal pattern of vertical distribution of water temperature in Dalneye L. based on summarized data for 1937-1974 (Krogus et al., 1987). Y-axis – depth of lake, m; X-axis – months. On isolines – water temperature, °C. Hatching in upper part of diagram – ice cover.

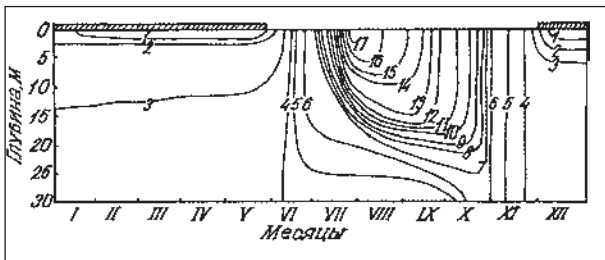


Fig. 15. Seasonal pattern of vertical distribution of water temperature in Blichneye L. (Kurenkov, 1975c). Y-axis - depth of lake, m; X-axis – months. On isolines – water temperature, °C. Hatching in upper part of diagram – ice cover.

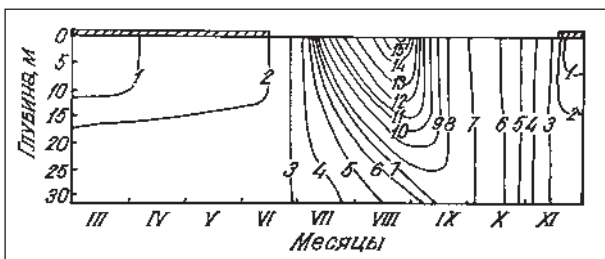


Fig. 16. Seasonal pattern of vertical distribution of water temperature in Azabach L. based on summarized data for 1951-1957 (Krokhin, 1972). Y-axis - depth of lake, m; X-axis – months. On isolines – water temperature, °C. Hatching in upper part of diagram – ice cover.

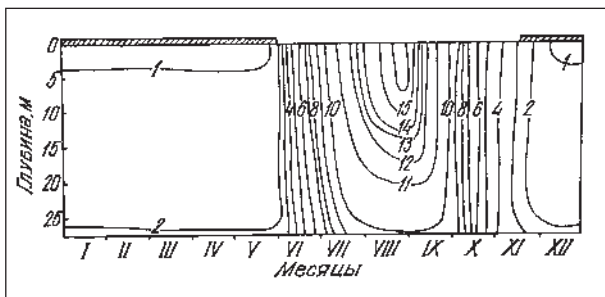


Fig. 17. Seasonal pattern of vertical distribution of water temperature in Nachikinskoye L. (Kurenkov, 1975c). Y-axis – depth of lake, m; X-axis – months. On isolines – water temperature, °C. Hatching in upper part of diagram – ice cover.

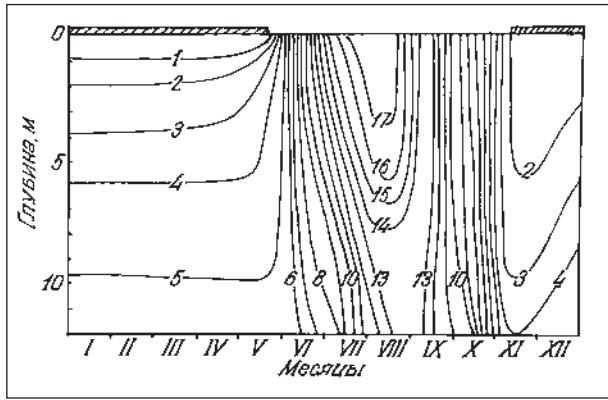


Fig. 18. Seasonal pattern of vertical distribution of water temperature in Khalaktyrskoye L. (Kurenkov, 1975c). Y-axis – depth of lake, m; X-axis – months. On isolines – water temperature, °C. Hatching in upper part of diagram – ice cover.

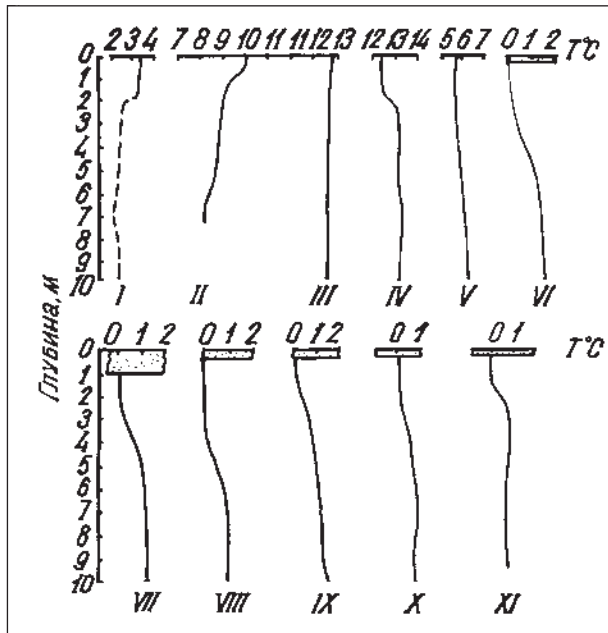


Fig. 19. Vertical distribution of water temperature in Nerpichye L. (Kurenkov, 1975c). Y-axis – depth of lake, m; X-axis – months. I – 22 June 1958; II – 22 June 1954; III – 26 July 1957; IV – 27 July 1958; V – 20 October 1957; VI – 10 May 1951; VII – 19 March 1957; VIII – 18 May 1957; IX – 23 April 1957; X – 22 February 1958; XI – 22 March 1958. Diagram shows ice cover at the time water temperature was measured.

ture gradients. However, a relatively maximum concentration of planktonic algae usually forms by the middle of July in the euphotic layer (0-30 m); by September–October, it sinks to the 100-200 m layer (Lepskaya, 1988).

The pelagic plankton of Kuril L. is depauperate, and consists mainly of two species of crustaceans (*Cyclops scutifer* and *Daphnia longiremis*) and nine species of rotifers (Rotatoria). *Cyclops scutifer* are the most abundant in the plankton, and serve as the main food of juvenile sockeye.

The ecology and dynamics of *Cyclops scutifer* abundance in Kuril L. were examined in detail by I. A. Nosova (1968, 1970, 1972, 1972a, 1986). More recently, studies on this species were continued by L. V. Milovskaya (1986).

The biology of *Cyclops scutifer* in Kuril L. is characterized by the absence of a pronounced seasonal rhythm of the life cycle, due to the hydrological regime of the lake. The vertical distribution of *Cyclops scutifer* is characterized by their mi-

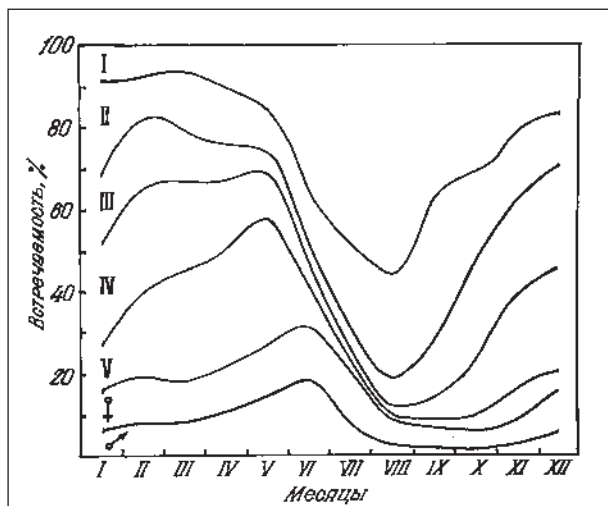


Fig. 20. Seasonal dynamics of age groups in *Cyclops scutifer* population of Kuril L. in 1985, % of the total numbers (L. V. Milovskaya – data provided specially for this book). Y-axis – frequency of occurrence, %; X-axis – months.

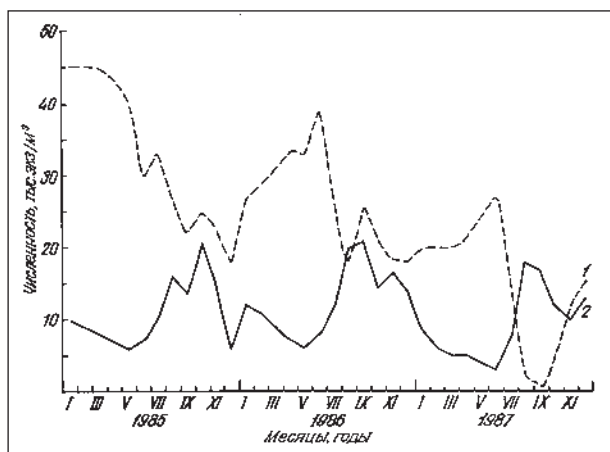


Fig. 21. Dynamics of abundance of *Cyclops scutifer* in Kuril L. during 1985-1987 (L. V. Milovskaya – data provided specially for this book). Y-axis – abundance, thou./m³; X-axis – months, years.

1 – nauplii, 2 – copepodites.

gration to depths of 200-300 m, and by the almost complete absence of adult individuals in the 0-25 m layer. Adult *Cyclops scutifer* trend mainly towards depths of more than 100 m (Nosova, 1968, 1972).

The approximate seasonal dynamics of the age groups and abundance of *Cyclops scutifer* are characterized in figs. 20 and 21.

The deepest distribution of *Cyclops scutifer* is noted at the beginning of summer and at the beginning of winter, during the homothermic periods. In August–September, during the period of marked temperature stratification, the main part of the zooplankton, with the exception of mature *Cyclops scutifer*, is concentrated in the warmest, 0-25 m, layer. As the temperature of the surface layer drops at the beginning of October, *Cyclops scutifer* go deeper. The winter distribution of the zooplankton depends on the ice cover; therefore, the vertical distribution of the zooplankton in Kuril L., which does not freeze over every year, varies from one winter to the next. The few observations carried out to study the daily dynamics of vertical distribution of the plankton in Kuril L. have shown that the diel migrations of both *Cyclops scutifer* and the majority of rotifers are quite intensive in March (Nosova, 1968, 1972, 1972a).

The dynamics of abundance of *Daphnia longiremis* in relation to the water temperature in the lake is characterized in fig. 22.

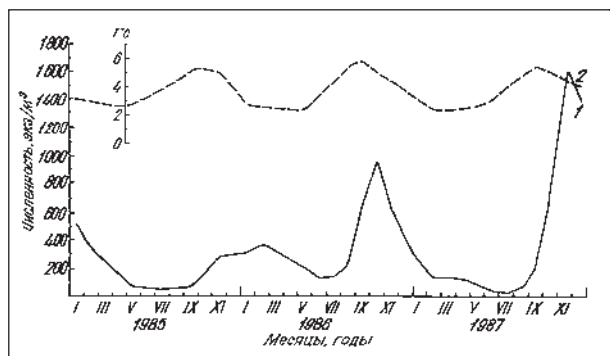


Fig. 22. Dynamics of abundance of *Daphnia longiremis* in Kuril L. during 1985-1987 (L. V. Milovskaya (data provided specially for this book). Y-axis – abundance, specimens/m³; X-axis – months, years.

1 – *Daphnia longiremis*, 2 – average temperature of water in 0-200 m layer, °C.

Data on the interannual variability in the abundance of *Cyclops scutifer* and *Daphnia longiremis* in Kuril L. are presented at the end of the book (Appendix, tables 14-15).

Kronotskoye Lake

The phytoplankton of Kronotskoye L. consists almost exclusively of diatoms (Bacillariophyta). Green (Chlorophyta) and blue-green (Cyanophyta) algae are noted in the warmest seasons, mainly in bays and mostly in shallow ones farthest from the lake.

As in the majority of other Kamchatkan lakes, *Melosira italica* subsp. *subarctica* is the dominant among the algae (up to 15,000 colonies/l). During certain years, a high level of development is also attained by *Asterionella formosa* (up to 2000 colonies/l). *Cyclotella* sp. and *Fragilaria* sp. (up to 1000-1500 colonies/l). Of the algae of other groups, *Microspora* sp. is noted (up to 500 colonies/l in 1956). *Staurastrum* sp. and *Gloeococcus* sp. are common, though scarce, and blue-green algae, *Anabaena spyrroides* and *Microcystis aeruginosa*, are found in small quantities in bay samples. Maximum development of algae takes place from the time the ice breaks up on the lake up to the middle of July. Minimum development is observed in August; a second peak of abundance is noted in September–October, but it does not usually reach the level of spring blooming (Kurenkov, 1978a).

Cyclops scutifer dominates among the pelagic crustaceans in Kronotskoye L. The pattern of the population structure and the dynamics of abundance of *Cyclops scutifer* in Kronotskoye L., plotted on the basis of a correlation of plankton samples for different years. is depicted in figs. 23, 24 and 25 (Kurenkov, 1978a).

Fig. 23 depicts the alternation of subpopulations. The lower graph (B) shows the course of the age changes in the cope-

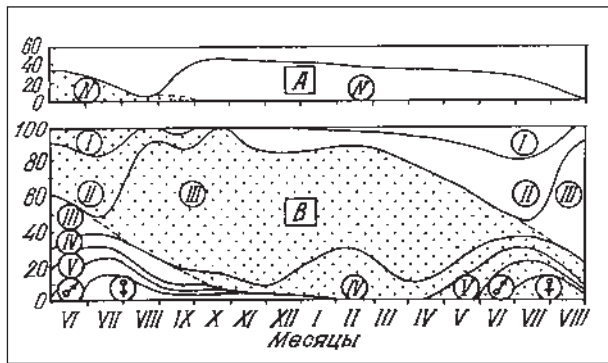


Fig. 23. Seasonal dynamics of abundance of age groups in *Cyclops scutifer* population of Kronotskoye L. (mean for 1973-1975) (Kurenkov, 1978a). Y-axis: upper part (A) – frequency of occurrence, specimens/l; bottom part (B) – % of total numbers; X-axis – months.

A – nauplii, B – copepodites.

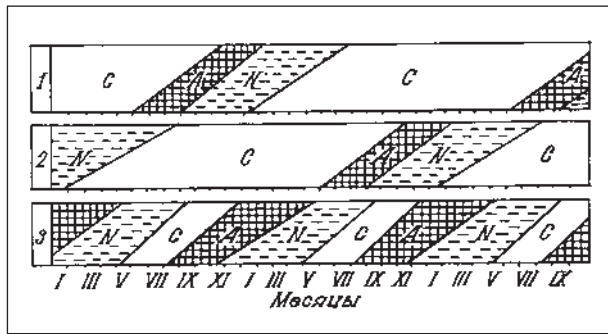


Fig. 24. Ecological cycles of pelagic copepods in Kronotskoye L. during 1973-1975, % of total number of individuals in populations (Kurenkov, 1978a). Y-axis – populations of crustaceans. X-axis – months.

1 – *Cyclops scutifer* – subpopulation of even-numbered year; 2 – the same of odd-numbered year; 3 – population of *Neutrodiaptomus angustiolobus*; N – nauplii, °C – copepodites I-V, A – adults.

podites. The total number of copepodites in each plankton sample was equated to 100 %. The values of relative abundance of each copepodite stage from the 1st one to the adult stage (males and females) were marked off on the vertical line.

During the breeding period in August–September, the abundance of hatched nauplii (A) begins to increase rapidly. These months can be regarded as the beginning of the life cycle of each new generation. During the winter period, the nauplii gradually pass into the first-second copepodite stage, and by the following summer (even-numbered year) they are almost completely in the third stage, in which they will basically spend the approaching winter. A rapid metamorphosis will take place during the following spring (odd-numbered year), and, as we have already mentioned, the cycle will be completed by the breeding of the matured individuals. Therefore, the first subpopulation spends the even-numbered year in the first stages of development (nauplius, copepodites I, II and III), while the second subpopulation, hatched in the preceding odd-numbered year, will complete its life cycle during that even-numbered year (dotted line denotes second subpopulation in the diagram). Thus, the two subpopulations develop in opposite phase (Kurenkov, 1978a).

The population dynamics of *Cyclops scutifer* in Kronotskoye L. (fig. 25) is characterized by a relatively latent curve with a dome-shaped rise in August–September when the copepodite young enter the plankton in masses. The abundance of these crustaceans can vary significantly from year to year. The highest peak of abundance during the years of our investigations (28 specimens/l) was noted at the beginning of August 1975. Copepodites II predominated in the plankton at this time. Similar numbers were noted in 1983 (fig. 25.1). There were also lean years when the numbers during this period did not exceed 14.000/m³, and in winter dropped to below 1000/m³ (fig. 25.2) (Kurenkov, 1978a).

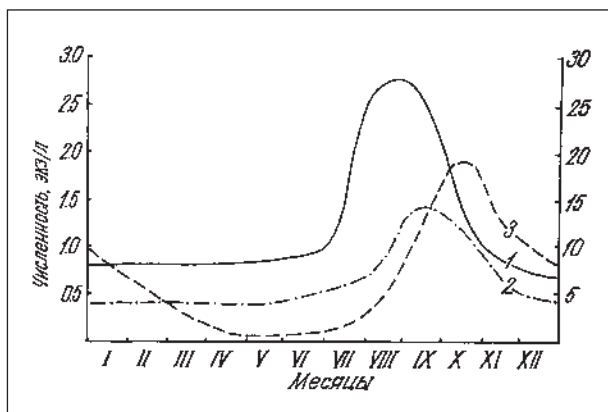


Fig. 25. Dynamics of abundance of pelagic crustaceans in Kronotskoye L. (Kurenkov, 1978a). Y-axis – abundance, specimens/l; X-axis – months.

1 – *Cyclops scutifer*, 1973 (right-hand ordinate); 2 – the same for 1969; 3 – *Daphnia longiremis*, average for 1969-1975 (left-hand ordinate).

Another species of pelagic copepods, *Neutrodiaptomus angustiolobus*, is represented by a monpopulation in Kronotskoye L. Its breeding period is extremely drawn out, which also determines the drawn out nature of the cycle of the whole generation (fig. 24). Individuals of the same generation, having appeared in the plankton in the order of their generations, develop at different times. For example, whereas the nauplii of the first generation develop up to copepodite at the coldest time of the year (December–May), the ones of the last generation complete their development during the warmest months

nearly half a year later. Therefore, the total time spent by the nauplii in the generation amounts to about 300 days. The time spent in the plankton by the other stages is also quite long. The whole period of a generation's existence from the appearance of nauplii of the first generation and up to the elimination of all the adults of the last generation constitutes one and a half years (Kurenkov, 1978a). More detailed data on the life cycle of *Neurodiaptomus angustilobus* are presented in a separate paper (Vvedenskaya, Kurenkov, 1978).

Neurodiaptomus angustilobus is far less abundant than *Cyclops scutifer*. The peak of the copepodites is noted in September–October. The highest abundance (2.7 specimens/l) was noted in 1971. It is usually 2-3 times lower during this period. The abundance of copepodites drops to 0.1-0.2 specimens/l in winter, when nauplii predominate in the population (Kurenkov, 1978a).

The third species of pelagic crustacean, *Daphnia longiremis*, is also relatively scarce; however, because of a large size, rapid breeding during the warm period and the capacity to form accumulations, it plays a significant, though brief, role in the diet of the sockeye (fig. 25.3) (Kurenkov, 1978a).

Dalneye Lake

The diatom *Stephanodiscus astraca* is the basic food of *Cyclops scutifer* in this lake (Kurenkov, 1978). The most complex structure of all the *Cyclops scutifer* populations studied in Kamchatka was noted in Dalneye L. We managed to make sense of this complex structure only after experiments were carried out in aquarium conditions. Correlating the duration of metamorphosis in the crustaceans to the water temperature in the lake (taking into account the vertical distribution of temperature and copepods of different stages), we succeeded in determining the relationship between the periods in which adult individuals and copepodites I appear in the populations. This relationship enabled us to identify the cohorts to which these individuals belonged (Kurenkov, 1973). The reproductive periods in the two most abundant cohorts coincide with the periods of spring and autumn circulation in the lake. The individuals of the third cohort reproduce in winter (Kurenkov, 1975b). The population structure and dynamics of abundance of *Cyclops scutifer* in Dalneye L. are depicted in fig. 26.

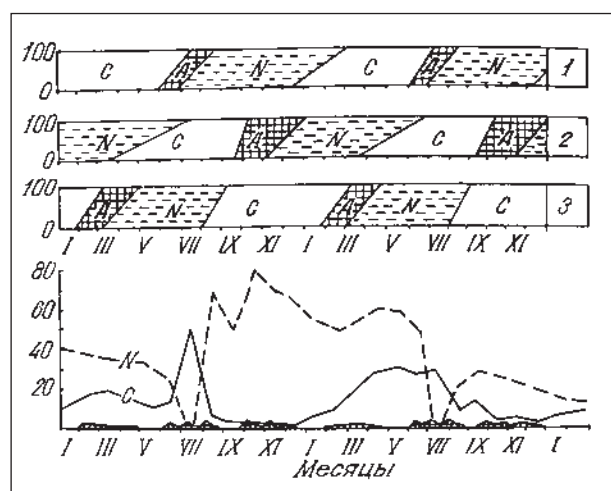


Fig. 26. Population structure (top) and dynamics of abundance (bottom) of *Cyclops scutifer* in Dalneye L., based on summarized data for 1965-1975 (Kurenkov, 1978). Y-axis: top (1, 2, 3) – % of total abundance of individuals in the population; bottom – abundance, specimens/l; X-axis – months.

1, 2, 3 – cohort Nos.; N – nauplii. C – copepodites I-V, A – adults.

The pelagic filter-feeding copepod *Neurodiaptomus angustilobus* is represented by a monopopulation with a one-year cycle in Dalneye L. Reproduction begins in January (in contrast to the majority of other freshwater Calanoida), and ends at the beginning of September, when the individuals of the older generation are eliminated and those of the younger generation reach the stage of copepodite III-IV. Their main food item is *Stephanodiscus astrae* (Kurenkov, 1970a, 1976).

The abundance of copepodites peaks in July. In August–September they are rapidly eliminated by *Cyclops scutifer* and fish. In September, this elimination decreases, and the highest abundance (1-2 specimens/l) is noted up to the end of the life cycle (Kurenkov, 1970a, 1976; Krogus et al., 1987).

The seasonal population dynamics of *Daphnia longiremis* is depicted in fig. 27; this species is encountered in the lake throughout the year. In November, a large part of the females forms ehippia, and dies off; however, a part of them survives through the winter and continues to grow, and even (rarely) produces parthenogenetic eggs. The most intensive reproduction of *Daphnia longiremis* in Dalneye L. takes place in June; it drops drastically by the beginning of August, completely repeating the path of the chlorophyll content curve. The second small increase in fecundity is associated with autumn blooming; it is vaguely defined, and occurs in September–October. These are the two periods that determine the occasionally observed double-peak curve of *Daphnia longiremis* abundance (Kurenkov, 1975a, 1978).

At the beginning of summer (July), *Daphnia longiremis* stay mainly in the upper 5-metre layer of the pelagic zone. In August–October (the period of maximum abundance), they spread throughout the 5-30 m layer (the lower part of the epilimnion, the thermocline and the upper layers of the hypolimnion), i.e. in much the same way as *Daphnia* species do in all the lakes of the temperate zone (Krogus et al., 1987).

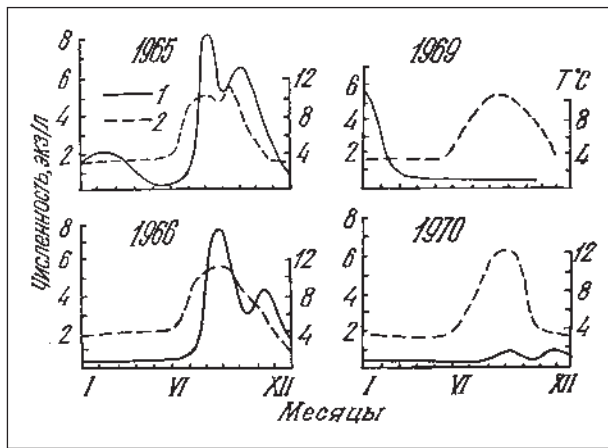


Fig. 27. Dynamics of abundance of *Daphnia longiremis* and the mean temperature in their habitat in Dalneye L. (Kurenkov, 1975a, 1975c). Y-axis – abundance, specimens/l (left); water temperature, °C (right); X-axis – months.

1 – *Daphnia longiremis*, 2 – water temperature.

Studying the vertical distribution of *Daphnia longiremis* in Dalneye L., B. P. Kozhevnikov (1968) established that they are distributed mainly in the upper 20 m layer of the lake, particularly during the second half of summer when their maximum abundance is observed. The mean temperature of this layer does not usually exceed 11°C (August, September), though the temperature of the surface layer does go up to 15.5°C. This circumstance, i.e. the absence of critical temperatures (above 14°C) in the pelagic zone, does not restrict the distribution of *Daphnia longiremis* in the lake, and they can be found in any layer, though they are encountered mostly in the thermocline, as we have already mentioned.

Azabach Lake

The phytoplankton of Azabach L. consists mainly of diatomaceous algae, among which *Melosira italica*, *Asterionella formosa* and *Synedra acus* predominate. During 1956–1960, the phytoplankton was extremely well developed as a result of fertilization by volcanic ash which fell into the lake watershed after a volcano erupted (Kurenkov, 1972).

The pelagic zooplankton here consists of crustaceans and rotifers that are commonly found in the large lakes of Kamchatka, and also includes a number of relict estuarine forms, *Cyclops scutifer* and *Daphnia galeata* are the most important foods in the diet of young sockeye in Azabach L.

In the *Cyclops scutifer* population of Azabach L., one can distinguish two cohorts, one of which is very scanty. The individuals of the main cohort reproduce in July–September. In winter, the population is mainly at the stage of copepodite III; the first adults appear around the time the ice breaks up (in mid June) (Kurenkov, 1972, 1976).

In the smaller part of the population (second cohort), metamorphosis takes place later. This subdivision explains why some of the nauplii are found in the plankton for such a long time (throughout the winter) (Kurenkov, 1972, 1976).

From 1981 through 1987, L. A. Bazarkina (archives of KoTINRO) noted a decrease in the numbers of *Cyclops scutifer* in Azabach L. towards the end of freeze-up, and a 2-fold increase in population abundance when these copepods began to reproduce after the lake ice broke up. Analysis of the dynamics of abundance and the development of the age stages of *Cyclops scutifer* gave grounds for assuming that the copepodites which appear in winter are not eliminated, but pass into a state of dormancy, otherwise the abundance of mature individuals would be lower than the winter minimum. Indeed, recent investigations in the Azabach L. watershed have shown that dormant *Cyclops scutifer* at the 5th copepodite stage are found in samples from the near-bottom layer of the pelagic zone of the lake (Bazarkina, 1993). Diapausing copepods have been found at stations in the lake where the bottom is covered with soft substrates and is not exposed to runoff currents. This more exact definition of the biology of *Cyclops scutifer* is extremely important when calculating the production of this species in the lake.

Figs. 28 and 29 depict the seasonal dynamics of abundance of the different age groups and the overall population dynamics of *Cyclops scutifer* in Azabach L.

The nauplii of *Cyclops scutifer* in Azabach L. are concentrated at the surface and near the bottom during the daylight hours. At night, migrating freely through the thermocline, they spread evenly through the open water. Copepodites I-II remaining in the depths for the greater part of the day. Their rise to the surface is observed at 05.00 hours. Copepodites III-IV ascend and descend three times, but do not form accumulations at the surface as they do so. Female *Cyclops scutifer* without eggs, as well as males, migrate freely through the thermocline and form significant concentrations in the 0-5 m layer in the middle of the night. Egg-bearing females do not perform such distant migrations, the latter being limited to the 15-metre layer (15-0 m). Most of the males and the eggless females of *Daphnia longiremis* stay above the thermocline around the clock, forming their maximum abundance at the surface. The highest surface concentration of egg-bearing females is observed at 01.00 hours. Over a 24-hour period, they migrate through the open water, penetrating deep into the thermocline. Mature *Cyclops scutifer* and *Daphnia longiremis* form significant concentrations in the upper layers of the lake during the night and at sunrise. This creates favourable foraging conditions for the young of the sockeye (Belousova, 1968).

The most recent investigations of L. A. Bazarkina (personal communication) have shown that, with a change in the species composition of the pelagic fish community of Azabach L. in 1980s and an increase in the pressure of *Cyclops scutifer*

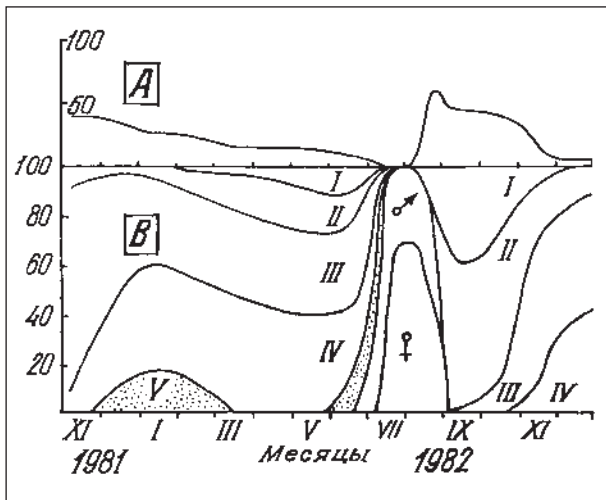


Fig. 28. Seasonal dynamics of abundance of age groups in *Cyclops scutifer* population of Azabach L. during 1981-1982 (L. A. Bazarkina – data prepared specially for this book). Y-axis – top (A) – frequency of occurrence, specimens/l; bottom (B) – total abundance, %; X-axis – months, years.

A – nauplii, B – copepodites.

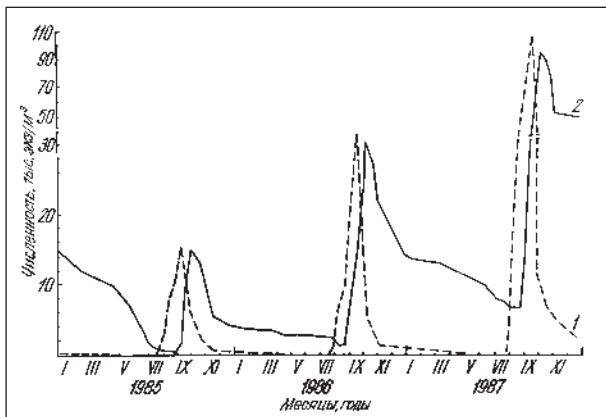


Fig. 29. Dynamics of abundance of *Cyclops scutifer* in Azabach L. during 1985-1987 (L. A. Bazarkina – data prepared specially for this book). Y-axis – abundance, thou./m³; X-axis – months, years.

1 – nauplii, 2 – copepodites.

consumers, the intensity of the vertical migrations of *Cyclops scutifer* has increased in comparison with the 1960s when S. P. Belousova conducted her research (1968).

The other important food organism, *Daphnia longiremis*, appears in July, reaches its maximum abundance (5-7 specimens/l) in September, and drops out of the plankton by the end of October. Its maximum biomass amounts to 90-230 mg/m³, and the average annual biomass does not exceed 20 mg/m³ (Kurenkov, 1972).

According to L. A. Bazarkina's data for 1981-1990 (personal communication), the maximum abundance of *Daphnia longiremis* in Azabach L. amounted to 19.3 specimens/l in September 1988, and 15.4 specimens/l in August 1981.

Data on the interannual variability of *Cyclops scutifer* and *Daphnia longiremis* abundance in Azabach L. are presented at the end of the book (Appendix, tables 16-17).

A similar pattern of change in the structure of the *Cyclops scutifer* population (fig. 28) exists in Nachikinskoye L. and Blizhneye L. and most likely in lakes Kursin, Dvukhyurtochnoye, Listvenichnoye and Tolmachevskoye. The dynamics of abundance of *Cyclops scutifer* and *Daphnia longiremis* in Nachikinskoye L. and Blizhneye L. hardly differs from the same indices of these species in Azabach L. (Kurenkov, 1975b, 1976).

Khalaktyrskoye Lake

Khalaktyrskoye L. is inhabited by Copepoda of the facultative pelagic complex, i.e. *Mesocyclops leucarti* and *Cyclops kolensis*; the first is predominantly a predator, and the second is a facultative predator. The water flea *Daphnia cristata* is also encountered in Khalaktyrskoye L. This species serves as the main food of young sockeye. In addition to this, the latter feed on chironomid larvae, but in small quantities. Copepods are characterized by various ecological cycles. Each of the two species inhabiting Khalaktyrskoye L. is represented by a monopopulation (fig. 30) (Kurenkov, 1978).

Mesocyclops leucarti is dicyclic, as in other middle-latitude geographical regions. Its first reproductive period coincides with the breakup of ice on the lake. The individuals of this generation mature by September. A second reproductive period follows. The second-generation copepods reach the stage of copepodite III-IV by the time the lake freezes over. In winter, these copepods live at the very bottom, but do not go into complete diapause; they continue to develop slowly, and reach maturity by spring.

Compared with this species, the second one, *Cyclops kolensis*, develops more slowly. It also reaches the stage of copepodite III by the time the lake freezes over, but its metamorphosis in winter ceases until the water begins to warm up in July. These copepods reach maturity in July, when the spring generation of *Mesocyclops leucarti* has already reached the stage of copepodite III-IV. The reproductive period of *Cyclops kolensis* lies between the respective periods of the first species (Kurenkov, 1978).

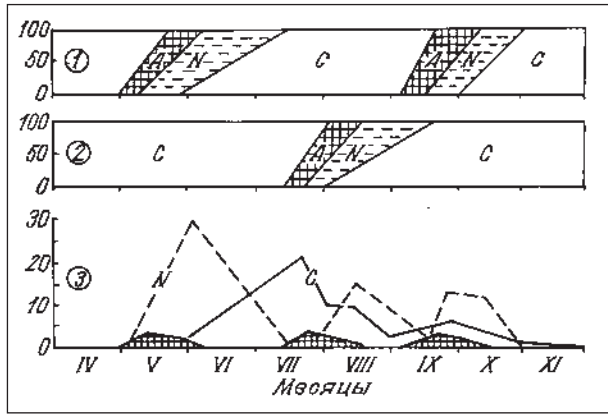


Fig. 30. Ecological cycles and dynamics of abundance of pelagic Copepoda in Khalaktyrskoye L., based on 1973-1974 data (Kurenkov, 1978). Y-axis – frequency of occurrence; 1-2 – % of the total numbers in the population; 3 – specimens/l; X-axis – months.

1 – *Mesocyclops leuckarti*. 2 – *Cyclops colensis*. 3 – total numbers of Copepoda
N – nauplii, C – copepodites I-V, A – adults.

The abundance of Cladocera, mainly *Daphnia cristata*, peaks in August–beginning of September, amounting to 25-30 specimens/l, and then falls drastically at the beginning of September (Kurenkov, 1976, 1978).

The vast majority of small lakes in Kamchatka is characterized by faunal complexes like the one in Khalaktyrskoye L. If a lake of this type is located in the tundra and has a higher than usual humus content, then the *Mesocyclops leucarti*, *Cyclops kolensis* and *Daphnia cristata* present in Khalaktyrskoye L. are usually accompanied by one or two species of copepods, mostly *Acanthodiptomus yamanacensis* and *Hetercope appendiculata* (or *H. borealis*). Small alpine lakes may have other specific complexes (Kurenkov, 1976, 1978).

Nerpichye Lake

Vigorous development of diatoms of the genera *Fragilaria*, *Diatoma*, *Melosira*, *Synedra* and *Cyclotella* (species not identified) is noted in the spring samples (May–June). The spring blooming of diatoms peaks by this time, and flagellates and green algae begin to appear, particularly *Pandorina* and *Pediastrum*. In June–September, the most vigorous development is noted in the blue-green algae, mainly *Anabaena spiroides*, the colonies of which reached an abundance of 400,000 specimens/l in 1957 (Kurenkov, 1967a).

The intensive exchange of waters between Nerpichye L. and the Kamchatka R., as well as the changes in salinity during high and low tides, make it difficult to assess the quantitative development of this lake’s zooplankton, especially the dynamics of its seasonal abundance.

Daphnia longispina attains the highest abundance among plankters. Up to 39,000 specimens/m³ (9 September 1957), and once (26 August 1960) even 96,000 specimens /m³, was recorded during the period of our investigations; however, these extremely high figures are probably incidental ones that reflect the presence of local stocks which form for a brief period in August–September. The numbers of the other species, namely *Acanthocyclops vernali*, *Eurytemora kurenkovi* and *Ectinosoma* sp. are considerably lower, and rarely exceed 1000 specimens/m³ even during the peak of abundance, while the numbers of *Tachidius distipes* rarely go up to 100 specimens/m³ (Kurenkov, 1967a, 1976).

I. I. Kurenkov (1976) studied the zooplankton of the brackish Nerpichye L., and determined the ecological cycles of some of the planktonic crustaceans (fig. 31).

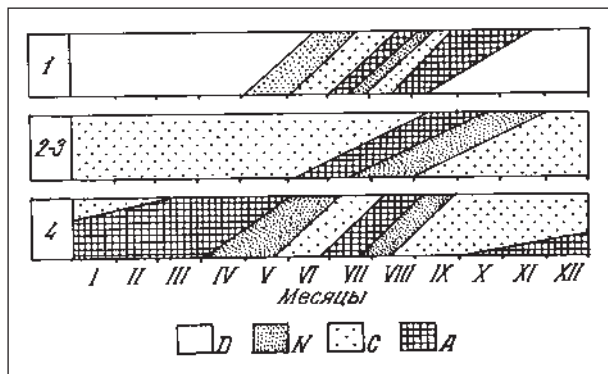


Fig. 31. Ecological cycles of some planktonic crustaceans in Nerpichye L. (Kurenkov, 1976). Y-axis – frequency of occurrence, % of total numbers in the population; X-axis – months.

1 – *Eurytemora kurenkovi*, 2-3 – *Ectinosoma* sp. and *Tachidius distipes*, 4 – *Cyclops vernalis*.
D – diapause, N – nauplii, C – copepodites I-V, A – adults.

Since the majority of the above-mentioned species reach their maximum abundance at the end of summer–beginning of autumn (depending on when the water is at its warmest), the biomass also peaks during this particular period. The adjacent periods are characterized by very low indices, as seen on the biomass dynamics curve where the peak is high, but narrow (fig. 32). By and large, the foraging conditions of young sockeye in the brackish Nerpichye L. can be evaluated as unfavourable (Kurenkov, 1967a, 1970, 1976), which is reflected in the fairly weak utilization of this body of water as a foraging ground (considering its large size) by the young of the sockeye in the Kamchatka R. watershed (Bugaev, 1984a).

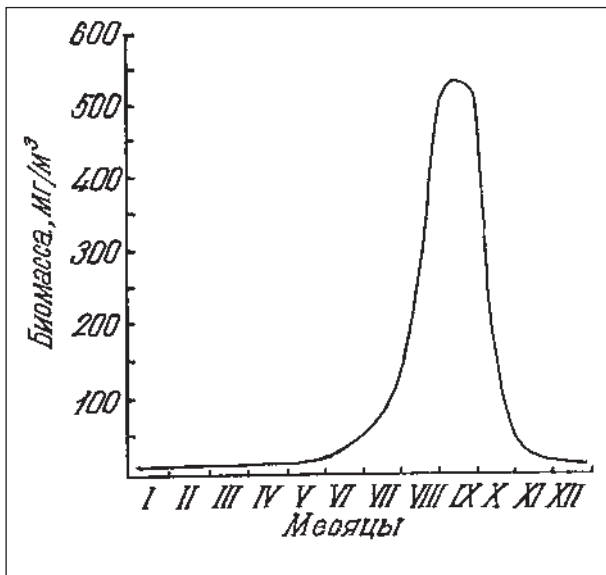


Fig. 32. Dynamics of the total biomass of planktonic crustaceans in Nerpichye L., based on summarized data for different years (Kurenkov, 1976). Y-axis – biomass, mg/m³; X-axis – months.

Section 8. Freshwater period of the largest Asian stocks of the sockeye (Kamchatka and Ozernaya rivers)

8.1. Spatial distribution of the sockeye populations of the Kamchatka R.

Based on an analysis of the scale structure in juvenile and adult sockeye, the degree of their infection with plerocercoids of *Diphyllobothrium* sp., as well as the growth and migrations of the young in the Kamchatka R. watershed (fig. 2), the following local second order stocks (sub-stocks) and their groups were established (Bugaev, 1983c, 1986a):

1. Group of local sockeye second order stocks of the upper and middle reaches of the Kamchatka R., the young of which migrate downstream to the sea as underyearlings (group “S”). While studying the scale structure in adult sockeye of certain local stocks of the Kamchatka R. watershed, we came across two groups of individuals which differed in the mean distance between the sclerites in the central part of the scales (fig. 33, 34). The existence of these two groups is traced over a number of years.

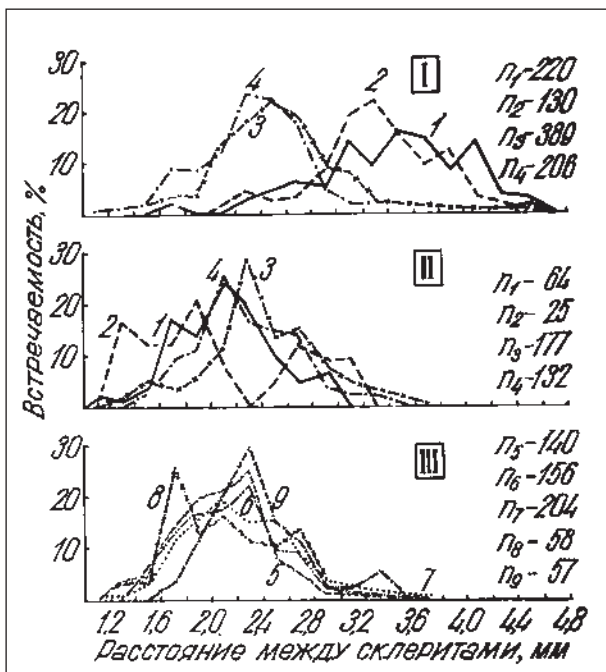


Fig. 33. Distribution of the average distance between sclerites in the first zone of growth (including the first ZAS) on the scales of adult and juvenile sockeye in the Kamchatka R. watershed (at 100x magnification). Y-axis – frequency of occurrence, %; X-axis – distance between sclerites, mm.

Underyearlings with fewer than 5 sclerites on the scales and juveniles and adults with fewer than 5 sclerites in the first zone of growth not included.

I – the distance between sclerites in the first zone of growth (including ZAS) on scales of adults of the early (spring) sockeye in 1976.

1 – upper reaches and uppermost tributaries of the Kamchatka R. where the sockeye is not infested with *Diphyllobothrium* sp.;

2 – spring-fed creeks and channels of the middle reaches of the Kamchatka R.; as an exception, material on the late (summer) sockeye of Ushkovskoye L. was used for additional information;

3 – tributaries of the middle and lower reaches of the Kamchatka R. where the sockeye is infested with *Diphyllobothrium* sp.;

4 – lakes (excluding Nerpichye L.).

II – the distance between sclerites on the scales of young sockeye from foraging waters in the vicinity of the Kamchatka R. near the village of Pushchino and the town of Klyuchi.

1 – Kamchatka R. near Pushchino; 2 – Kamchatka R. from the village of Milkovo to the Shapina River; 3 – oxbow lakes of the Kamchatka R. from the village of Dolinovka to the Tolbachik R.; 4 – “Ushkovskoye L.” springs.

III – the distance between sclerites on the scales of young sockeye from foraging waters around the town of Klyuchi – mouth of the Kamchatka R.

5 – floodplain lakes; 6 – Azabach L., and its side channel; 7 – main channel, lakes and abandoned channels of the Raduga R.; 8 – Kursin L.; 9 – mouth of the Kamchatka R.

The boundary between the established types of scales (fig. 33, 34) can be drawn within a 3.0-3.2 mm range (at 100x magnification), as we examined the distance between sclerites on the scales of juvenile sockeye from practically all of the Kamchatka

R. watershed (fig. 33), we could not find a single body of water in which foraging young sockeye would have more widely spaced sclerites. This brought us to the conclusion that the young sockeye of this area migrate seaward mainly as underyearlings without scales. Indeed, later investigations (Bugayev, Karpenko, 1983; Bugayev, 1984; Bugayev, 1987) confirmed the hypothesis that the formation of more widely spaced sclerites was due to the growth of the young fish in salty or brackish waters.

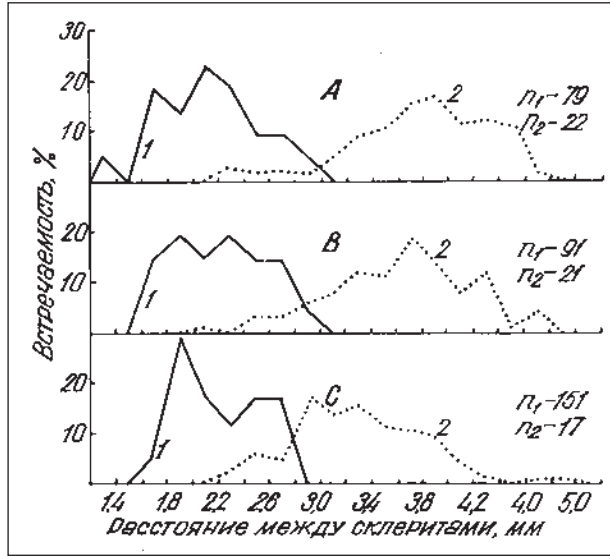


Fig. 34. Distribution of the average distance between sclerites in the first zone of growth (including the first ZAS) on the scales of adults of the early (spring) and late (summer) sockeye from some rivers of the Kamchatka R. watershed (based on summarized data for a number of years, at 100x magnification). Y-axis – frequency of occurrence, %; X-axis – distance between sclerites, mm.

A – Andrianovka R., B – Kirganik R., C – Nikolka R.
1 – late sockeye; 2 – early sockeye.



Fig. 35. Central part of scales in sockeye spawners of the Kamchatka R. (“S” and “V” groups).
1 – “S” group, Andrianovka R., 1977, early sockeye, AC (fork length) – 570 mm, female, age 0.3, length of freshwater period of life 0+, arrow marks supplementary ZAS;
2 – “S” group, Ushkovskoye L., 1977, late sockeye, AC – 680 mm, male, age 0.3, length of freshwater period 0+, no ZAS;
3 – “V” group, Kirganik R., 1978, late sockeye, AC – 605 mm, male, age 1.3, length of freshwater period 1+, arrow marks ZAS – annulus;
4 – “V” group, Nikolka R., 1978, late sockeye, AC – 510 mm, female, age 1.3, length of freshwater period 1+, arrows mark ZAS (first – annulus, second – supplementary).

The typical scales of the “S” group are depicted in fig. 35.1-2 (type “S”). Most “S” group scales have an indistinct or weakly defined central area characterized by the presence of one (often indistinct) river-type ZAS (zone of adjacent sclerites) (1). Less commonly, there are no ZAS in the central part of the scales (2). The ZAS illustrated in fig. 35.1 developed in salt water, and is a secondary structure which does not reflect the seasonal rhythm of growth.

Fig. 36 characterizes the presence of mature fish in the Kamchatka R. watershed after their downstream migration as underyearlings. Downstream migration to the sea as underyearlings is characteristic of mainly the early (spring) seasonal race of the sockeye salmon of upper and middle of stream of Kamchatka R. Only population of the late (summer) seasonal race of the sockeye, which migrates downstream to the sea as underyearlings is the sockeye of Ushkovskoye L., where the early form is practically never encountered.

The number of sclerites in the first and marginal zone of the central part of the scales in group “S” adult sockeye is usually equal to 5-6 and 2-3 respectively, i.e. it is slightly lower than in fish from areas in which the offspring of the sockeye do not migrate downstream as underyearlings (fig. 37). The adult fish of group “S” are not infected with *Dipyllobothrium* sp., and are predominantly of age 0.3.

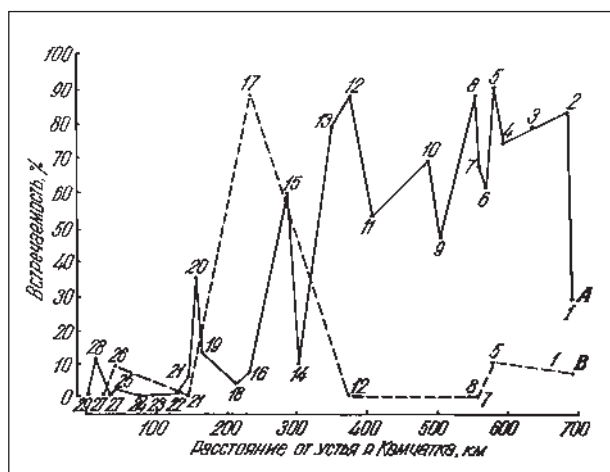


Fig. 36. Frequency of occurrence of sockeye spawners returning after downstream migration as underyearlings in the Kamchatka R. watershed. X-axis – distance from the mouth of the Kamchatka R., km Y-axis – frequency of occurrence, %.

A – early sockeye, B – late sockeye. Areas marked as in fig. 2.

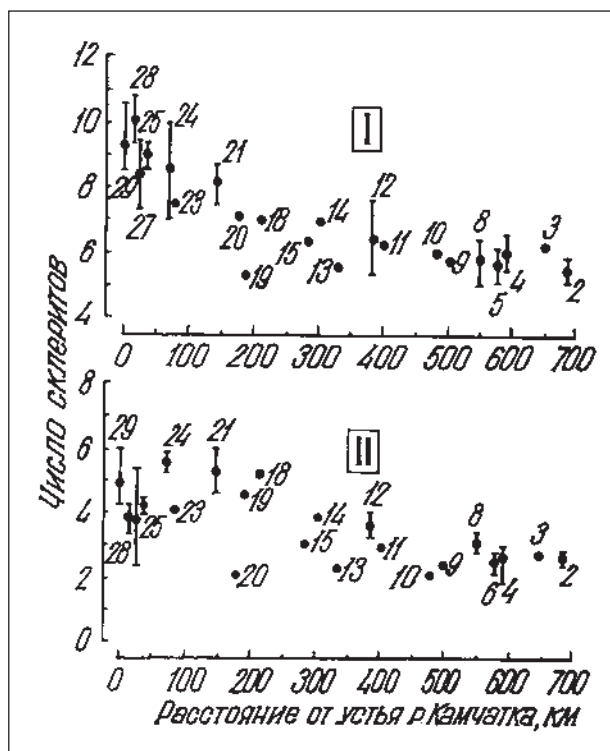


Fig. 37. Variation of the number of sclerites in the growth zones of the central part of the scales in adults of the early (spring) sockeye with one ZAS, depending on the distance between the tributary and the mouth of the Kamchatka R. Y-axis – number of sclerites; X-axis – distance from the mouth of the Kamchatka R., km.

I – first growth zone, II – marginal growth zone of central part of scales. Areas marked as in fig. 2.

2. Group of local sockeye second order stocks, the young of which feed and grow in the vicinity of the spawning grounds before migrating downstream (group “V”). Analysis of the available data has shown that, from the breeding area of group “S”, the late sockeye (except those of Ushkovskoye L.) migrate seaward as underyearlings in small numbers (Bugaev, 1984, 1986a), as the structure of their scales will tell (fig. 34, 35.3-4).

A survey has shown that a fairly large number of young sockeye feeds and grows on the spawning grounds in the breeding area of group “S” in the Kamchatka R. watershed, and spends the winter there (fig. 2). The following year, during the seaward migration down the river, a highly characteristic scale pattern forms in these fish (fig. 35.3), i.e. after 6-10 sclerites, several (mostly 6-8) more widely spaced sclerites appear. The first zone corresponds to the period of growth at the spawning grounds, and the second zone to the period of seaward migration. We attribute the latter to “compensatory growth” (Bugaev, 1984c, section 8.3.3). One of the causes of this compensation growth could be the migration of yearlings from the spawning grounds in the upper reaches of the Kamchatka R. to the middle and lower reaches where the temperature in the river and floodplain lakes in which young sockeye stop to forage briefly is higher. The removal of a stress factor, in this case a cooler temperature, can result in compensation growth (Mina, Klevezal, 1976). During certain years, there may not be any compensation growth on the scales of most of the late sockeye in the upper part of the Kamchatka R. watershed (fig. 35.4), the adult fish of group “V” are not infected with *Diphyllbothrium* sp., and are mainly of age 1.3.

3. Group of local sockeye second order stocks, the young of which feed and grow in Azabach L. prior to their seaward migration (group “E”). This grouping of local stocks whose young forage in Azabach L. before migrating downstream was established on the basis of the observed increase in the frequency of occurrence of fish with two ZAS in the central part of the scales in the lower part of the Kamchatka R. watershed (fig. 38), an increase in the percentage of fish with lake-type scales (fig. 39, tables 11, 12) (Bugaev, 1978), a rise in the incidence of *Diphyllbothrium* sp. infestation in the same area (fig. 40), an increase in the number of gill rakers (fig. 41), which is an indication of increased plankton

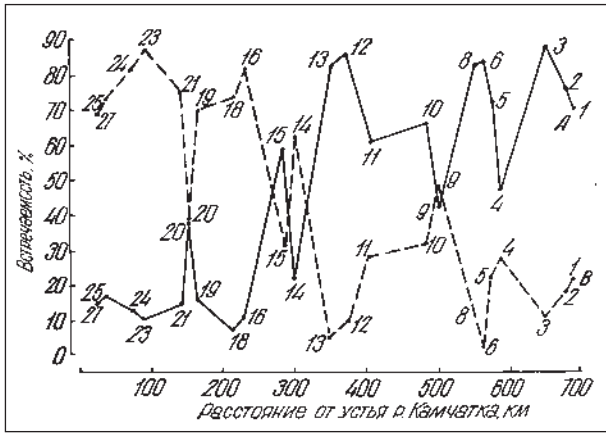


Fig. 38. Frequency of occurrence of adults of the early (spring) sockeye with one and two ZAS in the central part of the scales in river stocks of the Kamchatka R. watershed and Azabach L. Y-axis – frequency of occurrence, %; X-axis – distance from the mouth of the Kamchatka R., km.

A – sockeye with one ZAS, B – sockeye with two ZAS. Areas marked as in fig. 2.

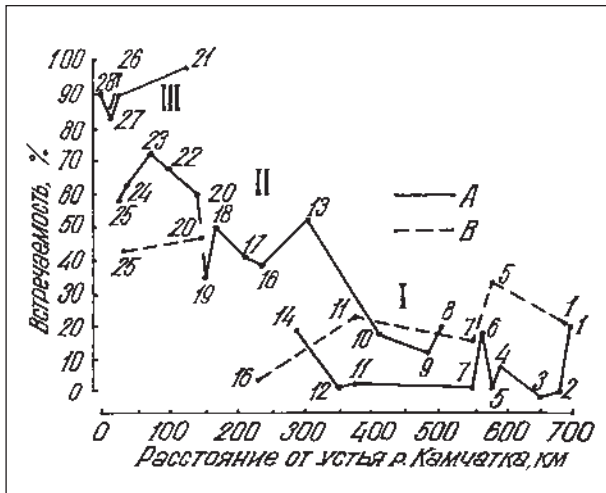


Fig. 39. Frequency of occurrence of sockeye spawners of the Kamchatka R. watershed with a "lake" ZAS on the scales (based on summarized data). Y-axis – frequency of occurrence, %; X-axis – distance from the mouth of the Kamchatka R., km.

A – early sockeye, B – late sockeye. Areas marked as in fig. 2. I – river stocks, fish not infested with *Diphyllobothrium* sp.; II – river stocks, some fish infested with *Diphyllobothrium* sp.; III – fish of lake stocks.

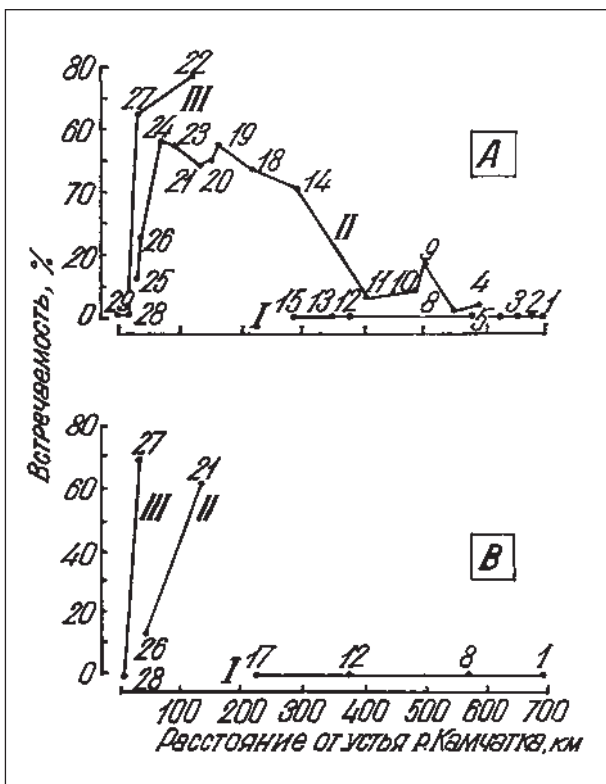


Fig. 40. Extensity of infection of adult sockeye of the Kamchatka R. watershed (males and females) with *Diphyllobothrium* sp. plerocercoids. Y-axis – frequency of occurrence, %; X-axis – distance from the mouth of the Kamchatka R., km.

A – early sockeye, B – late sockeye. Areas marked as in fig. 2. I – rivers with no infected fish; II – rivers with infected fish; III – lakes where the spawning of adults and the foraging of the young take place in the same watershed.

consumption by the fish, and on a study of the growth and migration of young sockeye in the Kamchatka R. watershed (Bugaev, 1983c).

It was found (Bugaev, 1981a, 1982, 1983c) that the young of the sockeye from the tributaries of the lower reaches of the Kamchatka R. migrate as underyearlings to Azabach L., located below these tributaries, where they spend the winter and then migrate to the sea the following year. After the migration to the lake in July–November, a supplementary ZAS, which is not an annulus, forms on the scales of these fry (Bugaev, 1981a; Bugaev, Bazarkin, 1987). Its formation can be attributed to the change in habitat with the move to a new foraging ground (Nikolsky, 1974). After a winter in the lake, an annulus forms on the scales of the sockeye yearlings of group “E” towards the end of June–beginning of July. At the time of downstream migration, the yearlings of group “E” have two ZAS on their scales; the first is a less pronounced (river-type) supplementary ZAS, and the second is the more distinct (lake-type) annulus. Fig. 42.1 depicts the central part of a typical scale from group “E” spawners.

Most of the group “E” spawners are of age 1.3, and are infested with *Diphyllbothrium* sp. quite extensively (fig. 40, Bugaev, 1982). Infestation with this parasite occurs after the young of the year migrate to Azabach L. (Bugaev, 1982).

4. Local sockeye second order stock of Azabach Lake (“A”). Analysis of the structure of the central part of the scales (freshwater growth) in adult sockeye of Azabach L. has shown that there is a negative correlation between the scale characteristics (size of radii, number of sclerites) and the abundance of the sockeye not only in Azabach L., but also in group “E” (Bugaev, 1983a), the existence of this correlation can be attributed to the fact that, in addition to the young fish of the Azabach L. stock, this lake is foraged by the young of group “E”, which constitute up to 50-70 % of all the juveniles foraging here (Bugaev, 1981a, 1982).

More than 70 % of the adult sockeye of stock “A” have two ZAS in the central part of the scales (fig. 42.2). This implies that these fish spend two years in fresh water. Unlike that of group “E” individuals, both of the ZAS in the central part of the scales of stock “A” individuals belong to the lake type (Bugaev, 1978). Using the method of age determination when data on the growth of juvenile fish are not available (Mina, 1973, 1976; Bugaev, 1983a), we recorded supplementary ZAS on the scales of stock “A” adults in an average 10 % of the cases. It is not excluded that the latter is due to the incomplete isolation of the populations (“A” and “E”), i.e. the migration of a small part of the brood stock from the tributaries of the lower Kamchatka R. to Azabach L., which is located below these tributaries. Nobody has ever analyzed the degree of isolation of the sockeye’s reproductive systems that are interrelated in much the same way as in stock “A” and group “E” (Bugaev, 1981a, 1986a). The adult fish of stock “A” are usually heavily infested with *Diphyllbothrium* sp. (fig. 40; Bugaev, 1982), and are mostly of age 2.3.

5. Group of local sockeye second order stocks, the young of which feed and grow in Nerpichye L. before migrating downstream to the sea (group “N”); local second order stock of Nerpichye L. (stock “N”). Analysis of the scale structure in adult sockeye of the Nerpichye L. watershed, one of the largest brackish lakes in northeastern Asia, has shown that about 8-9 % of the adult fish from the breeding area of group “E” have a scale structure similar to that of this stock (fig. 42.3). Despite the fact that we were unable to trace the migration of the young fish to Nerpichye L., the characteristic pattern of the central part of the scale suggests that underyearling sockeye migrate from the tributaries of the lower reaches of the Kamchatka R. to Nerpichye L. (Bugaev, 1984a). Most of the fish with this type of scale have two ZAS in the central part of it, the first one a river-type (usually weakly defined) ZAS, and the second one a lake-type ZAS. In the first zone of scale growth in adult fish, the distance between the sclerites is usually more than 3.0-3.2 mm (at 100x magnification) (fig. 43), as in the case with group “S”, this fact suggests that most of the underyearling sockeye of stock “N” and the fish of group “N” migrate downstream to the lake before their scales are formed. Indeed, we found that most of the underyearlings from the tributaries of Nerpichye L. migrated downstream to the lake without scales (Bugaev, 1984a). We consider the first weakly defined ZAS on the scales of individuals from stock “N” and group “N” to be a supplementary one, and, for some unknown reason, it is formed during the foraging period in Nerpichye L. The second ZAS is the annulus. Most of the adult fish of stock “N” and group “N” are of age 1.3, and are not infested with *Diphyllbothrium* sp. plerocercoids.

6. Local sockeye second order stock of Dvukhyurtochnoye L. (“D”). The stock of Dvukhyurtochnoye L. is distinguished from the other sockeye stocks and groups of the Kamchatka R. watershed by larger annual increments of the freshwater zone

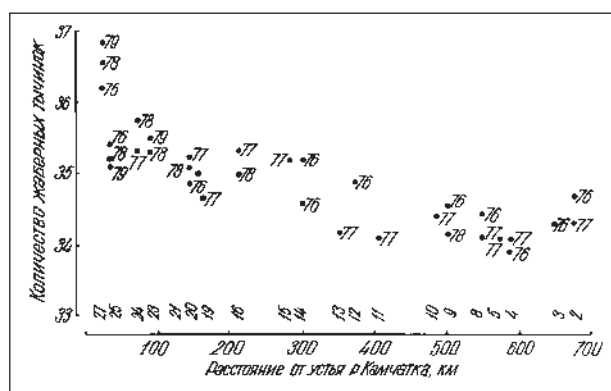


Fig. 41. Number of gill rakers on the first gill arch (from the left side) in adults of the early (spring) sockeye of the Kamchatka R. watershed in 1975-1979. Y-axis – number of gill rakers; X-axis – distance from the mouth of the Kamchatka R., km.

Figures near dots – years of sampling; lower row of figures – areas of sampling. Areas marked as in fig. 2.

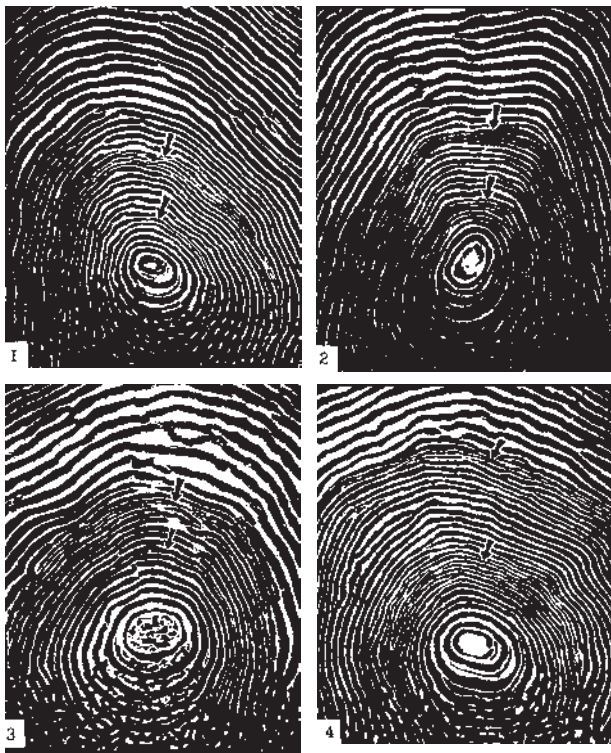


Fig. 42. Central part of scales in sockeye spawners of the Kamchatka R. watershed – “E” groups, “A” stocks, “H” stocks and groups and “D” stocks.

1 – group “E”, Bolshaya Khapitsa R., 1978b early sockeye, AC 580 mm, female, age 1.3, length of freshwater period 1+, arrows mark ZAS (first arrow – supplementary one, second arrow – annulus);
 2 – stock “A”, Azabach L., 1975, early sockeye, AC 570 mm, female, age 2.3, length of freshwater period 2+, arrows mark ZAS – annuli;
 3 – stock and group “N”, Nerpichye L., 1977, early sockeye, AC 570 mm, female, age 1+, arrows mark ZAS (first arrow supplementary one, second arrow annulus);
 4 – stock “D”, Dvukhyurtochnoye L., 1976, early sockeye, AC 575 mm, female, age 2.3, length of freshwater period 2+, arrows mark ZAS – annuli.

of the scales (fig. 44; Bugaev, 1987, 1989), there are usually more than 10 sclerites in the annual zones of the central part of the scales (fig. 42.4). The latter are easily distinguished from those of stock “A” (fig. 42.2). The observed ZAS are usually of the lake type. It is not difficult to determine the age of the fish of this stock. Most of them migrated downstream from the lake as two-year-olds. The scale structure in the adult fish of stock “D” is characterized by a low variability, which we attribute to a consistently low abundance of young sockeye in the lake. We believe that the low abundance of this stock is due to the lack of spawning grounds in the Dvukhyurtochnoye L. watershed. The adult fish of stock “D” are mainly of age 2.3, and are heavily infested with *Diphyllbothrium* sp. (fig. 40; Bugaev, 1982).

7. Local sockeye second order stock of Kursin L. (“K”). The Kursin L. system includes two lakes, the little (upper) Kursin and the big (lower) Kursin; the stream flowing out of the smaller of the two falls into the larger one. At the present time, practically all of the early sockeye of this stock spawns in the upper lake, and the late sockeye spawns in the lower one.

The adult sockeye of the Kursin L. stock are characterized mostly by two ZAS in the central part of the scales. Furthermore, the early sockeye differs from the late sockeye in the structure of the scales. The central part of the scales in the early sockeye of Kursin L. (fig. 45.1) is very similar to that of group “E” sockeye in the type and arrangement of ZAS, and, based on the available criteria of identification (Bugaev, 1986a), does not differ from it (fig. 42.1). We consider the first ZAS on the scales of the early sockeye to be a supplementary one which formed apparently as a result of the migration of the underyearlings from the upper lake to the lower one, and the second ZAS the annulus.

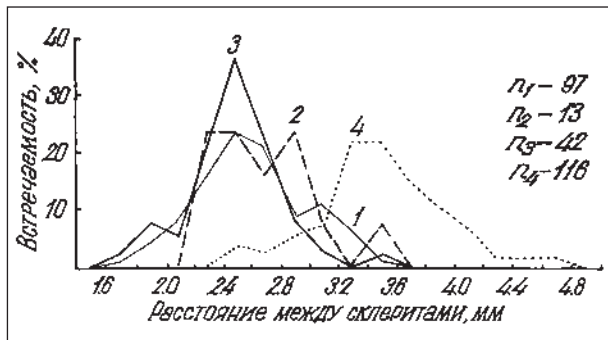


Fig. 43. Distribution of average distance between sclerites on scales in underyearlings and in the first zone of scale growth in yearlings and adults of the early sockeye of the Soldatskaya R. (at 100x magnification). Y-axis – frequency of occurrence, %; X-axis – distance between sclerites.

Individuals with fewer than 5 sclerites on scales or in first growth zone not included.

1 – underyearlings and yearlings caught in the Soldatskaya R. between 11 August and 17 October 1978;
 2 – underyearlings caught at the place where the Soldatskaya R. falls into Nerpichye L. on 20 August 1978;
 3 – spawners with one ZAS in the freshwater (central) part of the scales of the 1976-1978 spawning period;
 4 – spawners with two and three ZAS in the freshwater (central) part of the scales of the 1976-1978 spawning period.

In the freshwater zone of the scales in the late sockeye with two ZAS, there are 9-10 sclerites on the average in the first zone of growth, 6 sclerites in the second zone, and 2-4 sclerites in the marginal zone (fig. 45.2). The first is usually a lake-type ZAS, and the second one a river-type ZAS. The small number of sclerites in the second zone of growth and the weaker definition of the second ZAS implies that the second ZAS is a supplementary one (Mina, 1973, 1976; Bugaev, 1978). We still

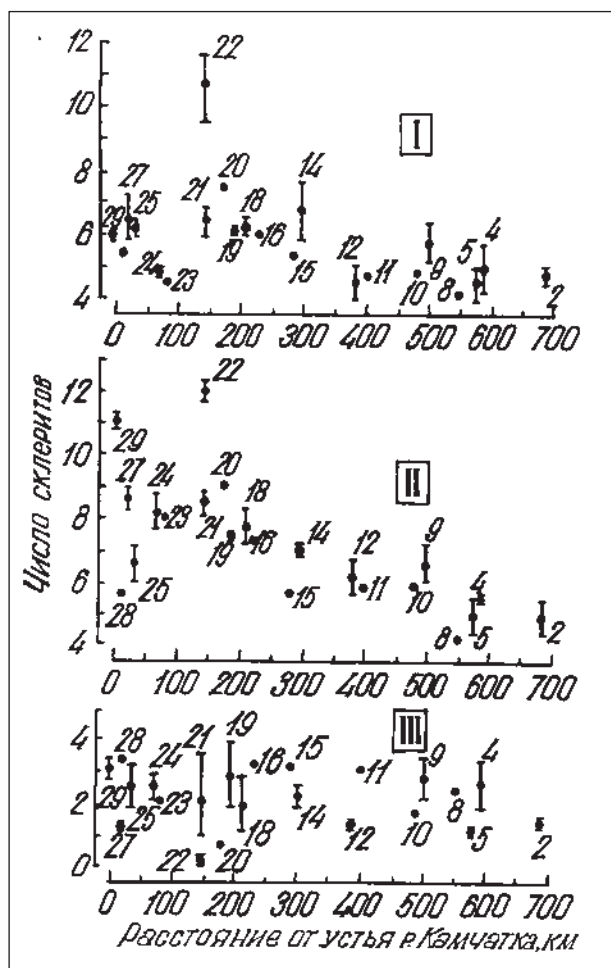


Fig. 44. Variation of the number of sclerites in the growth zones of the central part of the scales in early (spring) sockeye spawners with two ZAS. depending on the distance of the tributary from the mouth of the Kamchatka R. Y-axis – number of sclerites, %; X-axis – distance from the mouth of the Kamchatka R., km.

I – first growth zone, II – second growth zone, III – marginal growth zone of central part of scales. Areas marked as in fig. 2.

do not know what could have caused the formation of a supplementary ZAS on the scales of the juveniles of the late form of Kursin L. sockeye. We assume that this is related to the extremely favourable feeding conditions in the side channel connecting Kursin L. to the Kamchatka R. during the migration of late sockeye smolts (see Section 9.1).

As a result of our study on the scale structure in the adults of the early and late sockeye of Kursin L., we came to the conclusion that most of them are of age 1.3. The adult fish of stock “K” are not infested with *Diphyllbothrium* sp. plerocercoids, the migration of juvenile sockeye from the Kamchatka R. to the Kursin lakes has not been observed.

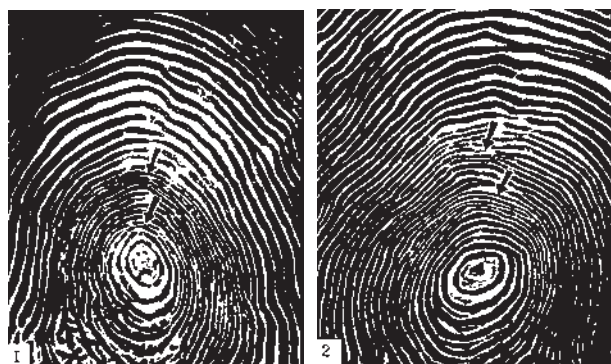


Fig. 45. Central part of scales in sockeye spawners of the Kamchatka R. watershed – stock “K”, early (spring) and late (summer) seasonal races.

– stock “K”, Kursin L., 1978, **early sockeye**, AC 600 mm, male, age 1.3, length of freshwater period 1+, arrows mark ZAS (first arrow the supplementary one, second arrow the annulus);
2 – stock “K”, Kursin L., 1976., **late sockeye**, AC 550 mm, female, age 1.3, length of freshwater period 1+, arrows mark ZAS (first arrow annulus, second arrow supplementary ZAS)

This study has shown that the sockeye stock of the Kamchatka R. has a complex population structure, and is made up of individual local second-order stocks and their groups. The observed differences in the structure of the central part of the scales and in the degree of infection of adult sockeye of the Kamchatka R. with *Diphyllbothrium* sp. are correlated with the biological characteristics of the young of certain stocks and groups within the river watershed.

All of the stocks and some of the above-mentioned groupings of sockeye have an early (spring) and a late (summer) seasonal race (“E”, “A”, “N”, “D”, “K”), but some groups have basically one seasonal race. e.g. “S” only an early one, and “V” only a late one; on the whole, their breeding areas coincide (fig. 2).

The sockeye stocks and groups differentiated by us in the Kamchatka R. watershed differ greatly as to their abundance. Table 13 presents the abundance ratio of the adult sockeye of the Kamchatka R. watershed for 1957-1991.

Table 11. Frequency of early sockeye brood stock with a "lacustrine" ZAS on the scales in Kamchatka R. watershed, %

Watershed	Year	One ZAS	Number of fish	Two ZAS		Number of fish
				First	Second	
Kamchatka R. (Pushchino village)	1973-1975	25.7	105	15.6	12.5	32
Kashkan R.	1976-1977	0.0	88	5.0	5.0	20
Kamchatka R. (Sharomy village)	1976	0.0	24	0.0	0.0	3
Kavycha R.	1976-1977	2.1	48	6.9	20.7	29
Andrianovka R.	1976-1977	0.0	97	6.5	6.5	31
Zhupanka R.	1974-1976	24.0	50	–	–	–
Kirganik R.	1976-1977	3.0	101	0.0	6.7	15
Kimitina R.	1976-1977	0.0	52	9.8	27.9	61
Kitilgina R.	1977	6.5	46	13.6	13.6	22
Shapina R.	1977	11.1	54	12.0	20.0	25
Nikolka R.	1963-1977	2.5	196	10.0	5.0	20
Tolbachik R.	1977	0.0	36	0.0	50.0	2
Bystraya-Kozyrevka R.	1976-1977	32.1	28	10.8	47.0	83
Shekhlun R.	1977	10.0	30	40.0	6.7	15
Kreruk R.	1978	–	–	4.3	34.8	23
Kryuki R.	1976-1978	36.8	19	5.8	38.7	191
Polovinnaya P.	1976-1977	17.6	17	4.0	49.3	75
Belaya R.	1977	12.5	8	14.3	57.1	7
Yelovka R.	1976-1978	60.6	40	20.2	51.2	203
Bolshaya Khapitsa R.	1976-1978	44.4	9	9.0	64.1	78
Raduga R.	1976-1978	74.2	31	11.6	51.4	138
Nizovtsevo L. (Raduga R. watershed)	1976-1977	60.0	10	10.4	53.2	77
Azabach L.	1963-1978	81.6	158	73.8	67.5	634
Kursin L.	1976-1978	85.0	40	50.8	50.8	65
Soldatskaya R. (Nerpichye L. watershed)	1976-1978	2.9	46	2.9	88.4	138
Dvukhyurtochnoye L.	1975-1978	100.0	12	85.0	81.0	153

Table 12. Frequency of late sockeye brood stock with a "lacustrine" ZAS on the scales in Kamchatka R. watershed, %

Watershed	Year	One ZAS	Number of fish	Two ZAS		Number of fish
				First	Second	
Kamchatka R. (Pushchino village)	1973-1978	23.4	81	21.2	6.1	66
Andrianovka R.	1958	36.3	22	28.6	0.0	7
Kirganik R.	1978	20.0	5	15.6	0.0	32
Nikolka R.	–	–	–	27.3	0.0	11
Ushkovskoye L.	1973-1978	1.5	476	11.8	7.8	51
Nizovtsevo L. (Raduga R. watershed)	1977-1979	45.9	37	1.4	40.8	71
Azabach L.	1972-1976	96.4	28	80.8	72.8	261
Kursin L.	1972-1976	92.7	41	80.0	38.0	100

Table 13. Ratio of abundance and age structure of second-order stocks and their groups in the Kamchatka R. watershed in 1957-1991 (Bugaev, Ostroumov, 1985, with addenda), %

Year	0.3	1.3				2.3	
	Group "S"	Group "V"	Group "E"*	Stock "K"	Stock and group "N"**	Stock "A"	Stock "D"
1957	5.3	21.5	50.7	0.1	5.7 (1.3)	15.6	1.1
1958	8.5	35.2	29.7	0.1	3.2 (0.7)	21.6	1.7
1959	10.7	13.7	57.7	0.1	7.5 (2.5)	9.0	1.3
1960	22.4	19.4	45.4	+	5.6 (1.7)	6.7	0.5
1961	33.9	12.1	44.0	0.1	5.5 (1.7)	3.1	0.7
1962	33.0	8.7	46.1	+	6.0 (2.0)	5.5	0.7
1963	26.5	9.1	49.5	+	6.0 (1.8)	7.8	1.1
1964	16.6	14.2	54.5	+	6.5 (1.8)	6.7	1.5
1965	19.3	9.4	48.7	0.1	7.1 (2.8)	12.0	3.4
1966	22.5	15.4	25.2	0.3	4.8 (2.7)	31.0	0.8
1967	16.3	9.7	31.6	0.1	3.8 (0.9)	35.4	3.1
1968	38.6	6.4	9.3	0.1	1.1 (0.2)	43.1	1.4
1969	38.3	4.0	29.6	0.1	3.8 (1.2)	23.0	1.2
1970	51.1	6.3	25.8	0.1	3.9 (1.5)	11.5	1.3
1971	14.6	5.4	46.7	0.1	5.9 (1.9)	21.2	6.1
1972	57.7	6.6	20.6	0.1	2.5 (0.7)	5.7	6.8
1973	22.6	1.7	54.7	0.2	5.7 (0.8)	7.1	8.0
1974	41.6	9.2	22.5	0.6	3.8 (1.5)	7.7	14.6
1975	35.2	5.1	45.3	0.1	4.5 (0.6)	4.2	5.6
1976	48.7	2.1	27.5	0.4	3.2 (0.7)	12.6	5.5
1977	42.7	2.5	31.5	0.1	3.1 (0.4)	16.5	3.6
1978	11.4	3.3	65.0	0.1	6.3 (0.6)	9.0	4.9
1979	16.3	4.9	48.2	0.3	4.9 (0.6)	21.3	4.1
1980	10.4	5.4	56.4	0.2	5.5 (0.5)	17.1	5.0
1981	18.1	6.1	45.2	0.3	4.7 (0.5)	20.8	4.8
1982	15.2	5.6	44.6	0.2	4.7 (0.9)	26.3	3.4
1983	18.4	4.6	36.6	0.1	3.5 (0.4)	33.6	3.2
1984	16.4	4.4	40.0	0.1	3.9 (0.2)	32.0	3.2
1985	13.2	8.9	24.4	0.1	2.6 (0.3)	38.4	12.4
1986	22.9	16.7	18.1	0.1	2.9 (1.3)	25.9	13.4
1987	31.8	4.9	22.0	0.2	2.6 (0.7)	28.6	9.9
1988	34.5	20.1	19.8	0.4	2.7 (1.0)	15.7	6.8
1989	31.9	8.9	23.6	0.2	3.6 (1.4)	14.1	17.7
1990	31.9	13.3	28.3	0.1	3.3 (0.8)	13.1	10.0
1991	15.3	13.3	33.7	0.3	4.0 (1.0)	23.4	10.0

Note. "+" signifies less than 0.1 %. *Group "N" individuals not entered here. ** Abundance of sockeye of stock "N" and group "N" are combined (partition of stock "N" shown in brackets).

8.2. Spatial distribution of the sockeye populations of the Ozernaya R.

Unlike the sockeye of the Kamchatka R., which spawn and forage mainly in the tributaries and in a number of lakes of the river watershed (Lagunov, 1940; Krogius, 1970; Ostroumov, 1972; Bugaev, 1983c, 1986a), the sockeye of the Ozernaya R. breed mainly in the Kuril L. watershed (fig. 5) (Krokhin, Krogius, 1937; Ostroumov, 1970; Yegorova, 1970; Selifonov, 1970, 1970a, 1975). The small Etamynk L., from which the Etamynk R. arises and then flows into Kuril L., is the second lake of the Ozernaya R. watershed where sockeye spawn and forage (Krokhin, Krogius, 1937; Ostroumov, 1970; Bugaev, 1976), but the abundance of Etamynk L. sockeye is very low and virtually incomparable to the abundance of Kuril L. sockeye.

From Kuril L., the young of the sockeye migrate downstream mainly at the age of 2 years; a small percentage of them (an average 9.1 %) is made up of three-year-olds. During certain years, some of the juveniles migrate downstream as yearlings (Selifonov, 1970, 1970a; Dubynin, Bugaev, 1988).

Most of the adult fish are of age 2.3 and 2.2 (Selifonov, 1975; Selifonov, 1982).

The sockeye of Kuril L. is characterized by interannual variability in growth, which depends on the level of development of the forage base and the changes in water temperature (Dubynin, 1986; Dubynin, Bugaev, 1988; Bugaev et al., 1989).

The adult sockeye of Kuril L. become heavily infested with plerocercoids of *Diphyllbothrium* sp. (Kononov, 1971).

The central part of a typical scale from adult sockeye of Kuril L. is depicted in fig. 46.1.

The sockeye of Etamynk L. basically spends two years in the lake; it becomes infested with *Diphyllbothrium* sp., but to a lesser degree than in Kuril L. (Bugaev, 1976).

A survey of Etamynk L. on 29-30 September 1974 showed that 80-90 % of the brood stock on the spawning grounds of this lake was made up of adult fish that had spent one year at sea, though this applied to only 5-6 % of the adult sockeye of



Fig. 46. Central part of scales in sockeye spawners of the Ozernaya R. watershed – lakes Kurilskoye and Etamynk.

1 – Kuril L., outfall of the Ozernaya R., 5 August 1985, AC 590 mm, female, age 2.3, length of freshwater period 2+, arrows mark ZAS – annuli;

2 – Etamynk L., Etamynk R., 21 August 1985, AC 550 mm, male, age 2.2, length of freshwater period 2+, arrows mark ZAS (first and second arrows – annuli, third arrow supplementary ZAS).

the Kuril L. watershed. We cannot tell how typical this is of the sockeye of Etamynk L., for we have no other data on the brood stock of this lake.

A typical central area of the scales of Etamynk L. adult sockeye is shown in fig. 46.2. The third ZAS (from the centre) is a supplementary one, and its formation is attributed to the migration of Etamynk L. smolts to Kuril L, and the short foraging period spent there. A supplementary ZAS probably forms as a result of a change in the ecological conditions of young fish, for no supplementary ZAS was observed in the smolts caught in Etamynk L. (Bugaev, 1976). We still do not know whether the juvenile fish migrate from Etamynk L. to Kuril L, as underyearlings, or yearlings.

The attempts to differentiate seasonal races in the Ozernaya R. stock of sockeye were unsuccessful (Krokhin, Krogius, 1937). A morphological analysis has shown that the Ozernaya sockeye stock includes a number of individuals which enter southern spring-fed creeks to spawn, and that these fish are smaller, with a short head and low body, and have weakly developed breeding colours (Krokhin, Krogius, 1937; Bugaev, 1976). This type of sockeye constitutes a small percentage of the total sockeye population of Kuril L. (Krokhin, Krogius, 1937; Yegorova, 1970a).

Unlike that of certain other sockeye stocks, the spawning migration of the Ozernaya R. sockeye, which begins with a large number of migrants from the end of July and continues up to the end of September (peaking at the beginning of August), does not indicate two seasonal races based on run timing, i.e. early (spring) and late (summer) (Krokhin, Krogius, 1937; Yegorova, 1970a; Krogius, 1983).

This being the case, some researchers (Yegorova, 1970a; Krogius, 1983) maintain that there are no seasonal groupings in the sockeye of the Ozernaya R. watershed, and consider the entire sockeye population of this river to be a late (summer) population.

This conclusion did not go undebated, since spawning in some tributaries of Kuril L. begins in the middle and sometimes even at the beginning of June (Selifonov, personal communication; Varnavskaya, 1988a), which is not typical of a late (summer) race.

N. V. Varnavskaya (1988a), using the method of electrophoresis in polyacrylamide gel, determined the frequencies of the polymorphic loci Ldh-B₁ and Pgm in consecutive samples of adult fish migrating to the spawning grounds and juveniles migrating to the sea. Local spawning groups (subpopulations) were studied from July to November 1985-1986. Altogether, more than 30 samples of adult sockeye caught in littoral and river breeding areas were examined. Analysis of the frequencies of the Ldh-B₁ gene in samples from the run of the brood stock showed an increase in the frequency of the Ldh-B₁ allele (slow) from the June samples (0.721-0.725) to the September ones (0.882-0.900). A similar picture was observed when downstream-migrant juveniles were studied in 1984-1986 (Varnavskaya, Dubynin, 1987). Early-migrating juveniles (beginning of June) are characterized by lower frequencies of the Ldh-B₁ allele (0.758-0.769) in comparison with the late-migrating ones (0.816-0.882). This conclusion is substantiated by the dynamics of genetic and biological indices in subpopulations during the spawning migration. The differences between the series of samples grouped according to the characteristics of the breeding ground and time of spawning proved to be statistically reliable, therefore, it is a proven fact that three ecological seasonal forms exist in Kuril L., namely the early river, late river and late littoral forms, and between the first and the third form we observe a high degree of reproductive isolation, which is responsible for the high level of genetic differentiation of the Ldh-B₁ locus ($t=2.7$; $P<0.01$). The late river form is characterized by intermediate values for all the criteria, which may be an indication of the more or less hybrid nature of this form, the exchange of genes between this form and the spring river and summer littoral forms is likely to be quite significant (Varnavskaya, 1988a).

The general level of heterogeneity, evaluated on the basis of the samples from spawning grounds, proved to be lower than in the sockeye populations of Azabach L. (Altukhov et al., 1983) and Nachikinskoye L. (Varnavskaya, 1984), the variability of the Ldh-B₁ gene frequencies is of a tempo-clinal nature (Varnavskaya, 1988a).

In 1986 and 1987, late-spawning subpopulations (October–November) were studied in greater detail. The sockeye subpopulations of the Etamynk R., in which spawning lasts from July to January, were examined several times. It can be said that, based on 1986-1987 data, the interannual differences between samples of one and the same local group are insignificant, whereas the frequency variations between the lake and the river spawning groups are quite significant. The maximum frequency range of the Ldh-B₁ allele was observed in 1986 (0.654-0.909), the gene pool of the Etamynk R. sockeye is the most variable; the frequency of the rare Ldh-B₁ allele was higher than usual in nearly all the samples there. This applies in particular to the early (July) and late (October–November) samples (N. V. Varnavskaya, personal communication).

The above data are unquestionably proof of the heterogeneity of the sockeye stock of Kuril L.

8.3. Seasonal rhythms of growth

The seasonal rhythms of growth manifest themselves on the fish scales in the form of annual zones of adjacent sclerites (ZAS), i.e. annuli, they appear as a result of the resumption of growth after its cessation at a certain time of the year (Chugunova, 1959; Birman, 1968; Bugaev, 1981). The ZAS that form during the growing season are considered to be supplementary ones.

The most accurate age data can be obtained by conducting systematic observations of fish growth with special attention paid to its seasonal rhythms (Mina, 1976; Mina, Klevezal, 1976). Comparative analysis of these rhythms and the growth rate of individuals from different bodies of water is a new trend in the study of natural sockeye populations, the reproduction and foraging of the young fish of the major stocks of this species within its range are, as a rule, confined to large and deep lakes (Krokhin, Krogius, 1937; Clutter, Whitesel, 1956; Koo, 1962; Foerster, 1968; Burgner, 1991) where the rhythms of growth are somewhat similar. This is probably why the question concerning the variability of the seasonal growth rhythms of young sockeye has evaded the scrutiny of researchers for so long. The first attempt in this direction was undertaken by F. V. Krogius (1970); this was later followed up by our own investigations (Bugaev, 1981, 1984b, 1991; Bugaev, Dubynin, 1991).

8.3.1. Linear growth of underyearling and yearling sockeye in the watersheds of the Kamchatka R. and Kuril L. (Ozernaya R.)

According to the data of Kamchatrybvod (Kamchatka Fish Department), the downstream migration of underyearling sockeye from the spawning grounds of the Zhupanka R. in the upper reaches of the Kamchatka R. (fig. 2) begins during the first or second ten-day period of May, peaks during the third ten-day period of May up to the first half of June, and is completed at the end of June–beginning of July (fig. 47), the underyearlings of the Chinook, chum, coho and char migrate downstream simultaneously with the underyearlings of the sockeye.

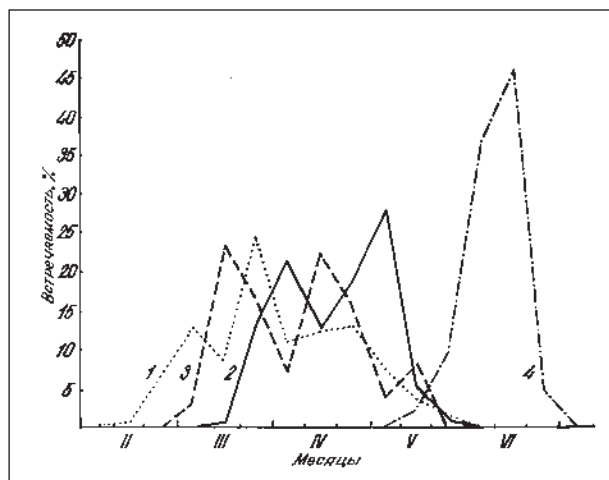


Fig. 47. Dynamics of downstream migration (by 10-day periods) of underyearling sockeye from the Zhupanka and Nikolka rivers (based on the data of Kamchatrybvod). Y-axis – frequency of occurrence, %; X-axis – months.

1 – Nikolka R., 1984; 2 – Nikolka R., 1989; 3 – Nikolka R., 1990; 4 – Zhupanka R., 1984.

Based on the long-term data of Kamchatrybvod (A. G. Urnyshev, V. P. Urnysheva, S. I. Sakharovsky, V. G. Davydov – archives of Kamchatrybvod) the downstream migration of underyearling sockeye from the Nikolka R. usually begins during the first days of March (less commonly at the end of February) and ends at the beginning of June. Fig. 47 illustrates the downstream migration of underyearling sockeye in 1989-1990. Underyearlings of the coho and char migrate downstream simultaneously with the sockeye. The largest number of underyearlings migrates downstream between 22.00 and 01.00 hours. By dawn, the number of fish caught in the traps drops sharply. The largest number migrates downstream along the banks. The downstream migration in open water is uniform. The downstream migration of underyearlings lessens abruptly on bright moonlit nights, and therefore we observe peaks of downstream migration (fig. 47). The size-weight characteristics of downstream-migrant underyearling sockeye are given in table 14.

Analysis of the correlation between the number of spawned out adult fish and the number of underyearling sockeye migrating downstream from the Nikolka R. in 1976-1991 points to the existence of two highly significant levels of correlation (fig. 48), but we have not yet established the causes of this.

From Ushkovskoye L. where a fish hatchery existed up to 1988, the young of the sockeye and other salmons (chum and coho) would be released at different times, but most of the sockeye usually migrated downstream at the end of April, their downstream migration took place mainly at night, but some of the juveniles entered the Kamchatka R. during the daylight hours as well. The length and weight of the sockeye underyearlings released from the nurseries of the Ushkovsky Fish Hatchery are given in table 15.

In the limnokrenes of the Azabach L. watershed, free-swimming sockeye fry were noted during the first days of April, the migration of sockeye fry from the spring-fed spawning grounds in the lake takes place from the end of April up to the end of June. The downstream migration begins at a low water level. A rise in water level at the beginning of May is accompanied by an increase in the number of migrants, which peaks on May 15-25th (Simonova, 1972). The size and weight of the sockeye underyearlings at the spawning grounds of Azabach L. are given in table 16.

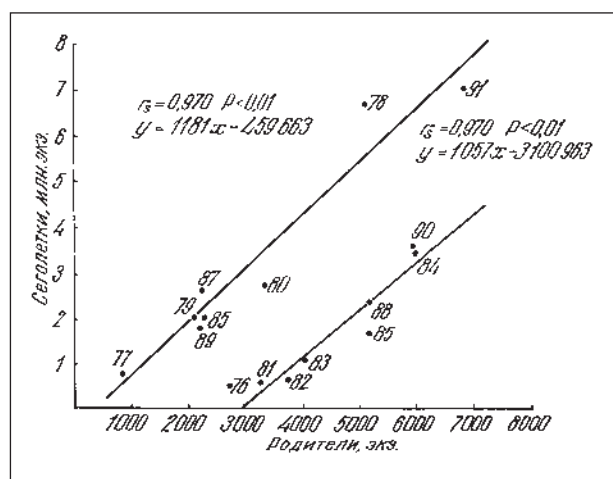


Fig. 48. Variation of the number of underyearling sockeye in the Nikolka R., depending on the numbers of spawned out adults of the early (spring) seasonal race of the sockeye (based on the data of Kamchatrybvod and A. G. Ostroumov's aerial survey data). **Y-axis** – abundance of underyearlings, mill. specimens.; **X-axis** – abundance of spawners.

Figures near dots denote year of downstream migration of under-yearlings.

Table 14. Length and body weight down stream migrating sockeye underyearlings, Nikolka R. 1977-1990 (Kamchatrybvod date)

Migra-tion year	Body length, mm						Body weight, mg					
	March		April		May		March		April		May	
	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average
1977	–	28.7	–	29.4	–	34.3	–	178.0	–	234.0	–	487.3
1978	–	30.4	–	31.2	–	33.7	–	155.8	–	244.6	–	412.8
1979	23-32	28.7	27-40	30.3	27-45	36.9	80-260	186.2	150-710	244.5	150-1070	548.8
1980	25-31	28.4	26-39	29.9	28-52	34.0	110-250	172.7	140-720	241.1	150-1620	422.8
1981	25-31	28.5	25-38	30.2	26-42	32.4	140-270	194.2	110-600	254.9	100-720	333.3
1982	26-31	28.7	27-45	30.1	27-45	35.1	98-270	194.3	150-1020	250.1	160-1040	479.3
1983	25-30	29.0	28-41	31.1	25-49	38.0	150-250	196.6	150-760	276.7	130-1370	627.7
1984	–	29.3	–	32.0	–	38.1	–	190.5	–	327.3	–	611.7
1985	–	29.5	–	33.4	–	37.0	–	210.9	–	355.1	–	544.8
1986	–	29.6	–	31.9	–	38.0	–	184.0	–	296.0	–	590.0
1987	–	29.0	–	35.0	–	33.0	–	178.0	–	375.0	–	349.0
1988	–	29.3	–	31.6	–	35.4	–	200.0	–	290.0	–	452.0
1989	–	28.0	–	32.6	–	37.0	–	226.0	–	355.0	–	573.5
1990	–	29.4	–	31.6	–	36.7	–	193.3	–	299.0	–	548.0

Note. Each sample consisted of from 50 to 100 exemplars.

Table 15. Average body length and weight of sockeye underyearlings released by the Ushkovsky Fish Hatchery in 1975-1979 (Kamchatrybvod data)

Year released	Date released	Body length, mm	Body weight, mg
1975	19.03-28.03	24.0	148.0
1976	24.04	27.0	160.0
1977	20.04	28.0	168.0
1978	30.03-24.04	27.0-26.0	155.0-177.0
1979	26.03	27.0	222.5

Table 16. Average body length and weight of sockeye underyearlings in Azabach L. Spawning grounds (Simonovs, 1972a)

Indicator	Creek No. 3			Creek No. 4		Creek No. 5	
	April	May	June	May	June	May	June
Body length, mm	27.9	27.9	28.3	28.5	29.2	28.4	28.7
Body weight, mg	187.9	188.1	182.0	195.9	237.0	183.8	194.5

We should note that the young of the sockeye from the Zhupanka and Nikolka rivers and Ushkovskoye L. migrate downstream to the sea mostly as underyearlings (Bugaev, Karpenko, 1983; Bugaev, 1984). As our investigations have shown, a downstream-migration peak is observed annually, usually on June 15-20th, in underyearling sockeye at the mouth of the Kamchatka R. During this period, underyearling sockeye without scales migrate downstream. The downstream migration lessens substantially in July, but it intensifies again during the first ten days of August. The dynamics of the downstream migration of underyearling sockeye to the mouth of the Kamchatka R. was illustrated earlier (Bugaev, Karpenko, 1983). Table 17 characterizes the size of individual underyearlings from the Kamchatka R. estuary and the number of sclerites on their scales.

Table 17. Body length and number of scale sclerites from sockeye underyearlings caught at the mouth of Kamchatka R., 1978-1989

Date, year	Length, mm		Number of scale sclerites		Number of fish
	Range	Average	Range	Average	
29.07-01.08.78	29-59	54.0	0-6	3.48	5
02-03.08.78	36-56	45.1	1-6	3.13	16
05-06.08.78	34-56	47.3	1-5	3.63	27
20-21.08.78	30-64	51.1	0-8	4.40	80
02-03.06.79	28-31	29.5	0-0	0.00	4
15.06.79	28-31	29.2	0-0	0.00	10
18-19.06.79	27-34	28.0	0-0	0.00	36
20.06.79	27-34	28.3	0-0	0.00	71
25-26.06.79	27-37	29.1	0-0	0.00	22
01-02.07.79	28-37	30.9	0-0	0.00	31
10-11.07.79	28-36	31.4	0-0	0.00	11
19-20.07.79	36-42	38.4	1-2	1.40	5
29-30.07.79	31-37	34.7	0-2	1.00	3
06-08.08.79	54-72	54.8	3-7	4.50	6
10-11.08.79	45-67	53.2	3-7	4.69	13
17-18.08.79	39-63	51.2	1-7	4.20	5

Note. For the purpose of statistical processing, in the event that some of the fish in the sample were scaleless the number of sclerites present were assigned the value of "0".

The initiation of scales in underyearlings sockeye (central area outlined by a single sclerite) in the Kamchatka R. watershed takes place at an average body length of 40 mm. This length is equal to 38 mm for the sockeye of Dalneye L., 40 mm for Karymaysky klyuch (Bolshaya R.) (Kroggius, 1957), and 40 mm for Kuril L. (Selifonov, 1970a).

We found that our data on the average rate of scale initiation in juvenile sockeye in the Kamchatka R. watershed depended on the time of sampling (fig. 49). If the scales were basically formed in the young fish and most of them already had 2-3 sclerites, the values of the mean length at which a central area outlined by a single sclerite was observed on the scales of underyearlings were higher on the average, and vice versa. On the average, the initiation of scales in underyearling sockeye takes place at a length of 40 mm in the Kamchatka R. watershed.

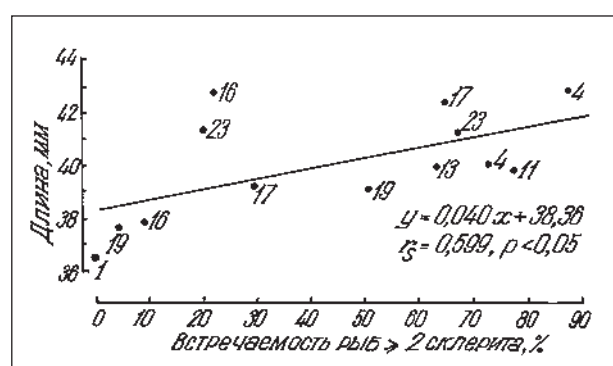


Fig. 49. Body length of underyearling sockeye at the moment of scale initiation (central area on scales limited to one sclerite). Y-axis – length of underyearlings, mm; X-axis – frequency of occurrence of individuals with two or more sclerites on the scales in samples, %. Areas marked as in fig. 3.

Let us now examine the linear growth of juvenile sockeye in the Kamchatka R. watershed (fig. 3) with the seasonal rhythm taken into account.

Our attempts to observe the linear growth of the sockeye in individual bodies of water proved successful only for groups of specimens from a number of small bodies of water where it was possible to fish off a significant part of the population and where the young fish stay all year (limnokrenes of the Kokhanok R., Ushkovskoye L., Kulpik L., oxbow lake of the Raduga R., etc.). Most of the bodies of water in the Kamchatka R. watershed are not inhabited by young sockeye all year round, and immature fish of the same age groups are encountered in them for a rather limited time. Practice has shown that 10-20 days after taking a sample of immature fish from a body of water such as this, it will in the majority of cases contain either no juvenile fish of the same age group, or will contain some immature fish of another age group or ones of the same age group but of a much smaller size than in the first sample from the same body of water. This is typical of the majority of floodplain

bodies of water in the Kamchatka R. watershed, where young sockeye are encountered only during the warm period of the year. Due to the fact that we seined the bodies of water quite thoroughly (usually 5-10 sets of a seine at different points), it was possible in some cases to anticipate the downstream migration of immature fish of one age group and the moving in of another. In large bodies of water, for example Azabach L., it was often impossible to catch fish of one and the same age group several days later without knowing the distributional tendencies of its components, as well as the tendencies of migration of the young from the tributaries of the lower Kamchatka R. to the lake (Bugaev, 1981a).

Having first grouped all the fish according to the number of ZAS on the scales, we compared the length of the young fish, which is recommended in the standard typical methods of age determination in cases where the accuracy of the latter is questionable (Mina, 1973, 1976). Having grouped the fish according to the number of ZAS, we were able to differentiate a group of underyearlings with one supplementary ZAS among the fish that had one ZAS on their scales (yearlings and underyearlings), these fish were quite numerous in some samples. As we picked out the underyearlings with supplementary rings, we recorded the time at which the annuli formed in a particular body of water or type of body of water (see Section 8.3.2), the rate of sclerite formation, the number of sclerites in the observed growth zones, and the time at which the young fish were caught. The later the supplementary ZAS form in the growing season, the easier it is to identify them and the higher the confidence level of determination of age.

For example, in the small floodplain lakes of the Kamchatka R. watershed, annuli form on the scales of young fish when the ice breaks up (in May or at the beginning of June), and one sclerite forms in 12.3 days on the average (Bugaev, 1981). Proceeding from this, we grouped the fish with one ZAS, caught at the end of July or later, with the underyearlings that had a supplementary ZAS on their scales if the marginal zone ended in the ZAS or if there was an increment of 1-2 sclerites after it. A small increment in sclerites after the ZAS was an indication of its recent formation, i.e. it was formed after seasonal growth was resumed.

The frequency of occurrence of individuals with one ZAS on their scales in the samples of underyearlings taken in the Kamchatka R. watershed at the end of August and in September increased somewhat (Bugaev, 1981a, 1986), which points to the fact that supplementary ZAS form during this period.

Without taking the underyearling samples from lakes Kursin and Azabachye into consideration, it can be said that the following tendency is observed: supplementary ZAS form more frequently on the scales of young fish from those bodies of water (fig. 3) where no, or practically no spawning takes place and young sockeye abound (oxbow lakes above the village of Tayozhnyi, Dedova Yurta, Kulpik L., lakes Kurazhechnoye, Kobylkino and Krasikovskoye, oxbow lake of the Raduga R.). To this list of lakes we can also add the "Ushkovskoye L." limnokrenes, despite the fact that this a large spawning ground. We have established that the immature fish of this stock migrate downstream to the sea as underyearlings (Bugaev, 1983c, 1984), while the young of other stocks utilize it as a foraging ground (Bugaev, 1984b).

A supplementary ZAS forms on the scales of young fish that migrate at the underyearling stage to forage in Azabach L. from the tributaries of the lower Kamchatka R. (Bugaev, 1981a), the data presented confirm G. V. Nikolsky's point of view that an ecological change can result in the formation of supplementary ZAS on the scales of fish (Nikolsky, 1974).

A high percentage of individuals with a supplementary ZAS on their scales (42 %) was noted by us in the underyearling sockeye of Kursin L at the beginning of September 1976. Knowing that the small Kursin lake is found in the watershed of the large Kursin lake and that sockeye spawn in both of them, one can assume that the underyearlings with a supplementary ZAS on their scales are the offspring of those from the small Kursin lake.

We attribute the formation of supplementary ZAS in both cases to the changes in the habitat of the young.

Having examined the linear size of underyearlings that have no ZAS on their scales (fig. 50), we can say that, despite the significant variations, their length will, on the average, increase with time. For underyearlings with a supplementary ZAS on their scales (fig. 51), it is difficult to perceive the increase in size. It is discerned only in the fish of certain bodies of water at certain time intervals. The underyearlings with one ZAS are somewhat larger than those without a ZAS on their scales (fig. 50, 51).

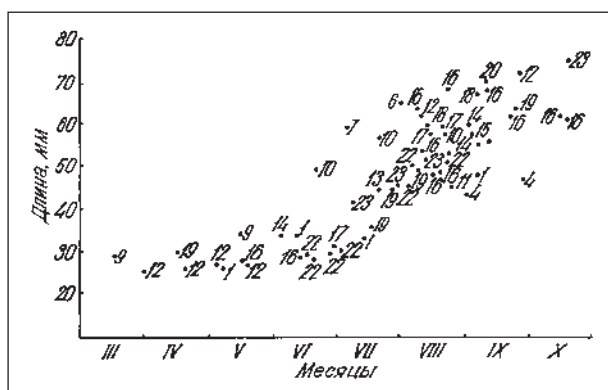


Fig. 50. Body length of underyearling sockeye (without ZAS on the scales) in some areas of the Kamchatka R. watershed during the growing season. Y-axis – body length, mm; X-axis – months. Areas marked as in fig. 3.

Due to the extensive size variability of the underyearlings, one can assume that the periods of scale initiation vary considerably as well. Based on our observations, the initiation of scales (central area circumscribed by one sclerite) in underyear-

lings of the Kamchatka R. watershed takes place from the end of May up to the end of September (mean period from the end of June to the beginning of July). F. V. Krogius (1970) has also noted considerable fluctuations in the period of scale initiation in the sockeye of the Kamchatka R.

Guided by the data in fig. 50 and the mean length of the young at the time of scale initiation (40 mm), one can conjecture the approximate periods of scale formation in young sockeye from different bodies of water in the Kamchatka R. watershed. The size variability observed in underyearlings can be attributed to the different periods of emergence of the alevins from the ground, which are determined by the hydrological characteristics of the different spawning grounds, the presence of seasonal races in the sockeye, and also by the different growth rates of the young fish in different types of waters. The variable rate of sclerite formation is evidence of this (Bugaev, 1981).

High positive correlations between the scale characteristics and the size-weight indices are indicated for the young of the sockeye (Clutter, Whitesel, 1956; Bugaev, 1989). Therefore, this implies that a high rate of scale growth is evidence of a high growth rate, and vice versa.

If we compare the length of yearling sockeye with one ZAS on their scales (fig. 51), we will see that individuals of similar size are encountered in different bodies of water in the Kamchatka R. watershed from April to October, though it can be said in some cases that individuals of certain bodies of water increase in size during the growing season.

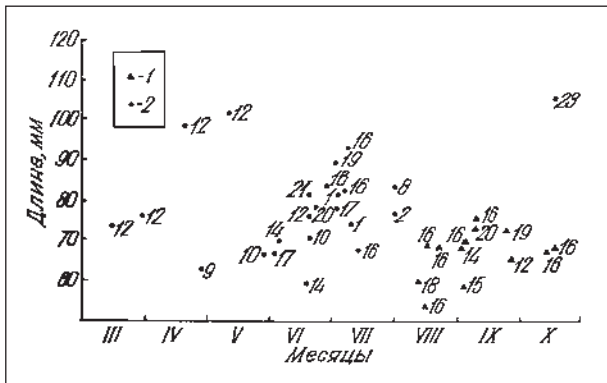


Fig. 51. Body length of underyearlings (with supplementary ZAS on scales) and yearlings of the sockeye in some areas of the Kamchatka R. watershed during the growing season. Y-axis – body length, mm; X-axis – months.

1 – underyearlings with supplementary ZAS; 2 – yearlings. Areas marked as in fig. 3.

Fig. 52 illustrates the length of underyearling and yearling sockeye in Azabach L. on the basis of 1979-1990 material, and fig. 53 the linear growth of underyearlings of stock “A” (Azabach L.) and group “E” (from the tributaries of the Kamchatka R.). The juveniles of stock “A” and group “E” from mixed trawl catches in Azabach L. were identified on the basis of an analysis of their size, scale structure, and the time and place of the catch, as recommended by us earlier (Bugaev, Bazarkin, 1987).

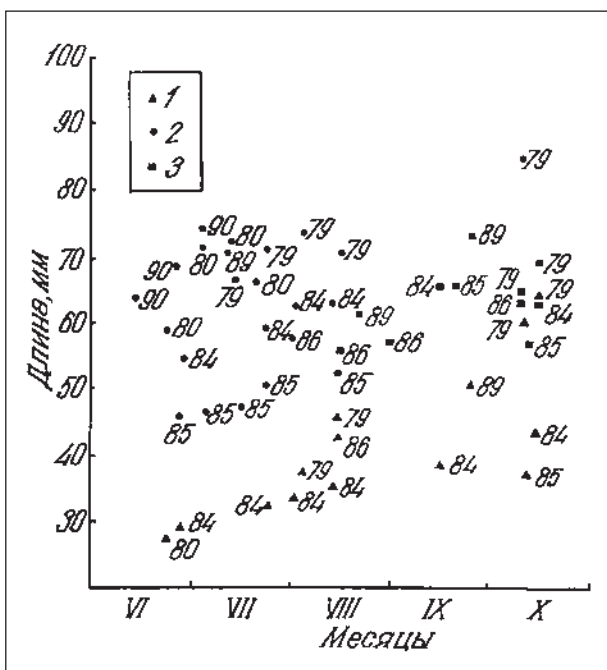


Fig. 52. Body length of underyearlings and yearlings of the sockeye of stock “A” and underyearlings of group “E” from Azabach L. during the growing season (based on 1979-1990 data), collected at station No. 2. Y-axis – body length, mm; X-axis – months. Figures near dots – year of catch.

1 – underyearlings of stock “A”; 2 – yearlings of stock “A”; 3 – underyearlings of group “E”.

When we analyzed the scales in yearlings with one ZAS, we noted that the number of sclerites in the first growth zone varied extensively, from 2-5 to 10-14. The size range of the underyearlings has already been mentioned (fig. 50, 51). Based on the material presented here, we can conclude that the number of sclerites in the first zone of scale growth is not the main

indicator of a true or false annulus, as it was said to be when the age of the Azabach L. sockeye was determined (Konovalov et al., 1971; Konovalov, 1980). Other scientists (Krogius, 1979; Selifonov, 1970) share our opinion that the number of sclerites in the first zone of scale growth in the sockeye is not the main indicator of supplementary scale structures (Bugaev, 1976, 1978, 1983a, 1983c).

The linear size of juveniles with two ZAS on their scales is very similar in different bodies of water in the Kamchatka R. watershed (with the exception of Azabach L. individuals) from April to July (Bugaev, 1986); however, an increase in size is quite noticeable in Azabach L. sockeye from June to September (Bugaev, 1986; Bugaev, Bazarkin, 1987).

Juveniles with two ZAS on their scales, except those from Azabach L, and Dvukhyurtochnoye L. (for which we have no data), are usually encountered in samples which include yearlings with one ZAS; however, they occur in small numbers. On the basis of a scale structure analysis of only a small number of sockeye from several bodies of water (lakes Nizovtsevo and Ushkovskoye, oxbow lake of the Raduga R.), we came to the conclusion that the fish with two ZAS on their scales may be two-year-olds (Bugaev, 1986).

The observed variability and significant transgression (even of mean values) in the size of the juvenile sockeye of the Kamchatka R. watershed with a different number of ZAS on their scales can be attributed to the nonsimultaneous emergence of the alevins from the redds, the variable rhythm of seasonal growth and the variable growth rate in different bodies of water. All of this is intensified by the fact that the growth rate of juvenile sockeye and the size of the downstream migrants can vary from year to year, depending on the level of the forage base, the abundance of immature fish and the temperature conditions during the year of the feeding migration (Burgner et al., 1969; Goodlad et al., 1974; Bugaev, 1983a; Bugaev et al., 1989; Burgner, 1991, etc. etc.)

The above summary indicates that, for the sockeye of the Kamchatka R. watershed, the size of the young, with the exception of underyearlings during the summer, cannot serve as the main criterion of age determination.

According to V. V. Azbelev and M. M. Selifonov (Selifonov, 1970a), the young begin to emerge from the ground in the Kuril L. watershed at the beginning of March, and this continues up to September. The alevins emerging from the ground in spawning creeks stay in the quiet backwaters and inlets for a short period, and then migrate to the lake. By the end of June, the young fish are usually 26-38 mm long (average 32 mm), and weigh 0.150-0.635 g (average 0.33 g). The emergence timing of the alevins and the periods of growth up to a certain length vary from year to year (Selifonov, 1970a).

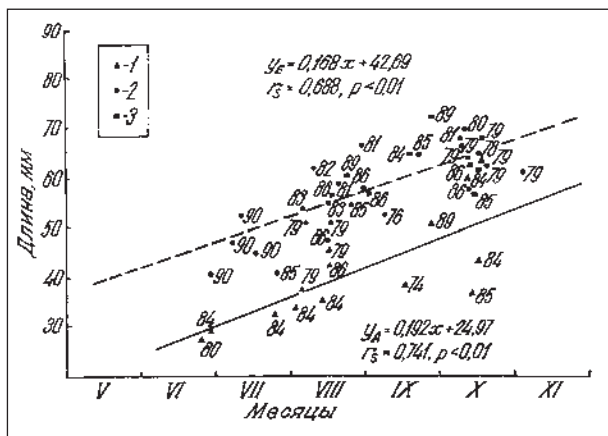


Fig. 53. Body length of underyearling sockeye of stock "A" and group "E" from the lake and side channels of Azabach L. during the growing season (based on 1976-1990 material). Y-axis – body length, mm; X-axis – months. Figures near dots – year of catch. 1 – underyearlings of stock "A", caught on the lake (station No. 2); 2 – underyearlings of group "E", caught in a side channel of Azabach L. (mainly near Dyakonovsky klyuch); 3 – underyearlings of group "E", caught in Azabach L. (station No. 2). In equations, "x" is number days from and after 01 June, "y" is body length.

Fig. 54 depicts the linear growth of underyearling and yearling sockeye in the Kuril L. on the basis of long-term trawl data. The increase in the body size of underyearling sockeye during the growing season is described quite well by the equation of regression. From the regression curve, one comes to the conclusion that scale initiation in the underyearling sockeye of Kuril L. takes place at the end of the second–beginning of the third ten-day period of August on the average (assuming that the scales are initiated when the fish is 40 mm long). For yearlings, the increase in body size during the growing season is of a more complex nature (fig. 54), as yearling sockeye resume their seasonal growth only after the smolts migrate downstream to the sea (Bugaev, Dubynin, 1991). Due to the small number of two-year-old sockeye in the catches after the downstream migration, we did not study the linear growth of this age group during the growing season.

Analysis of the growth rate of sockeye smolts prior to downstream migration on the basis of long-term data indicates that individuals which migrate downstream at an older age (2-3 years) have a slower growth rate than those migrating seaward at the age of 1-2 years (Selifonov, 1970a; Dubynin, Bugaev, 1988).

We do not have any data on the seasonal growth of juvenile sockeye in Etamynk L. (Kuril L. watershed).

8.3.2. Formation of the first annulus on the scales in juvenile sockeye of the Kamchatka R.

The juvenile sockeye of the Kamchatka R. watershed are characterized by uneven spacing between the sclerites that form on the scales during the growing season (fig. 55). Due to the absence of scales in underyearlings at the beginning of summer and the rapid downstream migration of yearlings from the majority of foraging waters during the same period, we did not manage to trace the changes in the distance between the sclerites forming during the growing season in any of the bodies of

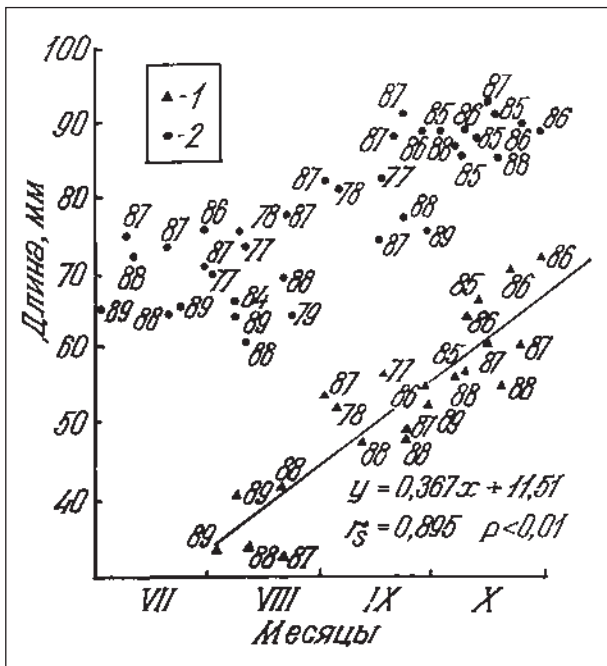


Fig. 54. Body length of underyearling and yearling sockeye of Kuril L. during the growing season (based on V. A. Dubynin's trawling material for 1977-1989). Y-axis – body length, mm; X-axis – months. Figures near dots denote – year of catch.

1 – underyearlings, 2 – yearlings.

water. Nevertheless, analysis of the data in fig. 55 leads to the conclusion that the distance between the sclerites forming in juvenile sockeye at the beginning and at the end of the growing season is significantly smaller than in the middle of it. The same was noted in the sockeye of the Wood R. watershed in Alaska (Koo, 1962), and in other fish as well (Vaganov, 1978), these facts suggest that, due to the irregular growth of the sockeye during the year following the formation of annuli on its scales, the adjacent sclerites on them are basically taken into consideration as indicators of both the completion and the resumption of growth. The appearance of annuli are preceded by sclerite deformation which is associated with the resumption of growth (Lapin, 1965). Prior to its resumption, there are no annuli on the scales of juvenile sockeye, despite the fact that the sclerites which correspond to the end of the growing season are in some cases quite closely spaced.

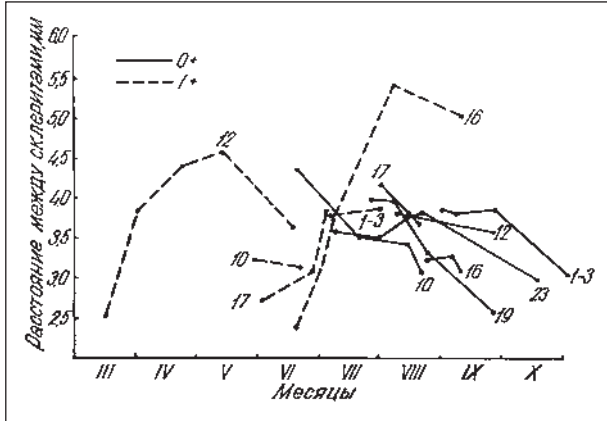


Fig. 55. Average distance between two outer sclerites on the scales of young sockeye from some bodies of water in the Kamchatka R. watershed (at 150x magnification). Y-axis – distance between sclerites, m; X-axis – months.

Areas marked as in fig. 3.

Analyzing the increase in the number of sclerites in the marginal zone of the scales in year-old sockeye, we noticed that it varied considerably, and this made it difficult to compare the periods of annulus formation on the scales of juveniles from different types of bodies of water. To determine the time that elapsed after the formation of the annuli, we made use of data from an observation of the length of time required for one sclerite to form on the scales of juvenile sockeye (fig. 18). On the basis of this information and the increments in the number of sclerites following the annuli, we determined the time that elapsed after their formation, which, together with the juvenile sampling dates, enabled us to determine the time at which the first annulus was initiated on the scales of fish from different types of bodies of water.

By examining the length of time it takes for one sclerite to form on the scales of underyearling sockeye (table 18), we see that they form at the slowest rate in fish from the upper reaches of the Kamchatka R. (limnokrenes of the Kokhanok R., and Ushkovskoye L.). The rate of sclerite formation in yearlings is similar to that of underyearlings from the same bodies of water (table 18). To determine the dates on which annuli form in the Kamchatka R. watershed, we accepted 20.7 days to be the average period of formation of one sclerite for underyearling and yearling sockeye samon in the upper reaches of the Kamchatka R, and spring-fed bodies of water, and 12.3 days for those in the lakes and abandoned river channels of the middle and lower reaches. Furthermore, in the cases where data on the rate of sclerite formation in foraging juveniles was available for a particular body of water, this data was applied directly (Kamchatka R. near the village of Pushchino, Kulpik L., Ushkovskoye L., old channel of the Raduga R., Nizovtsevo L., Azabach L.); otherwise, we used the average values obtained

by us (Nikolka R., Kurazhechnoye L., Kursin, side channel to Melkoye L.). Considering that the increments in the number of sclerites in the marginal zone of the scales in yearlings were not large, we do not expect any major deviations from these results as we come up with more accurate information on the time it takes for one sclerite to form on the scales of juvenile sockeye from certain bodies of water.

Table 18. Length of time required to form scale sclerites by sockeye underyearlings and yearlings in some sections of the Kamchatka R. watershed, days

Watershed	Underyearlings			Yearlings		
	Data, year	Average temperature during observation, °C	Duration of scale sclerite formation, days	Data, year	Average temperature during observation, °C	Duration of scale sclerite formation, days
Kamchatka R. at Pushchino	12.07-05.09.70	7.2	17.3	—	—	—
—“—	05.09-02.11.70	4.9	27.2	—	—	—
Kulpik L.	19.06-19.07.77	19.3	14.1	—	—	—
—“—	19.07-31.07.77	20.8	23.1	—	—	—
—”—	31.07-20.08.77	19.9	13.3	—	—	—
Lake border of Kokhanok R.	30.08-26.09.78	5.7	25.0	—	—	—
Ushkovskoye L.	09.08-26.09.78	6.2	20.3	29.03-20.04.78	3.5	20.0
—“—	—	—	—	20.04-11.05.78	5.0	18.9
Azabach L. (station No. 2)	—	—	—	13-23.07.79	12.5	14.7
—“—	—	—	—	23.07-04.08.79	14.0	8.2
—“—	—	—	—	04.08-14.08.79	16.0	13.3
Old bed of Raduga R.	15-26.78	13.6	12.4	09-22.06.79	7.2	9.0
—“—	26.07-07.08.78	12.9	12.9	22.06-02.07.79	9.0	11.5
—“—	07-22.08.78	13.0	9.2	02-12.07.79	11.0	12.8
Nizovtsevo L.	27.07-13.08.79	15.0	11.8	12-23.07.79	12.5	10.2
Soldatskaya R.	07-29.07.78	17.9	17.5	—	—	—
—“—	11.08-17.10.77	9.2	18.7	—	—	—

On the whole, the rate of sclerite formation on the scales of juvenile sockeye in the Kamchatka R. watershed can be described by means of a parabolic equation (fig. 56). Sclerites take the longest to form in low-temperature waters. In waters with temperatures approximating the optimal ones for the sockeye (Brett et al., 1969), the rate of sclerite formation was the highest, but then it again decreased as the water temperature in the same bodies of water continued to rise. Fig. 56 clearly depicts three groups of dots which correspond to these situations. In each group of lakes (fig. 56), except in the case of above-optimal water temperatures, the rate of sclerite formation during the growing season was accepted as constant (Bugaev, 1981). In shallow, easily warmed up lakes and abandoned river channels of the Kamchatka R. watershed (with depths of 1-1.5 m) where above-optimal water temperatures are observed during certain periods, the young of the sockeye and other salmons are encountered in noticeably high numbers only until the period of high temperatures sets in. With the onset of this period and later, practically no immature salmons are encountered in them. The sclerite formation data calculated by us for Kulpik L. during the period of high temperatures (fig. 56) are based on scant material (7-10 specimens per sample).

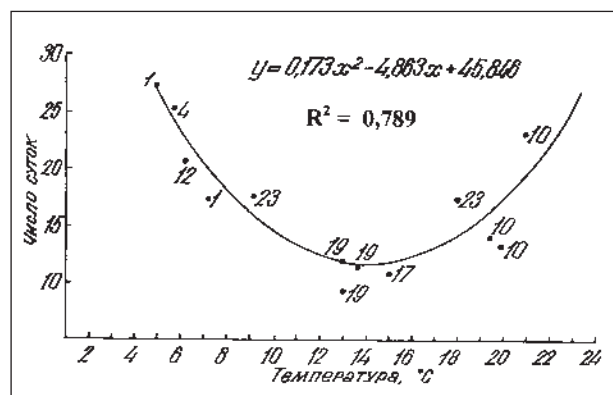


Fig. 56. Variation in the time of formation of one sclerite on the scales of underyearling sockeye, depending on the water temperatures in some foraging waters of the Kamchatka R. watershed. Y-axis – time of formation of one sclerite on the scales of fish, days; X-axis – mean water temperature during the investigation period, °C. Areas marked as in fig. 3.

The information obtained on the initiation dates of the first annulus in the sockeye of the Kamchatka R. watershed is presented in fig. 57. At first we noted the extensive time range of annulus formation, i.e. annuli form in February in spring-fed waters, and in June–beginning of July in lakes. The dates of formation of ZAS which reflect the seasonal rhythm of growth and are regarded as annuli can vary extensively (Nikolsky, 1974), and are correlated with both the winter–spring (Birman, 1968), and the spring–summer onset of growth (Chugunova, 1959) after its cessation at a certain time of the year.

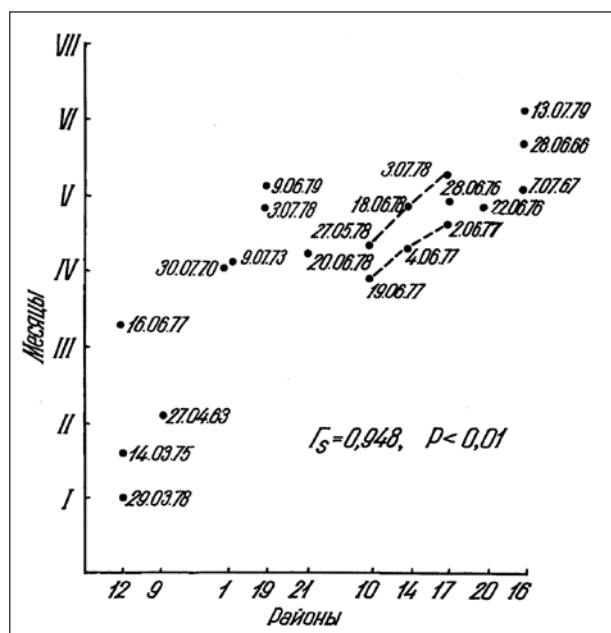


Fig. 57. Dates of formation of the first annulus on the scales of young sockeye in foraging waters of different types in the Kamchatka R. watershed. Y-axis – months; X-axis – sampling areas. Figures near dots denote – the dates on which juvenile sockeye were caught. Areas marked as in fig. 3.

The observed differences in the time of annulus formation on the scales of juvenile sockeye (fig. 57) appear to be related to an improvement in light conditions in the waters foraged by them. This improvement is determined by the winter–spring increase in daylight hours for bodies of water that do not freeze over, and by the time at which the ice cover breaks up for bodies of water that do freeze over (table 19). Due to the fact that the increase in daylight hours is gradual, the date given in table 19 for improved light conditions in non-freezing bodies of water is quite relative. On this date, there is three more hours of daylight (10 hours altogether) in comparison with the lowest values. This was based on the fact that we still observed the growth of young sockeye in the Kamchatka R. watershed with the day lasting this long (in the middle of October). Our later observations in the Kuril L. watershed (Bugaev, Dubynin, 1991) also showed that juvenile sockeye were still growing in October.

Spearman's coefficient of rank correlation between the time of improved light conditions in the bodies of water and the dates of annulus initiation in the juvenile sockeye of the same bodies of water (fig. 57, table 19) was very high, $r_s = 0.948$ ($P < 0.01$, $n = 19$). Let us examine the results obtained.

The time of breakup in the bodies of water that freeze over, which is associated with improved light conditions, is determined by the type of lake or channel, its geographic location in the Kamchatka R. watershed, and the hydrometeorological conditions of a particular year. The ice on the large and deep Azabach L. breaks up later (fig. 57, table 19) than on the smaller and shallower lakes Nizovtsevo and Kursin in the same area, and this affects the time of annulus formation on the scales of the fish. The abandoned river channel of the Kamchatka R., "Kulpik L.", and lakes Kurazhechnoye and Nizovtsevo are of similar depth (not more than several metres) and have a much smaller area than Azabach L.

Kulpik L. is located in the very centre of the Kamchatka R. valley, Kurazhechnoye L. is closer to its outskirts where the air temperature during the warm period of the year is somewhat lower, and Nizovtsevo L. is located in an even colder area (Vaskovsky, 1973; Bugaev, 1981). This is the order in which the ice cover on these lakes breaks up and the annuli on the scales of juvenile sockeye form (fig. 57, table 19). During the warmer years, the breakup occurs earlier, and this affects the time of annulus initiation. In 1978 for example, annuli formed later in the young sockeye from the above-mentioned three lakes, than in the warmer year of 1977 (Bugaev, 1981) (fig. 57, table 19).

By comparing the dates of annulus formation in juvenile sockeye caught in rivers, we can see (fig. 57, table 19) that, in 1978, annuli formed much earlier in the fish from the side channel of Melkoye L., and the old channel of the Raduga R., than in the sockeye of Nizovtsevo L., which is located in the same area. However, in the cases of river juvenile sockeye, we cannot be entirely certain that the landed fish had lived and overwintered in the area where they were caught, they may have come from other foraging waters of the watershed, and were caught during their seaward migration. The downstream migration of these juveniles from lakes to river channels prior to the formation of annuli on their scales can lead to earlier initiation of annuli due to the fact that rivers break up sooner than lakes. On the other hand, in rivers it is possible to catch juveniles that had migrated from lakes with annuli already formed, as for the juvenile sockeye caught in the Kamchatka R. near the village of Pushchino, we can say that the formation of annuli on their scales occurred within periods comparable with those of annulus formation in lakes. Since Kenuzhen L. (spawning and foraging grounds of the sockeye) is located several tens of kilometres up the Kamchatka R., it is quite possible that the landed fish were migrants from this lake.

Analyzing the dates of annulus formation in juvenile sockeye from the Ushkovskoye L. limnokrene, we noted (fig. 57) that, in 1977, the annulus formed much later than in 1975 and 1978. Knowing that the 1977 sample of juveniles was taken during the high-water period when the waters of the Kamchatka R. flood the limnokrene completely (Ostroumov, 1975b), we can say that the overwhelming majority of the sockeye caught by us were yearlings that had entered it to forage briefly, having overwintered in other bodies of water of the Kamchatka R. watershed where annuli are formed later.

When the data on the later resumption of growth after the winter lag in fish of older age groups was taken into account (Birman, 1968; Nikolsky, 1974), the established periods of formation of the first annulus on the scales of juvenile sockeye (fig. 57, table 19) could not be extrapolated to the formation of the second annulus. In 1979, we traced the formation of the annulus on the scales of individuals without a zone of adjacent sclerites and individuals with one ZAS in the sockeye of Azabach L. We found that the annuli in these two groups of Azabach L. juveniles were formed at practically the same time (Bugaev, 1981).

Table 19. Dates of improved light conditions and calculated dates of the formation of the annulus in sockeye scales in some plases of the Kamchatka R. watershed

Watershed	Year	Dates of improved light conditions	Dates of formation of the annular ring
Ice free:	1963	20.02	03.03
Nikolka R.	1975	20.02	19.02
Ushkovskoye L.	1978	20.02	01.02
—“—			
Freezing:			
Kamchatka R. near Pushchino village	1970	01.04*	01.05
—“—	1973	01.04*	03.05
Kulpik L.	1977	10.05	27.04
—“—	1978	20.05	11.05
Kurazhechnoye L.	1977	15.05	09.05
—“—	1978	25.05	27.05
Nizovtsevo L.	1976	01.06	28.05
—“—	1977	01.06	17.05
—“—	1978	05.06	08.06
Old side channel of Raduga R.	1978	20.05	25.05
—“—	1979	05.06	05.06
Azabach L.	1966	15.06*	20.06
—“—	1967	05.06	02.06
—“—	1979	20.06	05.07
Kursin L.	1976	10.06	26.05
Stream from Melkoye L.	1978	01.05*	08.05

*Indicated average dates of ice break up in watersheds.

According to our observations, the juvenile sockeye foraging in the Azabach L. watershed develop a supplementary ZAS at the end of summer or in autumn; this supplementary ZAS does not reflect the seasonal cessation of growth. An increase in the percentage of fish with ZAS at the end of August–September is evidence of the formation of ZAS at this time (fig. 58). Therefore, it is premature to regard all fish with two ZAS as two-year-olds in Azabach L. Due to the rare occurrence of fish with two ZAS in the catches, we still do not have any comparable data as to when the first and second annuli appear in sockeye from other areas of the Kamchatka R. watershed (Bugaev, 1981).

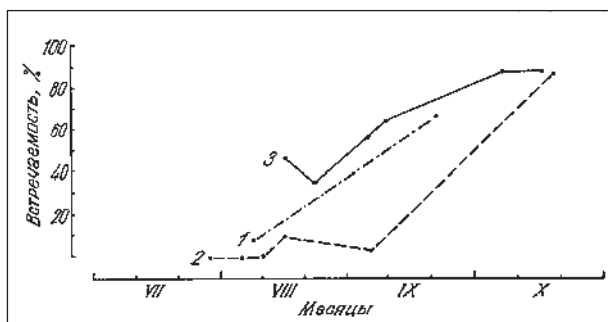


Fig. 58. Frequency of occurrence of underyearling sockeye with a supplementary ZAS on the scales in the Azabach L. watershed (based on 1965, 1976-1979 material). Y-axis – frequency of occurrence, %; X-axis – months.
 1 – side channel of Azabach L. (mouth), 11 km from its outlet (n=56 specimens);
 2 – side channel of Azabach L., 2 km from its outlet (n=228);
 3 – the water area of Azabach L. (n=313).

A comparison of material collected during the breakup of lakes indicates that annuli are usually present on fish scales in small and shallow bodies of water with average depths of 1-3 m (Nizovtsevo L., old channel of the Raduga R.), whereas they begin to form in the majority of individuals 10-15 days after breakup in large and deep bodies of water with average depths of up to 20 m (Azabach L.). The fact that annuli form on the scales of sockeye from large and deep lakes after their breakup has been known for a long time (Koo, 1962; Krogius, 1970; Marshall, 1978), and

has been applied to juvenile sockeye inhabiting different types of bodies of water (Krogius, 1970). For the small and shallow Etamynk L. with shoals (Kuril L. watershed), we already know of a case where an annulus was found on the scales of two-year-old sockeye at the time of breakup (Bugaev, 1976). This also supports our point of view that annuli form earlier in fish from small bodies of water after their breakup, than in fish from large and deeper waters where the growth of sockeye does not resume for a certain period of time. On the basis of F. V. Krogius concept (1970) that the annuli on the scales of juvenile sockeye in the Kamchatka R. watershed form after the ice breaks up, it was suggested that in small and shallow bodies of water without any significant inflow of ground waters which warm up more quickly, the activation of the metabolic processes and the onset of new growth following its cessation begins earlier than in fish from larger and deeper lakes which are characterized by greater inertia of the temperature processes, seasonal fluctuations in biomass and the abundance of food organisms. However, as our study has shown, the observed differences in the periods of annulus formation should also be correlated to the improvement in light conditions in the waters where the fish feed and grow.

For fish, light can serve as a stimulant or a depressant of growth, depending on the ecological characteristics of the species (Mina, Klevezal, 1976). Young sockeye grow better as the day becomes longer (Bilton, 1972). The earliest resumption of growth is noted in the Ushkovskoye L. limnokrene where the part closest to the spring does not freeze over in winter, and also in the "Nikolka R." rheokrene. The juvenile fish inhabiting these bodies of water have better temperature conditions than those living under the ice cover during this period, the daylight period increases first of all for the fish inhabiting spring-fed bodies of water that do not freeze over, and then for the fish of frozen-over waters only after breakup.

The daylight period begins to increase in January, which can activate the growth process in the young. In fish, the growth rate slows down in autumn and accelerates in spring, though the water temperature during the autumn months is the same as in spring; therefore, the change in the length of the daylight period regulates the growth rhythm (Mina, Klevezal, 1976). The presence of an ice cover is an obstacle which, for a certain time, masks the increase in the daylight period.

Since the breakup of slow-flowing rivers and lakes is a fairly long process, we believe that the open reaches and washed-out holes that form in the ice can noticeably improve the light conditions in small and shallow bodies of water, and virtually have no effect on the light conditions in large and deep ones. The breakup of certain areas in small and shallow bodies of water results in some local increase in water temperature due to warm-up, which is definitely conducive to the resumption of growth in the young fish. Furthermore, a high percentage of the young can migrate to the open parts in small bodies of water, since the total population in the latter is much smaller than the number of juveniles foraging in large lakes. This is probably the explanation for the presence of annuli on the scales of young sockeye in small bodies of water at the time of their breakup.

It is not excluded that the resumption of juvenile growth in different types of foraging waters coincides with a significant improvement in feeding conditions. For example, large mature Cyclopoida, a preferred food of juvenile sockeye, appear in Azabach L. in June (Kurenkov, 1972; Belousova, 1974). In spring-fed bodies of water, young sockeye feed mainly on benthic organisms (Kurenkov, 1964; Simonovs, 1972a; Bugaev, Nikolayeva, 1989). Benthic organisms are most abundant in slow-flowing spring-fed bodies of water and the upper reaches of rivers, their biomass being quite substantial as early as January and even higher in early spring (Levanidova, Kokhmenko, 1970). The combination of good light and feeding conditions, as well as the stability of temperature conditions, is probably responsible for the earliest resumption of growth in juvenile sockeye from spring-fed bodies of water in the Kamchatka R. watershed.

A similar comparative study of the tendencies of formation of ZAS on fish scales, which reflect the seasonal rhythm of growth (of annuli), can also be carried out for the sockeye of other bodies of water and for other species of Pacific salmon.

For example, in a one-time sample of two-year-old sockeye, taken on 19-20 June 1974 in lakes Kuril (a large and deep lake) and Etamynk (small and shallow), we noted that the second annulus had just formed in the individuals from Etamynk L. (fig. 59), while an increment of 2-3 sclerites was observed after the annulus in the fish from Kuril L. (Bugaev, 1976). In our

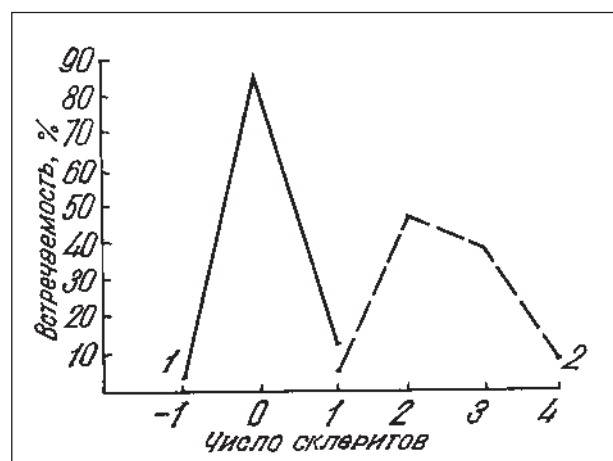


Fig. 59. Number of sclerites of the "new" growth in the marginal zone of the scales in two-year-old sockeye in a one-time sample (19-20 June 1974) taken in the watershed of Kuril L., and Etamynk L.

Y-axis – frequency of occurrence, %; X-axis – number of sclerites.

"-1" – without an annulus, "0" – newly formed annulus.

1 – Etamynk L. (n=49); 2 – Kuril L. (n=50).

opinion, this may have been due to the fact that, in 1974, the ice on Etamynk L. was just breaking up when the sample was being taken, while Kuril L. did not freeze over that year, which may have caused the earlier resumption of juvenile growth and the formation of annuli. This assumption is supported by the results of recalculations of the growth rate of downstream-migrant sockeye of Kuril L., in which the increments of the marginal zone of the scales during the years when Kuril L. does not freeze over are greater than in the years when it does (Selifonov, 1970a).

Our comparison of the timing of annulus formation in juvenile sockeye with the improvement of light conditions in the waters foraged by them has revealed certain perspectives on solving the practical tasks associated with more accurate definition of age concepts for some species of Pacific salmon, and that further comprehensive research in this direction can be of great theoretical interest.

In conclusion, a few words about the photographs of scales from underyearling and yearling sockeye from the Kamchatka R. watershed in order to illustrate the formation of annual and supplementary ZAS.

As seen in fig. 60, yearling sockeye from the non-freezing Ushkovskoye L. already have an increment of one sclerite (1) following the annulus at the end of March; in later samples (April and May), this sclerite is larger (2, 3), which proves that juveniles grow in this body of water in spring.

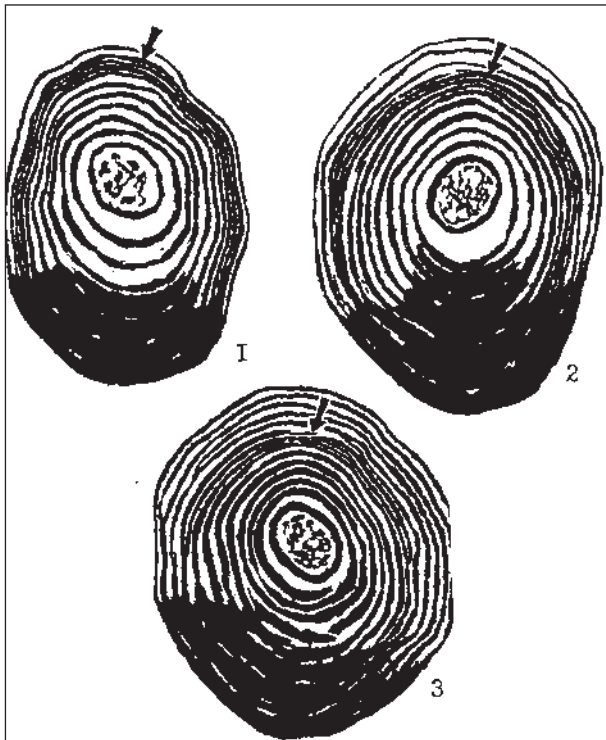


Fig. 60. Structure of scales in yearling sockeye from Ushkovskoye L., caught after resumption of the growing season.

1 – 29 March 1978, AC=86 mm; 2 – 20 April 1978, AC=96 mm; 3 – 11 May 1978, AC=99 mm. Arrows mark ZAS – annuli.

Fig. 61 depicts the scales of an underyearling caught in Kulpik L. (an abandoned river channel of the Kamchatka R.) in August without ZAS on its scales, as well as the scales of a yearling of the same generation, caught the following year in the second half of June after the annulus had formed.

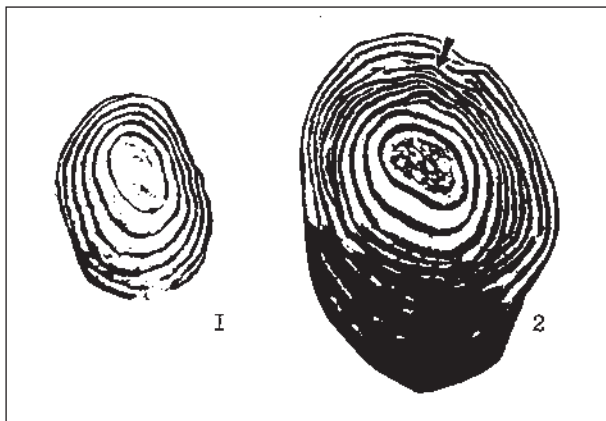


Fig. 61. Structure of scales in underyearling and yearling sockeye from Kulpik L.

1 – 20 August 1976, AC=59 mm, age 0+; 2 – 19 June 1977, AC=73 mm, age 1+. Arrow marks ZAC – annulus.

Fig. 62 depicts the scales of underyearling sockeye from Kurazhechnoye L, without a supplementary ZAS (1) and with one (2), at the beginning of September, as well as the scales of yearlings of the same generation the following year, in which an annulus had formed at the beginning of June (3, 4).

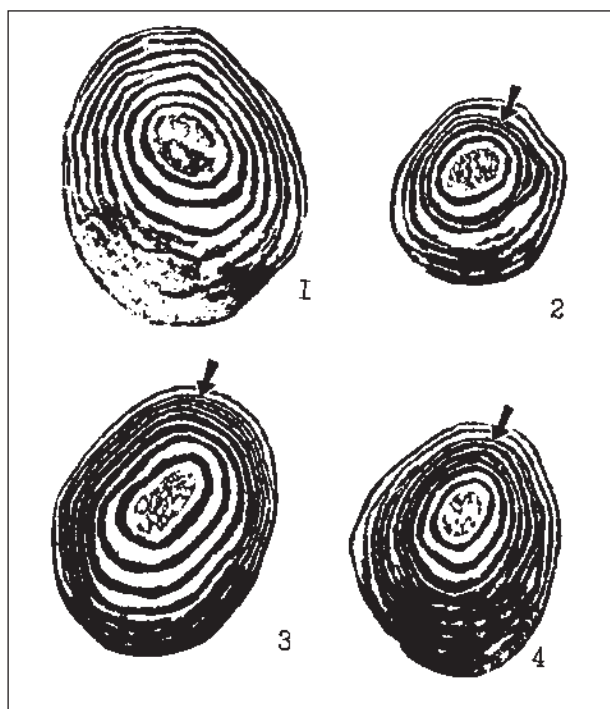


Fig. 62. Structure of scales in underyearling and yearling sockeye from Kurazhechnoye L.

1 – 2 September 1976, AC = 63 mm, age 0+;

2 – 2 September 1976, AC = 58 mm, age 0+, arrow marks supplementary ZAS;

3 – 4 June 1977, AC = 73 mm, age 1+, arrow marks ZAS – annulus;

4 – 4 June 1977, AC = 69 mm, age 1+, arrow marks ZAS – annulus.

The underyearling sockeye (fig. 63) caught in the lower reaches of the Yelovka R. at the end of June (1) and in the Kamchatka R. estuary in the second half of August (2) had no supplementary ZAS on their scales.

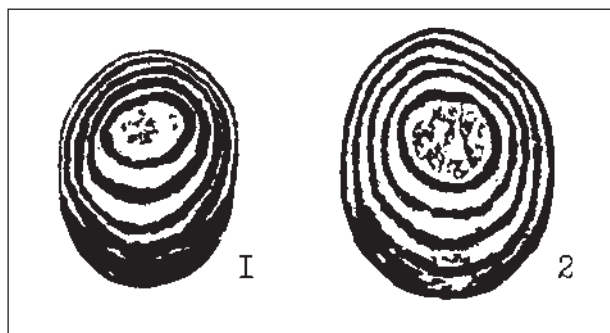


Fig. 63. Structure of scales in underyearling sockeye from the Yelovka R. and the mouth of the Kamchatka R.

1 – Yelovka R. (lower reaches), 25 July 1978, AC=57 mm;

2 – mouth of the Kamchatka R., 20 August 1979, AC=60 mm.

As we can see from fig. 64, there was no supplementary ZAS on the scales of a group “E” underyearling (Section 8.1) migrating to Azabach L. from the tributaries of the lower Kamchatka R. and caught in the Azabachye side channel at the beginning of September (1), but there was one in an underyearling caught at the beginning of October (2). An underyearling caught in Azabach L. in the middle of August had no supplementary ZAS on its scales (3), but one caught at the beginning of October did (4). The underyearling caught in August may have belonged either to stock “A” or group “E”, but the one caught in October definitely belonged to group “E”. A supplementary ZAS does not form in underyearlings of stock “A”.

Fig. 65 illustrates the formation of annual ZAS (annuli) on the scales of stock “A” yearlings caught in Azabach L. during the years of good feeding conditions (1, 2 – the juvenile fish are large) and poor feeding conditions (3, 4 – the juvenile fish are small) in the lake.

8.3.3. Compensatory growth in sockeye smolts of the Kamchatka R.

As shown in the previous section in which we examined the periods of formation of annuli in juvenile sockeye of the Kamchatka R. watershed, it takes an average 20.7 days for one sclerite to form in age 0+ and 1+ juveniles in cold spring-fed bodies of water, and 12.3 days in warmer lakes and abandoned river channels.

However, further investigations in the Kamchatka R. watershed have shown that the above data does not cover all the differences observed in the duration of sclerite formation in the sockeye of this body of water. For example, we noted a very high rate of sclerite formation in the sockeye smolts migrating from Azabach L. during the year of seaward migration, and because of this the sclerites were more widely spaced.

Considering the high positive correlation between body size and the structural characteristics of the scales in the sockeye (Clutter, Whitesel. 1956; Bugaev et al., 1989), one can assume that the growth rate increases drastically during this period. One can also expect an increase in the rate of sclerite formation in juvenile sockeye of the upper reaches of the Kamchatka R. during the year of seaward migration in comparison with the rate of their formation prior to downstream migration, as

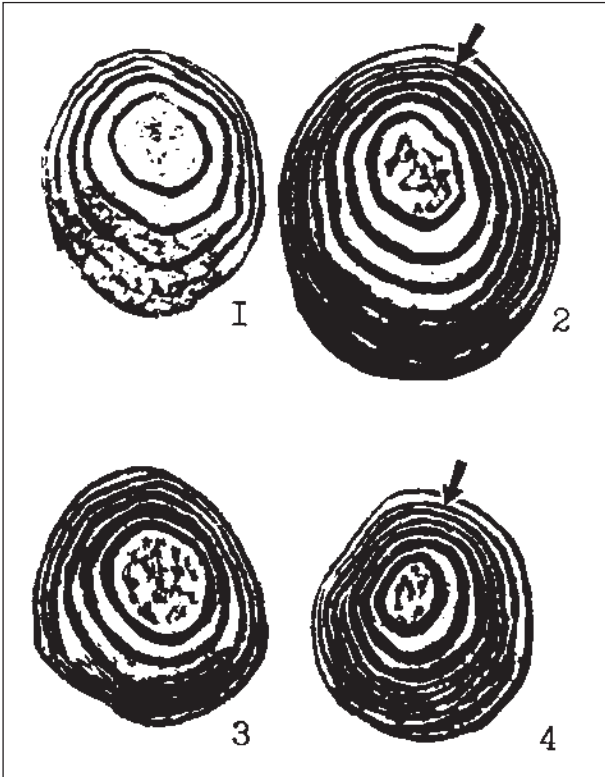


Fig. 64. Structure of scales in underyearling sockeye from the Azabach L. watershed.
 1 – side channel of Azabach L. near Dyakonovsky klyuch, 6 September 1979, AC=53 mm;
 2 – side channel of Azabach L. near Dyakonovsky klyuch, 16 October 1979, AC=63 mm, arrow marks supplementary ZAS;
 3 – Azabach L. (station No. 2), 15 August 1979, AC=61 mm;
 4 – Azabach L. (station No. 2), 6 October 1979, AC=64 mm, arrow marks supplementary ZAS.

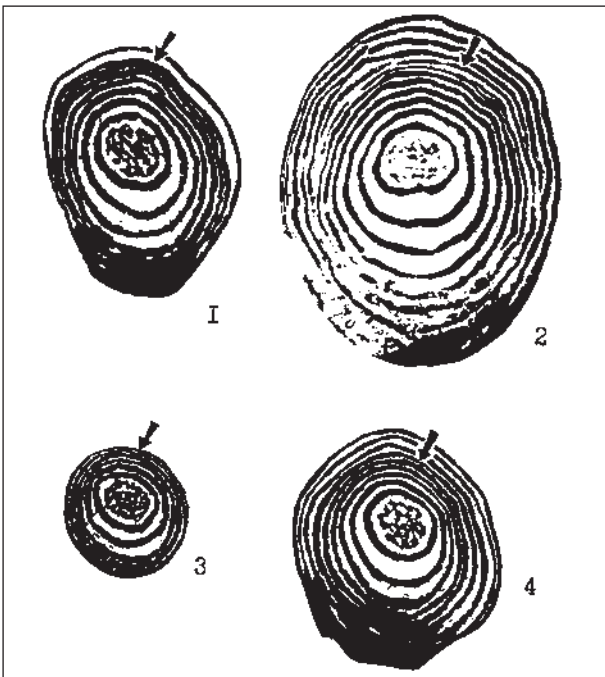


Fig. 65. Structure of scales in yearling sockeye of stock "A", caught in Azabach L. (station No. 2) after or at the time they resumed their growth after favourable (1, 2) and unfavourable (3, 4) foraging conditions.
 1 – 13 July 1979, AC=70 mm; 2 – 4 August 1979, AC=77 mm; 3 – 16 July 1987, AC=55 mm; 4 – 2 August 1987, AC=68 mm. Arrows mark ZAS – annuli.

a result, increments appear on the scales over short periods of time, and their origin is difficult to explain on the basis of the above-described concepts of scale growth.

As we studied the rate of sclerite formation on the scales of young sockeye caught in Azabach L., we noticed that it was higher in individuals with two ZAS, than in those with one ZAS (table 20) (Bugaev, 1984b, 1984c).

As we have already shown (Bugaev, 1981a. section 8.1), two forms of sockeye forage in Azabach L., stock "A" and group "E". Our analysis of the rate of sclerite formation in smolts of stock "A" and group "E" did not show any significant differences in the time it took for sclerites to form during the year of downstream migration in stock "A" and group "E" individuals, therefore, the results have been combined in table 20.

Measurement of the distance between the developing sclerites showed that it was greater in fish with one ZAS (having the highest rate of sclerite formation) than in fish with two ZAS (fig. 66). Due to the rapid downstream migration of young sockeye with two ZAS in 1980-1981, we were able to establish this fact only in 1979 material (fig. 67.3-4). During other years in Azabach L., we also encountered juvenile sockeye with more widely spaced sclerites in the marginal zone of the scales, which can be clearly seen in fig. 68.1.

Table 20. Variation in the time of formation of one sclerite on the scales of young sockeye salmon in the Azabach L. watershed in 1977-1981, days

Area catch	Data, year	Speed of sclerite formation, days			
		One ZAS	Number of fish*	Two ZAS	Number of fish*
Outlet of Azabach L. -- -- -- -- -- --	24.06-04.07.79	–	–	No growth	58 (77)
	04.07-13.07.79	–	–	12.2**	77 (68)
	13.07-23.07.79	–	–	6.6	68 (53)
	23.07-04.08.79	–	–	5.7	53 (36)
	23.06-03.07.80	–	–	12.8**	75 (79)
	03.07-12.07.80	–	–	5.9	79 (34)
Azabach L. (station No. 2) -- -- -- --	13.07-23.07.79	14.7	25 (39)	6.8	9 (27)
	23.07-04.08.79	8.2	39 (40)	6.7	27 (30)
	04.08-14.08.79	13.3	40 (14)	–	–
	23.06-03.07.80	–	–	No growth	29 (45)
	03.07-12.07.80	–	–	6.2	45 (27)
Azabach L. (station No. 3) -- -- -- -- --	23.06-03.07.80	–	–	6.7	24 (40)
	3.07-12.07.80	–	–	No growth	40 (13)
	12.07-20.07.80	11.9	15 (9)	6.2	13 (21)
	17.06-22.06.81	13.2	18 (25)	–	–
	22.06-04.07.81	12.1	25 (18)	–	–
	Total average	–	12.2	–	6.3

*Number before brackets – number of examples in previous sample, within brackets – in subsequent sample. **Data reliability was lower since growth had just recommenced and samples could include large quantities of fish in which growth had not yet begun. With regard to data differing significantly from the norm it was not included in the calculation of the average speed of sclerite formation.

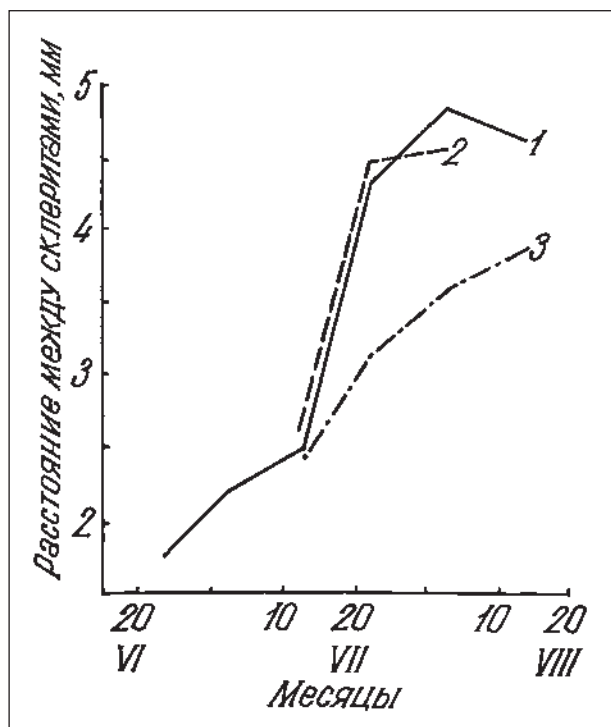


Fig. 66. Variation in the distance between sclerites on the scales of young sockeye in the Azabach L. watershed in 1979 (x150 magnification). Y-axis – distance between sclerites, mm; X-axis – months. 1 – outfall of side channel of Azabach L. (2 ZAS on scales); 2 – Azabach L., station No. 2 (2 ZAS on scales); 3 – Azabach L., station No. 2 (1 ZAS on scales).

Fish with a large increment of sclerites in the marginal zone of the scales, similar to that depicted in fig. 68.1, represent that part of the young which spends a longer time in the lake and is encountered in small numbers. The scale structure of juveniles from catches is evidence of this. For example, in 1979, when the young of the sockeye spent a long time in the lake, the increment in the marginal zone averaged approximately 5 sclerites by the end of downstream migration on August 14th. During warmer years, the increments are even smaller due to rapid downstream migration.



Fig. 67. Structure of scales in sockeye smolts of stock "A" and group "E", migrating from Azabach L. during different period of downstream migration and characterized by the presence of "compensatory growth" (caught at outfall of Azabach L. side channel).
 1 – stock "A", 13 July 1979, AC=104 mm, age 2+, arrows mark ZAS – annuli;
 2 – group "E", 13 July 1979, AC=107 mm, age 1+, arrows mark ZAS (first arrow – supplementary ZAS, second arrow – annulus);
 3 – stock "A", 4 Aug 1979, AC=108 mm, age 2+, arrows mark ZAS – annuli;
 4 – group "E", 4 Aug 1979, AC=112 mm, age 1+, arrows mark ZAS (first arrow – supplementary ZAS, second arrow – annulus).

As indicated in table 20, the rate of sclerite formation in the sockeye smolts of stock "A" and group "E" (with two ZAS on their scales) during the year of seaward migration averaged 6.3 days, though it took 12.2 days for one sclerite to form in the yearlings of stock "A". We have reason to believe that the rate of sclerite formation was the same (12.2 days) in the juvenile sockeye of group "E" during the first year of growth following migration to Azabach L. Evidence of this are the similar distances between sclerites in the first two zones of scale growth in the young of stock "A" and group "E".

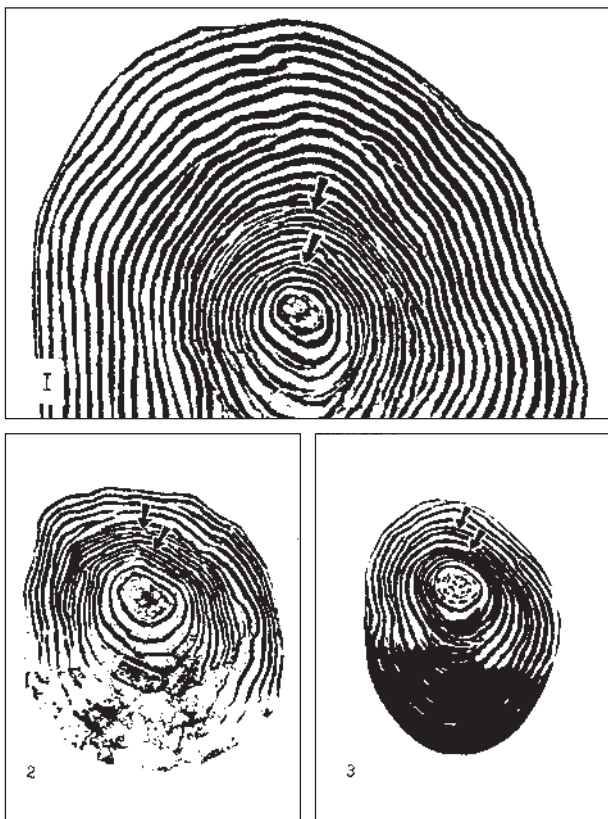


Fig. 68. Structure of scales in juvenile sockeye in some areas of the Kamchatka R. watershed, characterized by the presence of "compensatory growth".
 1 – Azabach L., group "E", 9 September 1976, AC=159 mm, age 1+, arrows mark ZAS (first arrow – supplementary ZAS, second arrow – annulus);
 2 – Ushkovskoye L., 16 June 1977, AC=106 mm, age 1+, arrows mark ZAS (first arrow – annulus, second arrow – supplementary ZAS);
 3 – Kamchatka R. (below Shapina R.), 31 July 1977, AC=79 mm, age 1+, arrows mark ZAS (first arrow – annulus, second arrow – supplementary ZAS).

We do not have any first-hand data on the rate of sclerite formation in yearlings of stock "A" and underyearlings of group "E" – after their migration to the lake. The absence of data for stock "A" individuals is due to their infrequent occurrence in catches, and in the case of group "E" to the fact that the migration of the underyearlings of this group to the lake lasts several months, and the growth of young sockeye during the first year of life is extremely variable.

In connection with the fact that the accelerated growth of scales due to the rapid formation of sclerites and wide spaces between them is typically observed during the year that the young migrate downstream to the sea, and considering the strong correlation between the scale characteristics and body length (Clutter, Whitesel, 1956; Bugaev et al., 1989; section 8.7.1). We can say that the growth rate of juvenile sock-eye salmon foraging in Azabach L. at this time is higher than the growth rate for the whole period preceding it.

The size of sockeye smolts from Azabach L. varies throughout the season of downstream migration. In 1979, for example, the mean length of individuals with two ZAS on their scales was 104 mm on June 24th, 95 mm on July 4th, 98 mm on July 13th, 105 mm on July 23rd and 110 mm on August 4th. The total number of sclerites in the first two zones of scale growth in these young fish averaged 16.20, 15.35, 15.00, 13.43 and 12.93 respectively. This fact indicates that young fish of a larger size at the beginning of the growing season are the first to migrate downstream. The size of the juveniles that migrated downstream from Azabach L. on 24 June–4 July 1989, for the most part before resuming their growth, showed the usual rate of growth the year before. Judging by the scale structure, the young fish which had been smaller than the downstream migrants before resuming their growth and migrated between 13 July–4 August 1979 began to grow again and, before migrating downstream (during the year of seaward migration), grew at a higher rate than in the preceding year. For instance, while it took 12.2 days for one sclerite to form in juveniles the year preceding the downstream migration, it took only 6.3 days in the year of the seaward migration (table 20); at the same time, the sclerites were 17–35 % more widely spaced in the year of the seaward migration than in the year before it (fig. 66). If the late-running juveniles had grown at the same rate in the year of the seaward migration as in the preceding year (years), the sea downstream migrants would definitely have been smaller on the dates indicated.

The situation arises where the juveniles of the later seaward migration, due to a higher growth rate, catch up in length to the larger [earlier] downstream migrants growing at sea during this period. The growth of individuals that are in all events involved in the situation where the differences in the size of individuals from the same age group diminish over a certain period in the process of growth can be classified as compensatory growth (Mina, Klevezal, 1976).

M. V. Mina and G. A. Klevezal (1976) group all the cases of compensatory growth in animals into the following two categories: 1 – growth which proceeds at a much higher rate than is typical (on the average) for “normally” developing individuals of a particular age, but is characteristic of “normally” developing individuals of a particular size (weight); 2 – true compensatory growth which proceeds at a rate exceeding not only the average growth of “normally” developing individuals of a particular age, but also the average growth rate of “normally” developing individuals of a particular size (weight).

D. F. Zamakhayev (1967) has reviewed in detail the research done in the field of compensatory growth. On the basis of this author’s data, it has been shown (Mina, Klevezal, 1976) that we now have some grounds for assuming that true compensatory growth does exist in fish, though it may manifest itself in various degrees in different species and in individuals of the same species at different stages of ontogenesis.

This study has shown that the largest juvenile sockeye migrate downstream to the sea mostly before resuming their growth or immediately after this, while the growth rate of smaller juveniles (judging by the scale structure) exceeds the growth rate of the large smolts the year before, i.e., the average growth rate of “normally” developing individuals of a larger size, which is the main indication of true compensatory growth (Mina, Klevezal, 1976).

The presence of compensation growth in the year of the seaward migration can also be anticipated in the young from other bodies of water in the Kamchatka R. watershed. Based on our observations, a scale structure similar to the one depicted in fig. 68.2-3 is typical of the freshwater (central) part of the scales of late adult sockeye from the upper reaches of the Kamchatka R. the presence of widely spaced sclerites in the marginal zone of the freshwater part of the scale in arabach sockeye (a special form of late sockeye of the Kamchatka R. watershed) was noted by A. G. Ostroumov back in 1965. According to our classification, the arabach sockeye belongs to group “V” (section 8.1). We have established that the zone with more closely spaced sclerites corresponds to the period of growth on the spawning grounds or in the tributaries of the upper reaches of the Kamchatka R. where the water temperature rarely exceeds 7–9°C because of a high discharge of ground water. Juveniles with a scale structure as in fig. 68.2-3 were caught after downstream migration from the spawning grounds in waters with a temperature of 14–16°C. A temperature of 16°C is considered to be the optimal one for the sockeye (Brett et al., 1969). Considering the short period spent by these young fish at the migration sites, it is unlikely that we will get any data on the rate of sclerite formation in them for the period of their seaward migration.

Nevertheless, some circumstantial data point to the fact that the rate of sclerite formation in the young of the late sockeye of the upper Kamchatka R. watershed for the year of the seaward migration can be significantly higher than the rate of sclerite formation prior to the downstream migration from the spawning area.

As we have already shown, it takes 20.7 days for one sclerite to form in young fish foraging in slow-flowing spring-fed bodies of water which do not freeze over, and these fish resume their growth during the winter–spring period. Taking into account the early resumption of growth, the first ZAS (from the centre) should probably be regarded as the annulus, and the second ZAS as the supplementary structure which apparently forms after downstream migration from the spawning grounds (fig. 68.2-3). Ecological changes can lead to the formation of supplementary structures on the scales (Nikolsky, 1974; Bugaev, 1976, 1981a).

As our investigations have shown, the formation of a supplementary ZAS on the scales of young sockeye in the vicinity of the spawning grounds is not a typical occurrence. If we regard the first ZAS as an annulus, knowing that annuli in young sockeye from spring-fed bodies of water are for the most part initiated not before the beginning of February (usually later) and taking into account the lower rate of sclerite formation on the scales of young sockeye from spring-fed bodies of water,

we should conclude that, at the time the fish were caught, there could not have been such a large increment of sclerites after the annulus with the low rate of sclerite formation (fig. 68.2-3). Proceeding from this, we can say that the young of the late sockeye of the upper Kamchatka R. watershed have a higher rate of sclerite formation after downstream migration from the breeding areas, than during the foraging period in the breeding areas.

Due to the lack of firsthand data on the growth and scale structure of late sockeye migrating downstream from the upper part of the Kamchatka R. watershed during the year of the seaward migration, we can, at this stage of our study, be certain of only the first type of compensation growth (Mina, Klevezal, 1976) for young sockeye of this grouping.

Let us now examine the factors which could have lead to the occurrence of compensation growth in young sockeye of the Kamchatka R. watershed during the year of the seaward migration.

One of the causes of compensatory growth in the young of late sockeye foraging in the areas of the spawning grounds during the first year of life may be the migration of young individuals from the upper reaches to the middle reaches of the Kamchatka R. where the water temperature in the river and floodplain lakes is higher. The removal of a stress factor, in this case a low temperature, can in some cases induce compensation growth (Mina, Klevezal, 1976). However, in young sockeye from Azabach L., a seasonal improvement in temperature conditions was observed for all of the young fish simultaneously (yearlings of stock "A", 2-year-old smolts of stock "A", yearling smolts of group "E"), but compensatory growth was noted only in smolts. If we assume that the change in growth rate during the seaward migration of the young depends on both hereditary and external (environmental) factors, then it is the hold-up of the young fish in the lake for a longer period than they were "programmed" to remain in fresh water which effects the hereditary component of the growth change program. This apparently holds true for the late sockeye of the upper reaches of the Kamchatka R. as well. This interpretation is not inconsistent with Tanner's hypothesis regarding the mechanism of compensation growth regulation in animals (Tanner, 1963).

Compensatory growth in sockeye smolts of the Kamchatka R. is accompanied by the formation of sclerites spaced at a distance that is intermediate between the distances observed in typical "freshwater" and typical "sea" sclerites. On the basis of this fact, we can assume that the "estuarine" (marine transitional) zones observed by a number of researchers (Birman, 1968; Zorbidi, 1974; Bugaev, 1978a) in Pacific salmon with a prolonged freshwater period can, in many cases, be of "freshwater" origin, and their formation may be caused by compensatory growth in fresh water during the year of seaward migration, as research has shown (Bugaev, 1984b), estuarine zones are most frequently encountered in late sockeye from the upper reaches of the Kamchatka R., the young of which spend their first year in the vicinity of the spawning grounds (Kamchatka R. near the village of Pushchino, Andrianovka R., Kirganik R., Nikolka R. spring), though they may not be encountered at all during certain years; these zones are less commonly observed in fish of the Yelovka R., and Azabach L.

It is interesting to note that the percentage of fish with an "estuarine" zone on the scales is higher in the late sockeye of Azabach L., than in the early sockeye. It can be assumed that these differences are determined by the smaller size of the juveniles of the late sockeye in the lake (due to the later spawning of its adults in comparison with the early sockeye, which in turn affects the time of its emergence from the ground). Compensatory growth is more characteristic of relatively small fish (Mina, Klevezal, 1976).

Compensatory growth should apparently be taken into account when studying the structure of the scales in the dwarf (residual) and freshwater (landlocked) forms of the sockeye and coho salmon of some bodies of water. In determining the age of these salmon with S. I. Kurenkov, we repeatedly noted that the sclerites were more widely spaced in the marginal zone of the scales, and found it difficult to determine the distance between them. S. A. Gorshkov (1977) noted similar structures on the scales of the freshwater forms of the Salmonidae.

Continued study of the conditions that lead to compensatory growth in Pacific salmon is extremely important both from the theoretical, and from the practical point of view, as the successful solution of this problem will enable us to apply our conclusions in fish management, as well as in the study of fish growth in natural populations. The latter is particularly important when determining the age of fish, for compensatory growth inevitably leads to the formation of more complex elements of identification structures.

8.3.4. Seasonal rhythms of growth in young sockeye of Azabach L. (Kamchatka R.) and Kuril L. (Ozernaya R.)

The onset and duration of the growing season in young sockeye were determined on the basis of scale structure by a number of researchers (Koo, 1962; Foerste, 1968; Marshall, 1978; Bugaev, 1981, 1983, 1984b, 1986; Bugaev, Bazarkin, 1987; Bugaev, Dubynin, 1991).

Bugaev (1981) noted that the time at which the first annulus forms (with growth resumption) in the young sockeye of the Kamchatka R. watershed – was correlated with the improvement of light conditions. In bodies of water that do not freeze over, the resumption of growth is timed to the winter–spring increase in the light period, and in waters that freeze over to the time of breakup. Depending on the type of body of water, its geographical location and the hydrometeorological conditions of a particular year, the dates on which the first annulus is formed may fall anywhere between the beginning of February (in slow-flowing spring-fed creeks or abandoned river channels) and the beginning of July (in lakes) (fig. 57). In small and shallow bodies of water (up to 3-5 m deep) and in rivers, annuli are usually noted on the scales of sockeye at the time of breakup, while in large and deep lakes (up to 30 m deep) the initiation of annuli in the majority of individuals begins 10-15 days after breakup.

There is no lake in the Kamchatka R. watershed that is similar to Kuril L. in its limnological characteristics. The largest lake in the Kamchatka R. watershed, Azabach L., freezes over annually; its maximum depth is 33 m, and its average depth

is 17 m (Krokhin, 1972). The maximum depth in Kuril L. is 316 m, and its average depth is 195 m (Nikolayev, Nikolayeva, 1991), and this lake does not freeze over every year.

Despite the fact that the growth of the young sockeye of Kuril L. has been studied quite thoroughly at different times (Selifonov, 1970, 1970a, 1974; Dubynin, 1986; Dubynin, Bugaev, 1988; Bugaev et al., 1989), the question concerning the length of their growing season in this body of water is still debatable, and the time of annulus formation still has to be determined. We also do not know when exactly the growing season for young sockeye of the Kamchatka R. watershed comes to an end.

As mentioned earlier (section 8.1), Azabach L. is the foraging ground of not only the juvenile sockeye of the stock that spawns directly in the watershed of this lake (stock "A"), but also the juvenile sockeye of stocks that spawn in the tributaries of the lower Kamchatka R. (group "E"), the offspring of these stocks migrate as underyearlings to forage in Azabach L. where they usually spend one winter and then migrate downstream to the sea at the age of 1+. Individuals of group "E" usually more numerous than those of stock "A". Based on our concepts (Bugaev, 1983a), most of the juveniles of stock "A" usually migrate downstream to the sea at the age of 2+. We also believe that there are periodic fluctuations in the abundance and prevalence of either age 1+ or 2+ individuals in the downstream migration of stock "A" sockeye smolts during different years (Kononov, 1980; Ostrovsky, 1987). M. Yu. Kovalyov (1989, 1990) has confirmed our data on the downstream migration of stock "A" sockeye as two-year-olds.

We should note that, after migration to Azabach L., underyearling sockeye of group "E" develop a ZAS on their scales; this is not an annulus, for the ZAS that form on the scales of fish during the growing period as a result of changes in habitat or other factors are considered to be supplementary ones (Nikolsky, 1974), as a result of the formation of a supplementary ZAS, yearling smolts of group "E" which migrate from Azabach L. together with two-year-olds of stock "A" are very similar to the latter, which makes identification of them a real problem.

The situation is much simpler when studying the freshwater period of Kuril L. and Azabach L. juvenile sockeye, since virtually only the juvenile sockeye of this stock forage here. The presence of juveniles from Etamynk L. in the Kuril L. watershed, the smolts of which migrate via Kuril L. (Bugaev, 1976), can be disregarded because of their low numbers. From Kuril L., the young of the sockeye migrate downstream to the sea mainly at the age of 2+. A small part of this group (an average 9.1 %) is made up of age 3+ individuals. The downstream migrants also include yearlings (Selifonov, 1970, 1970a). Shortly after the fertilization of Kuril L., the percentage of yearlings increased considerably, and the number of two- and three-year-olds decreased in the downstream migration (Dubynin, Bugaev, 1988).

In connection with the observed significant changes in smolt size (Dubynin, Bugaev, 1988; see section 8.4), we began to ponder the causes of the interannual differences in the size of the fish during each season of growth.

At the present time, we can confidently say that, throughout the growing season, the rate of sclerite formation in sockeye from some bodies of water is more stable than the fluctuation in the distance between the sclerites (Koo, 1962; Bugaev, 1981, 1983c, 1984b). Some researchers believe that the difference in the number of sclerites (the size) in juvenile sockeye from various bodies of water during different years of growth is due to the difference in the length of the growing season, presuming that the timing of both the onset and the end of the growing season is variable (Goodlad et al., 1974). However, we should mention that these researchers did not conduct firsthand observations on the seasonal growth of juvenile sockeye from the beginning to the end of it, but rather based their conclusions on the periods of the downstream migration of underyearlings from the spawning grounds to the lake, and on the number of sclerites present in the growth zones of the adult fish (Goodlad et al., 1974).

Analysis of the number of sclerites in the marginal zone of the scales in sockeye smolts from lakes Kuril and Azabach over a number of years during the year of the seaward migration has shown (fig. 69) that this number increases in the Azabach L. smolts of the later run, but no such correlation is observed in the smolts of Kuril L.

At the same time, the increase in the number of sclerites in the smolts from Kuril L. was often greater in the years when the lake did not freeze over (1982, 1984), than in the years when it did (1979, 1985, 1987). However, the presence of an ice cover is not the main factor affecting the number of new sclerites in smolts, for despite the fact that the lake did freeze over in 1980, the increase in their number that year was the highest (fig. 69). Earlier, M. M. Selifonov (1970a) noted a strong and statistically reliable correlation between the water temperature at a depth of 10 m and the growth rate of individuals in the year of the seaward migration. Taken together with these data, the correlations observed in fig. 69 are, as a whole, an indication of a more complex relationship. A combination of factors (food supply, abundance of juveniles, water temperature, the presence of an ice cover in winter, etc.) probably play a role here.

If we compare the periods of annulus formation in sockeye smolts migrating downstream from lakes Kuril and Azabach, we see that annuli begin to form earlier in Kuril L. smolts even in the years when this lake freezes over. We believe that these differences are due primarily to the fact that Kuril L. is located farther south and undergoes breakup sooner (in the middle or at the end of May) than Azabach L. (at the beginning or in the middle of June). Our investigations have shown that practically all the juvenile sockeye in the watershed of Azabach L. resume their growth in the fairly short time of 20-30 days, and 70 % of them even in 10-15 days (Bugaev, 1981; Bugaev, Bazarkin, 1987). As a result, an increment in sclerites after the annulus is observed in the later smolts (fig. 69). On the other hand, the smolts from Kuril L. display a fairly "standard" increment after the annulus throughout the year of downstream migration. This can be due only to the fact that the resumption of growth and the formation of annuli occur first in the juveniles migrating downstream later in the season. One can assume that, prior to downstream migration, the resumption of growth is delayed in the juveniles migrating downstream last, and the annulus does not form for a certain period, as indicated by the small number of sclerites in the marginal zone of the scales in samples of fish taken at the end of downstream migration (fig. 69).

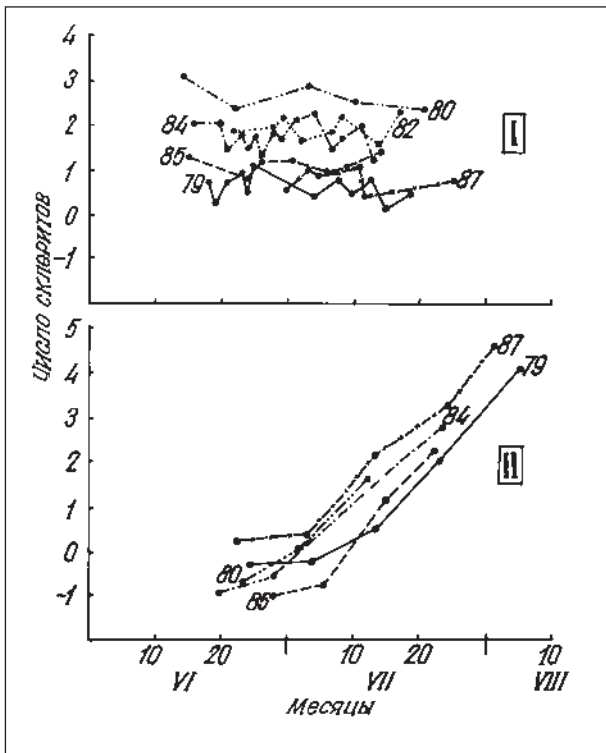


Fig. 69. Variation in marginal zone of scales in sockeye smolts from Kuril L. and Azabach L. during downstream migration. Y-axis – number of sclerites, after annulus; X-axis – months.

“-1” – without annulus, “0” – with newly formed annulus. I – Kuril L., II – Azabach L.

If we examine and compare the changes in the marginal zone of the scales in juvenile sockeye caught at the outfall of the Ozernaya R. from Kuril L., and in juveniles caught in the lake, we can see that the number of sclerites in the marginal zone of the scales in juvenile sockeye foraging in the lake begins to increase after the downstream migration of the smolts has come to an end.

This fact indicates that the Kuril L. juvenile sockeye which stay behind to forage resume their seasonal growth (after its autumn–winter–spring cessation) only towards the end or after the migration of the smolts. In other words, the resumption of seasonal growth occurs practically simultaneously in the sockeye smolts of Azabach L. and the juveniles remaining in the lake to forage (fig. 69, 71), where as the seasonal growth of Kuril L. juveniles is resumed first of all in the smolts migrating downstream earlier, then in the smolts migrating later, and finally in the juveniles remaining to forage in the lake for another one or two years (fig. 69, 70). It should be said that, in some cases, the smolts migrating from Azabach L. are observed to have a somewhat larger number of new sclerites in comparison with those caught at the same time in the lake (Bugaev, Bazarkin, 1987). Such differences point to the fact that, in some cases, the Azabach L. sockeye shows a tendency towards earlier resumption of growth in earlier-migrating individuals, but never to the same extent as in the Kuril L. sockeye.

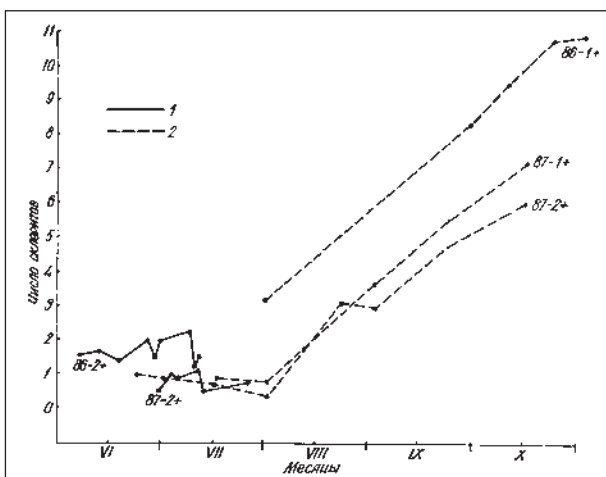


Fig. 70. Variation in marginal zone of scales in smolts and foraging juveniles of the sockeye in Kuril L. during the growing season of 1986-1987. Y-axis – number of sclerites; X-axis – months.

“-1” – without annulus, “0” – with newly formed annulus. 1 – smolts, 2 – foraging juveniles.

Despite the fact that the resumption of seasonal growth in the Azabach L. occurs practically simultaneously in downstream migrants and juvenile sockeye remaining in the lake to forage (fig. 69, 70), we recently found that, during certain warm years, the annuli in the juveniles remaining in the lake form somewhat sooner (fig. 72) than in the smolts. The opposite is observed during the colder years, i.e. the smolts resume their growth earlier than the juvenile sockeye remaining in the lake to forage. We believe that these differences are caused by the fact that a vast shallow area (“Tun-

dra”) with depths of 1-3 m exists in Azabach L., and the ice disappears from it earlier than in the main deeper part of the lake. Furthermore, we have noted that the differences in the breakup time of the shallows and the deeper part of the lake are smaller during the warmer years, and greater during the cold years. We presume that, during the warm years, many of the juvenile sockeye remaining in the lake to forage migrate to the shallows, and resume their growth before the smolts do. However, during the cold years, the smolts are the first to migrate to the shallows. Most of the juveniles remaining in the lake to forage migrate to the shallows only when the smolts begin to migrate downstream, the data obtained by us from trawl catches confirms this.

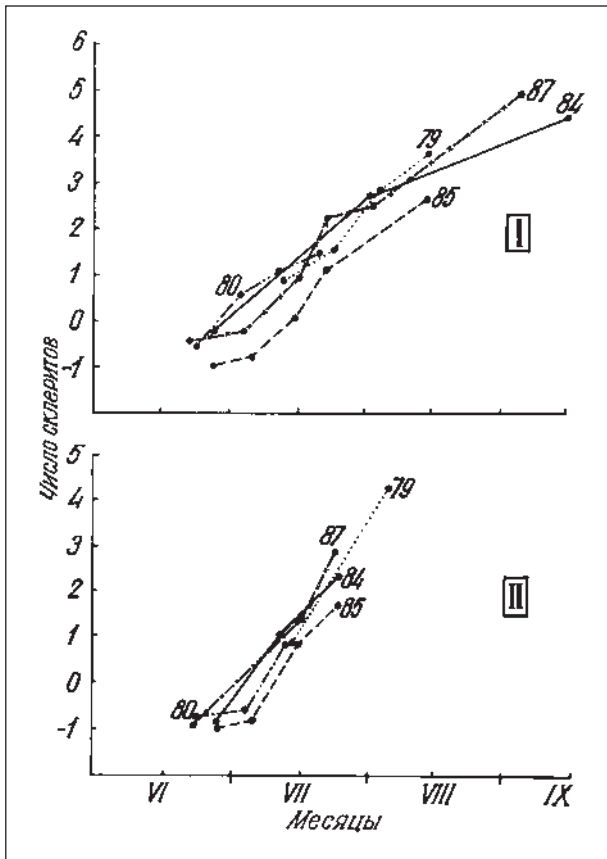


Fig. 71. Variation in marginal zone of scales in smolts and foraging juveniles of the sockeye in Azabach L. (station No. 2) during the growing season of 1979-1980 and 1984-1987. Y-axis – number of sclerites; X-axis – months.
 “-1” – without annulus, “0” – with newly formed annulus.
 I – age 1+ (one ZAS); II – age 1+ - 2+ (two ZAS).

We again wish to emphasize that our elaboration on the periods of annulus formation in the juvenile sockeye of the Azabach L. watershed does not alter our main conclusion that, on the whole, the resumption of seasonal growth and the formation of annuli in sockeye smolts and in juvenile sockeye remaining in the lake to forage is essentially more simultaneous than in the juvenile sockeye of Kuril L.

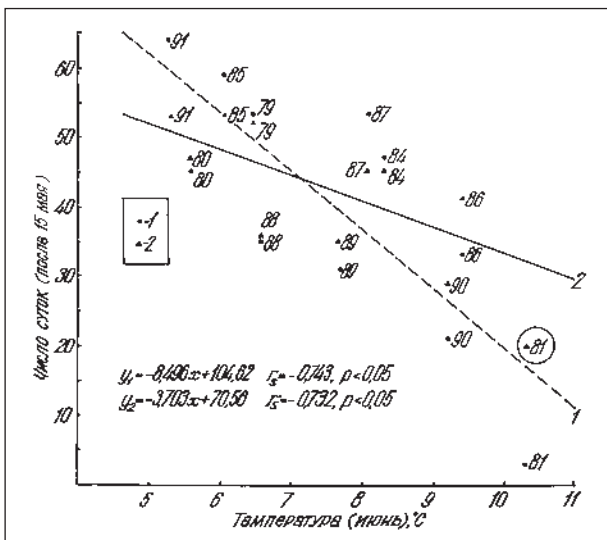


Fig. 72. Dates of formation of annuli in yearling sockeye of stock “A” (caught in Azabach L.) and sockeye smolts of stock “A” and group “E” (caught at outfall of Azabach L. side channel). Y-axis – number of days (after May 15th) when an annulus formed on the scales; X-axis – daily average air temperature in June at Ust’-Kamchatsk, °C.
 1 – yearlings of stock “A” (age 1+); 2 – smolts of stock “A” (age 2+) and group “E” (age 1+).
 The figures near the dots denote the year in which the material was collected. When calculating the equations, the lines of regression for 1981 (circled) were not taken into account, the 1981 values were determined by the formula $Y = 0.571X + 18.41$ ($r_s = 0.933$, $P < 0.01$, $n = 10$), where “x” denotes the date on which the first annulus formed in the yearlings of stock “A” (number of days after May 15th), and “y” denotes the date of annulus formation in smolts (number of days after May 15th).

This study was a continuation of our earlier investigations on the rate of sclerite formation in the sockeye of Azabach L. (Bugaev, 1984b). As we can see from table 25, the smolts of group “E” and stock “A” in 1979-1980 were much larger than in

1984-1987. Because of these differences, we examined all the data on the rate of sclerite formation for these particular periods (table 21). We have not presented any data on the forage base of young of the sockeye for these periods due to the fact that there were no studies conducted on this in the Azabachye L. watershed during 1970-1980.

Table 21. Average speed in the formation of one sclerite in young sockeye scales in the Azabach L. watershed in 1979-1987, days

One ZAS			Two ZAS		
Date	Average	Number of observations	Date	Average	Number of observations
Outlet of Azabach L.					
–	–	–	3.07-4.08.1979-1980	6.1±0.3	3
–	–	–	27.06-1.08.1984-1987	6.8±0.5	8
–	–	–	27.06-4.08.1979-1987	6.6±0.4	11
Azabach L. (stations No. 1-3)					
17.06-14.08.1979-1981*	12.2 ±0.9	6	23.06-4.08.1979-1980	6.5±0.1	5
27.06-5.09.1984-1987	11.9 ±1.1	13	22.06-23.07.1984-1987	8.9±0.9	13
17.06-5.09.1979-1987	12.0 ±0.8	19	22.06-4.08.1979-1987	8.3±0.7	18

*To make data more representatative during a period of good growth (1979-1980) we included two values for 1981, without the inclusion of the above data the speed of the formation of one sclerite was 12.0±1.4 days.

The larger size of the juveniles in 1979-1980 definitely indicates that the foraging conditions during this period were better than in 1984-1987. It is a well-known fact that the growth rate of the sockeye depends on the food supply (Krogius, 1961; Goodlad et al., 1974; Dubynin, 1986; Bugaev et al., 1989; Burgner, 1987, etc.), and this applies to the sockeye of Azabach L. as well (Bugaev, 1983a; Bugaev, 1987; Bugaev et al., 1993), though some researchers disclaim or disregard this relationship for the Azabach L. sockeye (Konovalov, 1980; Ostrovsky, 1987, 1987a, 1988; Kovalyov, 1988, 1989, 1990). Analysis of the data in table 21 has brought us to the conclusion that, despite the decrease in the size of the fish in 1984-1987 as compared with 1979-1980, the juvenile sockeye did not display any significant changes in the rate of sclerite formation during the studied period of the growing season.

Since the smolts and the juvenile sockeye that remain in Azabach L. to forage have a different rate of sclerite formation (Bugaev, 1984b), the somewhat longer formation of one sclerite in individuals with two ZAS caught in the lake in 1984-1987 as compared with 1979-1980 (table 21) can be attributed to the fact that the percentage of individuals remaining in the lake for another winter increases in the samples during the years of poor juvenile growth in Azabach L.

Our conclusions are also supported by the fact that similar results were obtained for the smolts of the Azabach L. side channel in 1979-1980 and 1984-1987, and the fact that it took slightly longer (6.5 days) for one sclerite to form in the fish from the lake in 1979-1980, as compared with the fish from the headwater of the side channel (6.1 days), i.e. the 1979-1980 samples from the lake may have included a few individuals which did not migrate downstream, but remained in the lake till the following year. In 1984-1987, the percentage of these fish was undoubtedly higher because of the deterioration of foraging conditions, and this could have affected the results.

Taking into account our own conclusion that approximately the same length of time is required for one sclerite to form during a “good” and a “bad” year of juvenile growth at least up to the middle of August (table 21), we examined the data combined for all the years according to the months. We found that the formation of one sclerite in individuals with one ZAS took 14.5±1.9 days in June (n=3), 10.2±0.9 days in July (n=11), and 14.4±0.4 days in August (n=5). Only the July figures (6.6±0.4 days, n=11) were available for the smolts with two ZAS from the headwater of the side channel, the time it took for one sclerite to form in juvenile sockeye from the lake equalled 9.6±1.5 days in June (n=3), and 8.0±0.8 days in July (n=15).

The differences in the rate of sclerite formation observed by us for the period studied during the growing season may actually be the result of some irregularity in the time of their formation. However, considering the small volume and collected nature of the material, as well as the biological characteristics of the sockeye foraging in Azabach L., we still tend to interpret the results somewhat differently. For instance, the July increase in the rate of sclerite formation in juveniles with one ZAS from the lake (stock “A”) can be attributed to the fact that yearling smolts with one ZAS could have been present among these juvenile sockeye, but the smolts from Azabach L. have a much higher rate of sclerite formation than the juveniles remaining in the lake to forage (Bugaev, 1984b, table 20). The slower rate of sclerite formation in June and August can be explained by the fact that growth is resumed in June—beginning of July, and the samples taken at this time may include individuals which have not yet resumed their growth, and the August samples may contain group “E” underyearlings with recently initiated supplementary adjacent sclerites, which could be mistaken for stock “A” yearlings. In the lake individuals with two ZAS, the slower rate of sclerite formation in June can also be explained by the fact that the growing season in juvenile sockeye from Azabach L. is just beginning, and the samples may include individuals which have not yet resumed their growth.

When we just began to study the rate of sclerite formation in stock “A” and group “E” sockeye foraging in Azabach L. (Bugaev, 1984b), we compared the rate of sclerite formation in individuals from the two mentioned samples, but did not note any significant differences, therefore, all further investigations were carried out without distribution of the rate of sclerite formation in stock “A” and group “E” individuals.

Since we now have more material at our disposal, we studied the rate of sclerite formation in stock “A” and group “E” sockeye smolts with two ZAS on their scales, which were caught in the headwater of the Azabach L. side channel during 1979–1991. Based on these combined data we found that it took 6.6 ± 0.5 days for one sclerite to form in stock “A” individuals, and 6.7 ± 0.5 days in group “E” ($n=17$ in both cases). A comparison by means of Student’s t-test showed no significant differences.

Let us now examine the time it takes for one sclerite to form in the juvenile sockeye foraging in Kuril L. We have much less material on this than on the Azabach L. sockeye. Based on summarized data, it took 11.4 ± 0.6 days for one sclerite to form in Kuril L. sockeye of age 1+ (31 July to 22 October) during 1976–1987 ($n=12$), and 13.9 ± 1.6 days in individuals of age 2+ (from 31 July to 15 October) ($n=8$). When we compared the duration of sclerite formation in yearlings, we found that it took 11.3 ± 0.3 days for one sclerite to form in August–September ($n=7$), and 11.6 ± 1.4 days in October ($n=5$), as we can see, the differences are not very great, but more samples must be taken from this lake as well.

The study showed that it also took approximately the same length of time for one sclerite to form in stock “A” yearling sockeye foraging in Kuril L. Based on the increment in the marginal zone of the scales (in the “plus”), the rate of sclerite formation in yearling and two-year-old sockeye of Kuril L. and the number of sclerites in the growth zones of the scales of age 2+ and 3+ smolts prior to downstream migration, we calculated the periods in which the growing season comes to an end in this body of water (table 22). Our calculations were based on the fact that it took 11.4 days for one sclerite to form in yearlings, and 13.9 days in 2-year-olds, as indicated in table 22, the estimated time of completion of the growing season in the juvenile sockeye of Kuril L. is the third 10-day period of October–middle of November for age 1+ individuals, and the middle of October–beginning of December for age 2+ individuals, i.e, the range of the values obtained is much wider in age 2+ juveniles than in age 1+ individuals. Fish of age 2+ usually cease to grow sooner (table 22).

The estimated periods of growth cessation in the juvenile sockeye of Kuril L. are highly inconsistent with freeze-up time on the lake, which usually takes place in the second half of January–February; however, by the time the fish stop growing, the day has become much shorter. Considering that newly formed sclerites of the following year are in some cases included in the annulus when the sclerites in the growth zones are being counted (Bugaev, 1981), the data in table 22 on the cessation of the growing season in the juvenile sockeye of Kuril L. should be accepted with some degree of correction. Considering that the annuli in Kuril L. sockeye are highly indistinct and usually consist of two adjacent sclerites, basically only one newly formed sclerite might in some cases be included in the annulus here, therefore, the correction for earlier cessation of the growing season should be minimal (only several days) in this case.

Table 22. Calculated dates of the termination of growth in young sockeye in Kuril L.

Year of downstream migration	Number of sclerites on smolt scales		Foraging year	Catch date and number of sclerites in marginal area of scales on foraging young		Increase in the number of sclerites before growth stoppeds		Data growth stopped	
	2+ (second year)	3+ (third year)		1+	2+	1+	2+	1+	2+
1977	11.1	7.0	1976	30.08(5.5)	30.08(3.2)	5.6	3.8	02.11	22.10
1978	12.3	9.2	1977	19.09(9.3)	19.09(7.4)	3.0	1.8	23.10	14.10
1978	9.6	10.9	1978	06.09(5.6)	06.09(4.6)	4.0	6.3	22.10	03.12
1986	8.7	7.8	1985	19.10(6.4)	–	2.3	–	14.11	–
1987	11.6	8.6	1986	30.10(10.4)	29.09(6.1)	1.2	2.5	13.11	03.11
1988	9.4	7.9	1987	15.10(7.2)	15.10(6.1)	2.2	1.8	09.11	09.11

We estimated the approximate periods of growth cessation in stock “A” juveniles using the scales of smolts from the headwater of the Azabach L. side channel, which had been identified by a method suggested earlier (Bugaev, Bazarkin, 1987). As indicated in table 23, the cessation of growth in stock “A” juvenile sockeye during the observation period occurred at the beginning of September–beginning of October, which was probably due to their variable food supply in the lake. In late autumn, the young of the sockeye in Azabach L. feed exclusively on *Cyclops scutifer*. One can assume that their growth will continue for a longer period during the years of high abundance of *Cyclops scutifer*, and vice versa.

Table 23. Calculated dates of the termination of growth in young sockeye stock “A” in Azabach L.

Year of down-stream migration	Number of sclerites on scales of smolts, aged 2+, in the second year	Foraging year	Data growth stopped in young of stock “A”, aged 1+	Increase in the number of sclerites before growth stoppeds	Data growth stopped in young of stock “A”, aged 1+
1980	7.54	1979	14.08(3.57)	3.97	01.10
1985	5.60	1984	13.08(3.64)	1.96	06.09
1986	6.22	1985	14.08(2.59)	3.63	27.09
1988	6.59	1987	05.09(4.89)	1.70	25.09

As our investigations have shown, the juvenile sockeye of the Kuril L. watershed are characterized by exceptionally long periods of seasonal growth resumption and annulus formation. Seasonal growth was resumed first by the smolts that started the downstream migration, then by the midseason migrants, and finally by the late smolts. The juveniles remaining in the lake to forage resumed their seasonal growth by the end of, or after the completion of the smolt migration from the lake. Having resumed their seasonal growth, the smolts migrated downstream straightaway. Evidence of this was the similar number of “newly grown” sclerites following the annulus in the samples from the beginning, the middle and the end of the downstream migration.

The late resumption of growth in the juvenile sockeye remaining in Kuril L. to forage is also confirmed by the results of an analysis of the correlation between the number of sclerites in the growth zones of the scales in age 2+ juveniles (age 1+ and 3+ individuals not included in the analysis due to their low abundance) and the abundance of *Cyclops scutifer* (the principal food of juvenile sockeye in the lake), which was carried out during a study of the interannual variability of the central part of the scales in the sockeye brood stock of Kuril L. (see section 8.7.3). It was found that the closest correlations between the number of sclerites and the abundance of *Cyclops scutifer* existed in August–October. The weak correlations noted at other times are indirect proof that this period (August–October) is the main period of growth in the juvenile sockeye of Kuril L.

Experimental data show that the seasonal rhythm of growth may be endogenous in some cases. In one and the same population, some individuals may have a distinct endogenous seasonal rhythm of growth, and others an exogenous one (Mina, Klevezal, 1980). In areas with a continental climate, the former have a selective advantage, i.e., their relative abundance increases from generation to generation. In areas with a mildly continental climate, the endogenous seasonal growth rhythm itself probably does not lower the adaptedness of the individuals, but disturbances of the genetic mechanism which effects a distinct endogenous rhythm are not noted by means of selection, and therefore the variability of the rhythm increases (Mina, Klevezal, 1980).

In a model, Azabach L. can be viewed as an analogue of an area with a continental climate, and Kuril L. as an area with mildly continental climate, since the first lake warms up and cools down much more quickly than the second one (Krokhin, Krogus, 1937; Krokhin, 1972).

It is a known fact (Mina, Klevezal, 1976, 1980) that the seasonal change in light conditions can serve as a time indicator for animals to resume their seasonal growth.

Let us examine the available data on the vertical distribution of juvenile sockeye in these lakes during the period of growth resumption, since the water, on the strength of its limited transparency, can serve as a unique “isolator” for the fish against any seasonal changes in light conditions related either to an increase in the light period of the day, or to the breakup of ice on the water.

The echo-sounding surveys conducted in the Azabach L. watershed have helped us to establish that schools of juvenile sockeye in this lake at the end of June–beginning of July stay mainly at depths of 8–10 m during the day, and at 0–5 and 0–8 m during the night (Nikolayev, Bugaev, 1985). According to the data of echo-sounding surveys conducted in the Kuril L. watershed in June, schools of juvenile sockeye stay at depths of 40–60 m during the daytime. In the process of diel vertical migrations, the schools disperse, and an echo sounder at night records a field of discrete targets at depths from 0 to 55 m (Nikolayev et al., 1982; Nikolayev, 1988a, 1990).

This fact does not exclude the possibility that some of the juveniles during this period do not rise to the surface at all during the 24 hours.

The observed diel vertical migrations of juveniles in lakes Azabach and Kuril are quite consistent with the vertical migrations of the zooplankton they feed on in these lakes (Belousova, 1972; Nosova, 1968, 1972), the same type of relationship has been noted for the sockeye of Babine L. (Narver, 1970), Dalneye L. (Krogus, 1974), Washington L. (Eggers, 1978) and many of the other lakes inhabited by this species (Burgner, 1991).

If we proceed from the hypothesis that the seasonal improvement of light conditions is one of the main factors of growth resumption for the sockeye, which, in a natural environment, coincides with a rise in temperature and a good or simultaneously improving forage base (Bugaev, 1981); then the noted characteristics of growth resumption in the young sockeye of Kuril L. can be partially explained by their vertical distribution. For instance, a comparison of echo-sounding survey data indicates that, unlike the young of Azabach L., the juvenile sockeye in the pelagic zone of Kuril L. inhabit the very deep layers of water. The evidence that the resumption of growth is delayed in some of the juvenile sockeye of Kuril L., as well as the data on the night distribution of fish in this lake, suggest that not all of the immature fish immediately migrate to the upper illuminated layers and resume their growth during the period of growth resumption after overwintering. With the limited transparency of the water for the young fish living (overwintering) in the deep layers of water (several tens of metres deep), the effect of better light conditions due to the breakup of ice on the lake or a longer light period during the winter–spring (in the years when the lake does not freeze over) will be much lower. With depth, the degree of isolation from the changes in light conditions (“the timer”) increases. Furthermore, we know that some individuals may have a different sensitivity to this “timer” (Mina, Klevezal, 1976, 1980).

For the sockeye of Azabach L., the seasonal improvement in light conditions as a result of the breakup of the ice cover, considering the shallowness of the lake in comparison with Kuril L., will be more perceptible and intense. Because of this, the period of growth resumption for the immature fish in Azabach L. is probably shorter than in Kuril L. Another important factor here is that the water mass in Azabach L. warms up more quickly than in Kuril L., since the latter, being larger and deeper, is a much colder lake on the whole (Krokhin, Krogus, 1937; Krokhin, 1972).

Whereas the fairly quick resumption of growth in the sockeye of Azabach L. can be attributed to the general improvement in light conditions and the warming up of the lake after breakup, the same explanation suits the sockeye of Kuril L., for it is not specified why the juveniles that remain in the lake for another year instead of migrating downstream are the last to resume their growth.

The foraging conditions in both lakes are highly variable from year to year, but we still have no data to prove that this has any fundamental effect on the vertical distribution of the fish in these lakes.

Judging by the numbers of spawned out adult fish and the more complex age structure, the abundance of juvenile sockeye foraging in Kuril L. at the same time is much higher on the whole than in Azabach L., despite the fact that the juveniles from the tributaries of the lower reaches of the Kamchatka R. migrate to Azabach L. to forage (Bugaev, 1981a).

Considering the proximity of the Kuril L., and Azabach L. areas (Krokhin, Krogius, 1937; Krokhin, 1972), we can say that the wider range of vertical distribution of the young during the foraging period (in addition to the effect of the nighttime distribution of the zooplankton) in Kuril L. is to some extent determined by the higher abundance of juvenile sockeye in this lake, and serves as a special energy-saving adaptation during the foraging period. The feeding of young sockeye in a narrower range of depths would lead to an increase in the concentration of juveniles, an increase in intraspecific competition and, therefore, an increase in the energy spent on the search for food.

An important circumstance affecting the length of the growth resumption period of juvenile sockeye in lakes Azabach and Kuril may be that the juvenile sockeye of Kuril L. resume their growth only under conditions of intraspecific competition, whereas the young sockeye of Azabach L. resume their growth under conditions of intra- and interspecific competition. During the summer–autumn period, the anadromous form of the threespine stickleback, *Gasterosteus aculeatus* (*trachurus* morph), migrates to Azabach L. to spawn, and underyearling pond smelt (*Hypomesus olidus*) to forage; this lake is also home to the freshwater form of the threespine stickleback (*leiurus* morph). The abundance of these food competitors of juvenile sockeye (Foerster, 1968; Burgner et al., 1969; section 8.5.3) exceeds the abundance of the latter during certain years (Bugaev, 1988). Due to the presence of interspecific competition, it is better for the young sockeye foraging in Azabach L. to resume their seasonal growth as soon as possible. In turn, the sockeye population foraging in Kuril L., due to the absence of interspecific competition, apparently must adhere to the intraspecific hierarchy during the resumption of seasonal growth.

Considering the higher abundance of juvenile sockeye in Kuril L. as compared with Azabach L., one can assume that the later resumption of growth noted by us in the juveniles remaining in the lake for another year is an adaptation of this population to the specific conditions in this lake. This differentiated resumption of the growing season for the juveniles migrating downstream and those staying behind to forage can occur only in the case where the resumption of growth and the differentiated sensitivity to “the timer” are largely controlled by internal (genetic) factors, which is not inconsistent with the current concepts of animal growth (Mina, Klevezal, 1976, 1980).

In conclusion, we present material which illustrates the formation of annuli on the scales of young sockeye in the Kuril L. watershed (figs. 73, 74). Photographs of scales depicting the formation of annuli and supplementary structures on the scales of sockeye in the Azabach L. watershed were presented earlier (figs. 64, 65).

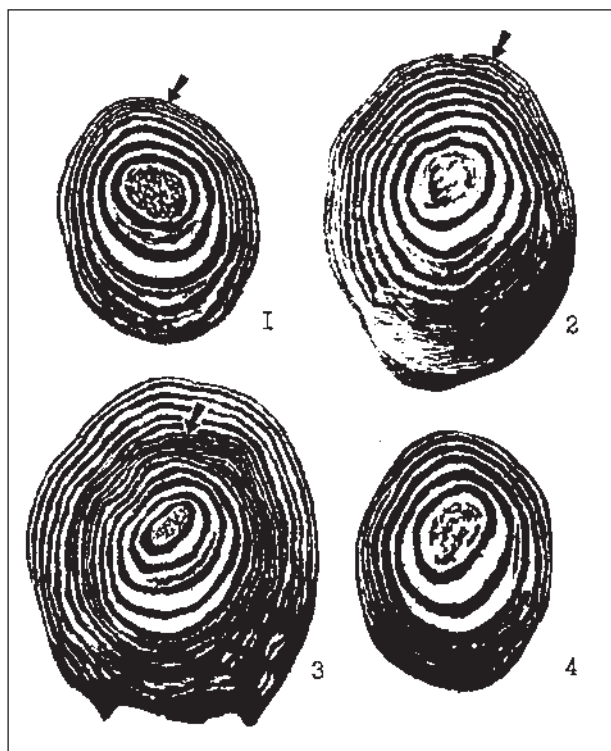


Fig. 73. Structure of scales in yearling and underyearlings sockeye from Kuril L. Arrows mark ZAS – annuli.

1 – 1 August 1987, AC=72 mm, age 1+; 2 – 1 August 1987, AC=78 mm, age 1+; 3 – 23 Sept 1987, AC=95 mm, age 1+; 4 – 15 October 1987, AC=63 mm, age 0+.

As seen in fig. 73, an annulus had just formed on the scales of yearlings at the beginning of August (1-2), and a fairly significant increment in sclerites was observed after the ZAS on the scales of these yearlings at the end of September (3). No supplementary ZAS were observed on the scales of underyearling sockeye in the middle of October (fig. 73.4).

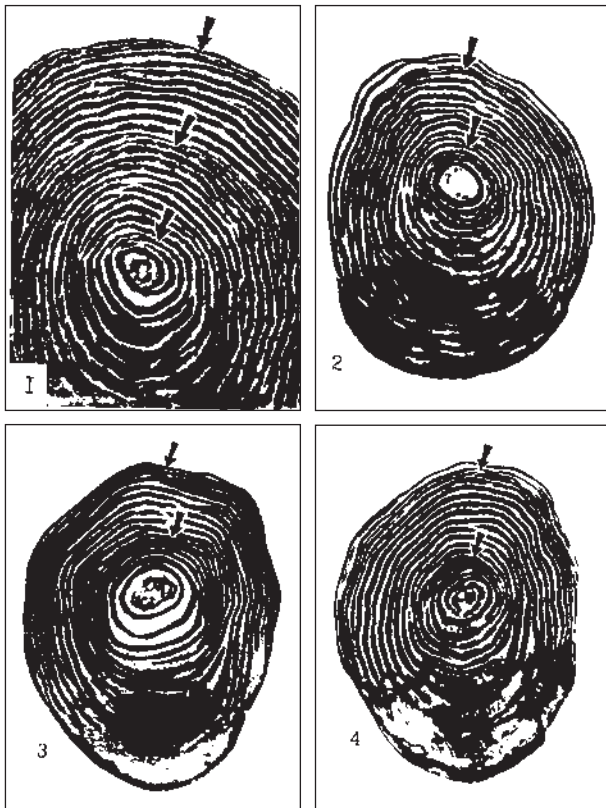


Fig. 74. Structure of scales in sockeye smolts from Kuril L. (outfall of the Ozernaya R.) and Etamynk L. Arrows mark ZAS – annuli.

1 – Etamynk L., 20 June 1974, AC=136 mm, age 3+; 2 – Kuril L., 23 June 1984, AC=103 mm, age 3+; 3 – Kuril L., 2 July 1985, AC=97 mm, age 3+; 4 – Kuril L., 6 July 1987, AC=106 mm, age 3+.

In a probable age 3+ sockeye smolt from Etamynk L. (Kuril L. watershed, fig. 5), which was caught in the lake at the time of its breakup at the end of the second ten-day period of June, the annulus on the scales had just formed (fig. 74.1). In age 2+ sockeye smolts of Kuril L., which were caught during different years at the outfall of the Ozernaya R., a fairly standard increase was observed at the time of downstream migration at the end of June–beginning of July, i.e. an annulus had just formed, or 1-2 “newly grown” sclerites were present on the scales (fig. 74.2-4), though the breakup of Kuril L. during these years occurred about a month earlier.

8.4. Downstream migration and qualitative characteristics of sockeye smolts migrating from Azabach L. and Kuril L. (Ozernaya R.)

The living conditions of the young in fresh water have a significant effect on the abundance of the mature part of the sockeye population (Krogius, 1951, 1961; Koenings, Kyle, 1995). The survival of the sockeye at sea is directly related to the qualitative characteristics of the smolts, particularly the body length and weight of the fish (Foerster, 1954, 1968; Ricker, 1962; Johnson, 1965; Koenings, Barket, 1987; Koenings et al., 1993). Let us examine the interannual variability of the size-weight indices in sockeye smolts migrating from lakes Azabach and Kuril. We have already discussed the downstream migration of underyearling sockeye in the Kamchatka R. watershed (see section 8.3.1).

Azabach Lake

The dynamics of downstream migration of sockeye smolts migrating from Azabach L. was studied by us with the help of periodic trawling in the headwater of the channel flowing out of Azabach L. (fig. 4), these studies were begun comparatively recently, in 1979, and are still underway (after a break in 1981-1983). Fig. 75 depicts the dynamics of downstream migration of sockeye from Azabach L. over a number of years, as indicated in this diagram, the dynamics of downstream migration of sockeye depends on the temperature of the water at the outfall of the Azabach L. side channel. Based on the data available to us, the size of the sockeye smolts in the side channel appears to be related to the number of individuals that later return to the Kamchatka R. watershed (section 11.2, fig. 125).

In the juvenile sockeye that forage in Azabach L., the number of zones of adjacent sclerites on the scales (ZAS), i.e. the annuli and supplementary rings, does not always correspond to the age of the fish in question. This is due to the fact that underyearling sockeye migrate to the lake from the tributaries of the lower Kamchatka R. every year from July to November

to forage and spend the winter there, and because of this change in habitat, a supplementary ZAS, which is not an annulus, forms on the scales. According to our estimate, about 50-70 % of all the immature sockeye of the Kamchatka R. watershed forages in this lake, and the juveniles entering the latter to feed and grow can constitute up to 60-70 % of all the young sockeye foraging in the lake (Bugaev, 1981a, 1983a).

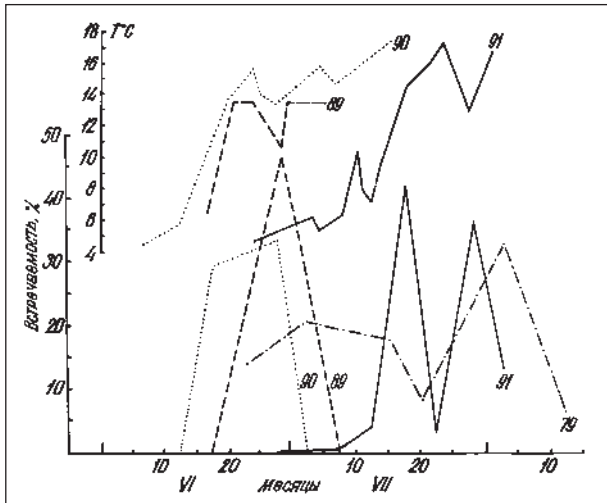


Fig. 75. Dynamics of downstream migration of sockeye smolts from Azabach L., based on trawling data (by 5-day periods, per minute of trawling). Y-axis: lower graph – frequency of occurrence, %; upper graph – water temperature at outfall of Azabach L. side channel at the time of trawling, °C; X-axis – months.

We again remind you that the young sockeye from the tributaries of the lower Kamchatka R. (group “E”) that forage in Azabach L. migrate downstream at age 1+, and those of the Azabach L. stock (stock “A”) at age 2+, as a result of the ecological changes after their migration to the lake, the juveniles from the Kamchatka R. tributaries develop a zone of adjacent sclerites on their scales; this is not an annulus, since it is formed during the growing season in immature sockeye. Despite the fact that mainly juveniles with two zones of adjacent sclerites migrate from Azabach L., the young fish from the tributaries are mainly of age 1+, and the young of stock “A” are of age 2+.

A method of differentiating the sexually mature fish of stock “A” and group “E” has already been developed (Bugaev, 1986a). Based on the method of adult identification, a method for identifying smolts of stock “A” and group “E” was proposed (Bugaev, Bazarkin. 1987). Later investigations in which the structure of smolt scales was compared with that of mature fish of the same year-classes (Bugaev et al., 1993) showed that the scale characteristics of the smolts and mature fish of stock “A” matched quite well.

Each year, smolts migrate from Azabach L. with two ZAS on their scales, though in 1987 individuals with one ZAS were encountered more frequently (table 24). Analysis of scales from stock “A” adults that had returned in 1989-1991 did not show a higher than usual frequency of occurrence of individuals that had migrated downstream as yearlings. This indicates that the sockeye with one ZAS that had migrated downstream in 1987 belonged mainly to group “E”, the higher than usual occurrence of individuals with one ZAS in 1987 (table 24) can be attributed to the fact that the foraging conditions in Azabach L. in 1985-1986 were very poor, and, after the migration of group “E” underyearlings to the lake, the growth of these young fish was worse than usual, as a result, the supplementary ZAS and the annulus next to it were in some cases accepted as one ZAS.

Table 24. ZAS number of sockeye smolt scales of downstream migrants from Azabach L., %

Migration year	One ZAS 3CC	Two ZAS	Three ZAS	Forth ZAS	Number of fish
1979	3.7	92.8	3.5	–	346
1980	3.5	93.5	3.0	–	201
1984	0.6	96.2	3.2	–	157
1985	2.3	90.4	7.3	–	220
1986	4.6	89.2	6.2	–	65
1987	25.0	62.9	11.7	0.4	240
1988	6.6	88.0	5.0	0.4	241
1989	3.5	71.7	23.0	1.8	283
1990	3.6	89.7	6.7	–	165
1991	5.4	87.1	7.2	0.3	333

Table 25 presents the size-weight characteristics separately for stock “A” and group “E” sockeye smolts from Azabach L., as we can see from this table, these characteristics changed considerably over the period of our investigations.

Table 25. Body length and weight of sockeye smolts migrating from Azabach L. in 1979-1994

Migrating year	Stock “A”, age 2+			Group “E”, age 1+		
	Range	Average	Number of fish	Range	Average	Number of fish
1979	81-125	102.60 ± 0.60	149	72-120	97.70 ± 0.70	197

Migrating year	Stock "A", age 2+			Group "E", age 1+		
	Range	Average	Number of fish	Range	Average	Number of fish
--	5.55-18.86	11.61 ± 0.25	--	3.50-19.24	10.59 ± 0.25	--
1980	77-117	95.30 ± 1.30	57	60-112	89.30 ± 0.70	130
--	4.60-15.00	8.57 ± 0.31	--	2.40-13.50	7.28 ± 0.16	--
1984	70-104	88.90 ± 0.70	88	68-104	83.20 ± 0.90	69
--	3.10-11.45	6.84 ± 0.18	--	2.65-10.64	5.53 ± 0.23	--
1985	67-95	78.40 ± 0.60	91	63-92	77.60 ± 0.50	129
--	2.90-6.00	4.43 ± 0.13	--	1.80-8.70	4.19 ± 0.11	--
1986	64-89	76.60 ± 2.30	11	54-88	74.20 ± 1.00	54
--	2.70-6.50	4.16 ± 0.41	--	1.70-6.50	3.83 ± 0.15	--
1987	68-99	82.09 ± 0.69	68	56-97	77.67 ± 0.51	172
--	3.70-11.00	6.08 ± 0.17	--	1.85-10.01	5.04 ± 0.12	--
1988	68-109	95.59 ± 0.69	140	63-109	92.25 ± 0.96	101
--	3.50-13.80	8.77 ± 0.18	--	3.40-14.00	8.92 ± 0.24	--
1989	78-118	99.23 ± 0.53	178	73-111	93.38 ± 0.92	105
--	4.90-14.30	10.21 ± 0.15	--	3.80-13.70	8.85 ± 0.23	--
1990	75-113	98.42 ± 0.63	84	62-108	81.58 ± 1.16	81
--	4.10-14.60	9.76 ± 0.19	--	2.60-12.90	5.88 ± 0.26	--
1991	75-122	100.86 ± 0.88	136	68-115	88.24 ± 0.54	197
--	4.80-18.80	11.25 ± 0.27	--	4.00-14.90	7.42 ± 0.14	--
1992	83-112	103.85 ± 0.36	171	83-111	97.24 ± 0.30	223
--	6.20-14.90	11.54 ± 0.12	--	5.10-13.80	9.91 ± 0.09	--
1993	94-128	112.05 ± 0.32	287	79-116	97.19 ± 0.56	224
--	8.50-22.40	15.67 ± 0.13	--	5.10-17.20	10.29 ± 0.17	--
1994	99-134	118.76 ± 0.53	195	68-116	86.77 ± 0.90	132
--	9.60-26.60	18.18 ± 0.23	--	3.40-18.80	7.56 ± 0.26	--
1995	78-116	96.86 ± 0.35	278	63-105	91.50 ± 0.93	104
--	3.50-15.70	9.58 ± 0.11	--	2.10-12.40	8.24 ± 0.26	--

Note. Upper values – body length according to Schmidt (Pravdin, 1966), in mm; lower – body weight in grams.

Each year, males predominate in the downstream migration, both in stock "A" and in group "E" individuals, and we have not yet observed any fundamental differences in the sex ratio of this stock and group. The proportion of females (based on combined data) was 46.2 % in 1979, 43.9 % in 1980, 42.7 % in 1984, 49.5 % in 1985, 46.9 % in 1987, 41.5 % in 1988, 40.3 % in 1989, 49.1 % in 1990, 40.5 % in 1991, and 38.7 % in 1992.

Kuril Lake

The dynamics of downstream migration of sockeye smolts from Kuril L. was studied with the help of a fyke net set up on the weir at the outlet of the Ozernaya R. (Selifonov, 1970a; Dubynin, Bugaev, 1988).

Table 26 characterizes the dynamics of downstream migration of Kuril L. sockeye smolts in 1975 through 1991, and fig. 76 gives a more visual picture of the dynamics of downstream migration for a number of years. Analysis of the table and diagram has shown that the dynamics of downstream migration of the young varies considerably from year to year.

As a result of hydroacoustic surveys in the Kuril L. watershed. A. S. Nikolayev (personal communication) established that the duration of the downstream migration of the nucleus of the immature sockeye population was determined by the degree of water warm-up. The duration of downstream migration was found to have the highest correlation with the mean temperature of the 0-50 m layer of water in August ($r=-0.80$, $P<0.01$, $n=10$).

The downstream migration of the young sockeye of Kuril L. (fig. 76) takes place somewhat earlier than that of Azabach L. sockeye (fig. 75), but the dynamics of downstream migration has certain common features. During the years when two clearly defined peaks of downstream migration were observed in the Kuril L. sockeye (1979, 1991), two peaks of downstream migration were also observed in the sockeye from Azabach L., which is an indication of the unidirectional effect of climatic conditions during the years of downstream migration.

Table 26. Seasonal dynamics of sockeye smolts migrating from Kuril L. (V.A. Dubynin, personal communication), %

Migrating year	01-05.06	06-10.06	11-15.06	16-20.06	21-25.06	26-30.06	01-5.07	06-10.07	11-15.07	16-20.07	21-25.07	26-31.07	01-5.08	06-10.08	Number of fish
1975	—	—	3.9	28.9	29.7	18.0	6.2	9.4	3.9	—	—	—	—	—	128
1976	—	0.7	—	0.7	12.8	14.3	5.2	21.0	9.8	3.0	2.3	21.8	8.3	—	133
1977	0.1	0.3	5.4	47.9	35.3	8.0	1.8	1.1	0.1	—	—	—	—	—	1116
1978	—	8.7	9.9	12.4	34.7	27.3	5.8	—	0.8	0.4	—	—	—	—	242
1979	—	—	0.1	4.3	35.5	1.1	6.9	26.2	18.1	4.0	1.4	1.4	0.6	—	941
1980	—	—	25.3	4.3	16.4	29.7	19.0	2.2	1.7	0.3	1.1	—	—	—	1187
1981	0.8	4.3	25.5	42.0	18.1	5.8	2.3	1.1	0.1	—	—	—	—	—	1931
1982	0.6	1.1	1.0	—	24.5	55.6	4.7	7.2	2.1	2.6	0.3	0.1	0.2	—	2015
1983	—	—	1.3	95.6	1.1	0.4	0.2	0.5	0.7	0.1	0.1	—	—	—	8860
1984	—	—	0.3	10.5	38.7	18.0	9.5	11.9	8.7	2.0	0.3	0.1	—	—	688
1985	—	—	7.3	7.1	7.6	10.5	31.5	18.3	17.3	0.4	—	0.1	—	—	1066
1986	1.2	1.7	3.4	2.6	1.3	35.3	29.9	15.3	8.1	0.2	0.9	3.8	—	—	846
1987	—	—	—	0.9	1.0	2.4	9.4	38.6	37.9	3.0	2.9	0.5	—	—	790
1988	—	—	5.0	11.1	12.1	18.2	35.3	11.3	4.5	0.4	1.6	0.7	0.1	—	556
1989	—	—	6.9	19.8	17.5	21.7	10.4	8.9	5.5	5.8	2.8	—	—	—	2393
1990	—	3.7	58.9	14.2	19.0	3.0	1.2	—	—	—	—	—	—	—	331
1991	2.8	17.9	11.3	1.9	2.1	5.8	28.2	10.5	8.8	8.8	1.9	—	—	—	468

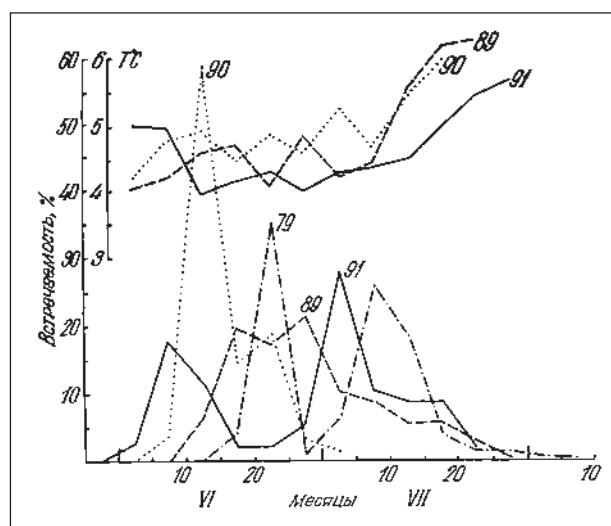


Fig. 76. Dynamics of downstream migration of sockeye smolts from Kuril L. (Ozernaya R.), based on catches with a fry net (by 5-day period). Y-axis: lower graph – frequency of occurrence, %; upper graph – water temperature at outfall of Ozernaya R. at 20.00 hours, °C; X-axis – months.

As we have already mentioned, the young of the sockeye spend mainly two years in Kuril L. before migrating downstream to the sea. Some (several percent) are juveniles migrating downstream after spending three years in the lake. During certain years, yearlings are encountered in large numbers in the downstream migration (Selifonov, 1970, 1970a, 1974; Dubynin, Bugaev, 1988).

After fertilization measures were carried out in Kuril L. in 1981, which was followed by unplanned natural fertilization of the lake by volcanic ash from the Alaid volcano that same year, and as a result of an increase in the abundance of sockeye spawners in the Kuril L. watershed since 1977-1978 (and up to the present) (Selifonov, 1986, 1988), a drastic increase in the relative number of yearling smolts has been noted in the downstream migration during certain years. The first high-frequency peak for yearlings was observed in 1985, four years after the shower of volcanic dust and the mineral fertilization of the lake, and then again in 1989 and 1991 (table 27).

Table 27. The age composition of sockeye smolts in Kuril L. (Dubynin, Bugaev, 1988; with addenda), %

Migrating year	Age 1+	Age 2+	Age 3+	Number of fish
1975	3.9	82.8	13.3	128
1976	45.4	38.7	15.9	132
1977	2.1	95.0	2.9	392
1978	4.9	82.7	12.4	242
1979	0.8	92.9	6.3	659
1980	1.8	91.9	6.3	320
1981	0.3	87.7	12.0	375
1982	5.2	82.5	12.3	464
1983	16.7	71.1	12.2	353
1984	22.7	74.9	2.4	666
1985	38.8	55.1	6.1	516
1986	9.2	86.6	4.2	381
1987	5.8	90.4	3.8	313
1988	1.3	83.9	14.8	384
1989	20.2	76.4	3.4	627
1990	5.1	85.2	9.7	196
1991	30.8	61.2	8.0	425

Three adjacent generations of young sockeye, i.e. underyearlings, yearlings and two-year-olds feed and grow in the lake together. After hatching out, the alevins spend some time in the littoral zone of the lake, and during this period are in no way food competitors of the juveniles; in the second half of summer, they move into the pelagic zone. All through the foraging season, they come in contact with one-year-olds and the non-migrant part of the two-year-olds.

Table 28 contains the size-weight characteristics of the sockeye smolts that migrated from Kuril L. in 1975 through 1991.

Data on the growth rate of sockeye smolts that migrated downstream from Kuril L. during 1975-1991 are presented in table 29. Analysis of the growth rate shows that the older smolts have a slower growth rate (two-year-olds in the first year, and three-year-olds in the first and second years). The same was noted earlier by M. M. Selifonov (1970a).

Table 30 gives the size-weight characteristics of the sockeye smolts of Kuril L. during periods varying in the abundance of spawned out adults. In the past, 1943-1967 were considered to be the years of high abundance (prior to fertilization), and 1968-1977 the years of low abundance (Dubynin, Bugaev, 1988). Our most recent investigations have shown that it is more correct to regard 1943-1963 as the years of high abundance, and 1964-1977 as the years of low abundance of spawned out adults (table 30). We based this conclusion on a graphic analysis of the inter-annual dynamics of spawner escapement, the

Table 28. Body length and weight of sockeye smolts migrating from Kuril L. in 1975-1991 (Dubynin, Bugaev, 1988; with addenda)

Migrating year	Age 1+			Age 2+			Age 3+		
	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
1975	53-91	73.0 ± 6.5	5	76-126	102.8 ± 1.1	106	103-139	125.5 ± 2.8	17
—	1.1-7.5	3.7 ± 1.12	—	2.2-18.4	10.6 ± 0.3	—	9.2-25.0	18.2 ± 1.2	—
1976	62-109	95.5 ± 1.1	60	83-131	108.0 ± 1.8	51	92-144	117.6 ± 3.3	21
—	1.3-12.8	8.0 ± 0.3	—	5.2-21.2	12.6 ± 0.6	—	6.5-27.5	16.0 ± 1.4	—
1977	50-93	65.1 ± 4.7	8	83-126	109.4 ± 0.4	373	102-129	113.8 ± 3.0	11
—	0.9-6.2	2.3 ± 0.6	—	5.3-18.0	11.8 ± 0.1	—	9.1-17.9	12.9 ± 1.0	—
1978	55-94	87.0 ± 3.0	12	89-128	103.6 ± 0.5	200	105-134	118.8 ± 1.4	30
—	1.1-8.1	6.1 ± 0.6	—	6.5-17.8	10.0 ± 0.1	—	10.5-18.6	14.6 ± 0.4	—
1979	77-97	87.6 ± 3.2	5	80-118	97.0 ± 0.3	612	98-128	112.3 ± 1.0	42
—	3.8-7.6	5.6 ± 0.6	—	4.5-13.1	7.7 ± 0.1	—	7.8-17.4	11.9 ± 0.3	—
1980	84-91	85.0 ± 2.7	5	80-113	95.4 ± 0.3	295	97-133	106.1 ± 1.9	20
—	4.6-6.5	5.4 ± 0.3	—	3.8-12.4	7.6 ± 0.1	—	8.4-20.4	10.6 ± 0.6	—
1981	—	73.0	1	80-110	93.1 ± 0.3	329	100-118	107.5 ± 0.7	45
—	—	3.7	—	4.0-11.6	7.3 ± 0.1	—	8.2-14.0	10.7 ± 0.3	—
1982	47-94	82.1 ± 2.2	24	78-111	93.6 ± 0.3	383	92-117	105.0 ± 1.2	57
—	0.8-7.9	5.1 ± 0.3	—	3.7-12.3	7.6 ± 0.1	—	7.1-14.2	10.4 ± 0.4	—
1983	47-97	83.7 ± 1.0	59	80-120	99.2 ± 0.5	251	104-129	117.0 ± 0.9	43
—	0.7-8.6	5.3 ± 0.2	—	4.1-15.5	9.0 ± 0.1	—	10.1-19.4	14.2 ± 0.4	—
1984	53-114	93.8 ± 0.7	151	79-129	106.5 ± 0.4	499	102-167	116.0 ± 3.3	16
—	1.3-13.1	7.6 ± 0.1	—	4.3-19.3	10.7 ± 0.1	—	9.6-44.4	15.8 ± 1.7	—
1985	51-108	84.9 ± 0.4	200	79-129	100.7 ± 0.6	284	103-136	116.3 ± 0.5	32
—	0.7-10.4	5.4 ± 0.1	—	4.3-17.9	8.8 ± 0.2	—	9.0-19.3	13.4 ± 0.5	—
1986	67-105	85.8 ± 1.3	35	83-121	100.9 ± 0.5	330	94-118	107.2 ± 1.3	16
—	2.5-10.0	5.7 ± 0.3	—	4.5-14.2	8.9 ± 0.2	—	7.0-14.4	11.3 ± 0.4	—
1987	57-97	83.7 ± 2.5	18	81-110	95.0 ± 0.3	283	94-119	105.8 ± 2.2	12
—	1.0-6.7	4.6 ± 0.4	—	4.0-12.8	6.9 ± 0.1	—	7.0-14.0	9.7 ± 0.6	—
1988	84-95	88.2 ± 2.1	5	81-117	99.7 ± 0.4	321	93-120	108.1 ± 0.7	58
—	4.4-7.5	5.8 ± 0.5	—	4.6-14.7	8.0 ± 0.1	—	7.2-14.3	10.0 ± 0.3	—
1989	77-100	87.3 ± 0.4	127	78-120	97.2 ± 0.3	479	93-139	109.8 ± 2.0	21
—	3.8-8.2	5.6 ± 0.1	—	3.7-13.3	7.6 ± 0.1	—	6.2-20.3	10.9 ± 0.7	—
1990	54-85	70.8 ± 3.6	10	76-120	100.0 ± 0.6	167	100-120	108.6 ± 1.1	19
—	0.8-4.6	2.6 ± 0.4	—	2.7-13.2	7.8 ± 0.1	—	7.8-13.5	9.9 ± 0.3	—
1991	44-99	84.1 ± 0.7	131	68-116	94.2 ± 0.5	260	95-118	106.3 ± 0.9	34
—	0.6-7.9	5.0 ± 0.1	—	2.3-13.7	7.0 ± 0.1	—	6.0-12.6	9.6 ± 0.2	—

Note. Upper values – body length according to Semidt (Pravdin, 1966), in mm; lower – body weight in grams.

Table 29. Growth rates of sockeye smolts of various ages in Kuril L. in each year of freshwater growth (Dubynin, Bugaev, 1988; with addenda), mm

Foraging year	Age 1+	Age 2+		Age 3+		
	The first foraging year	The first foraging year	The second foraging year	The first foraging year	The second foraging year	The third foraging year
1972	—	—	—	48.6	—	—
1973	—	56.5	—	50.9	27.8	—
1974	59.2	55.6	39.5	68.6	23.6	45.1
1975	78.9	62.6	45.1	50.1	25.2	38.8
1976	56.6	50.8	40.0	46.6	30.9	20.3
1977	81.2	60.4	46.2	52.9	37.7	32.8
1978	74.6	57.5	35.1	51.8	27.1	27.2
1979	71.0	53.2	27.4	48.3	22.3	25.6
1980	65.0	49.8	32.8	49.0	25.0	26.7
1981	73.7	59.4	37.9	53.4	32.7	27.5
1982	71.7	50.9	33.2	48.2	28.2	27.7
1983	82.4	58.4	47.9	50.5	32.7	32.1
1984	78.5	62.8	38.3	51.4	22.8	33.8
1985	73.8	51.3	31.2	48.8	24.1	26.6
1986	81.9	61.1	40.2	52.1	27.9	31.0
1987	77.4	54.2	35.3	49.7	26.1	26.4
1988	79.2	63.1	37.9	49.6	30.6	28.4
1989	70.2	57.6	35.6	—	27.3	27.1
1990	75.8	—	31.0	—	—	24.8

Table 30. Average body length and weight of Kuril *L. sockeye* smolts during periods of varying brood stock abundance (Dubynin, Bugaev, 1988, with addenda and changes)

Age	Indicator	Before fertilization					After fertilization				
		1946-1966	1967-1980	1981-1982	1983-1984	1985-1986	1987-1988	1989-1990	1991	1981-1991	
2+	Body length, cm	8.5-10.7 9.19	9.4-11.0 10.17	9.3-9.4 9.35	9.9-10.7 10.30	10.1-10.1 10.10	9.5-10.0 9.75	9.7-10.0 9.85	9.4 9.40	9.3-10.7 9.83	
	Body weight, g	5.9-10.2 7.71	7.6-12.6 9.93	7.3-7.6 7.45	9.0-10.7 9.85	9.8-8.9 8.85	6.9-8.0 7.45	7.7-7.8 7.70	7.0 7.00	7.0-10.7 8.15	
3+	Body length, cm	9.8-13.5 10.76	10.3-12.8 11.45	10.5-10.8 10.65	11.6-11.7 11.65	10.7-11.6 11.15	10.6-10.8 10.70	10.9-11.0 10.95	10.6 10.60	10.5-11.7 10.98	
	Body weight, g	8.3-15.4 11.54	9.6-21.1 13.92	10.4-10.7 10.55	14.2-15.8 15.00	11.3-13.4 12.35	9.7-10.0 9.85	9.9-10.9 10.40	9.6 9.60	9.6-15.8 11.45	
Spawning brood stock, mill. of specimens		1.732	0.557	1.400	1.375	1.200	3.085	2.675	2.050	1.153	

Note. Upper values – range of values in different years; lower values – mean values for given period.

abundance and biomass of the food zooplankton, the specific size of the foraging grounds (volume of water per fish), as well as the body length and weight of the sockeye smolts of Kuril L.

Based on the maximum size of two-year-old smolts in 1983 and 1984 (10.3 and 9.85 g), we can conclude that the maximum length and mass of the fish after the 1981-1982 fertilization were of the same order of magnitude as in the period of low abundance when an average 2.5 times fewer adult fish spawned in Kuril L. However, compared with the highly abundant years and with the escapement of spawners averaging the same, two-year-old sockeye smolts after fertilization were 12.0 % longer and 27.8 % heavier than those of the 1943-1963 spawning seasons (table 30), these figures are somewhat different from those presented earlier (Dubynin, Bugaev, 1988), but it would be more correct to use them from the point of view of the population dynamics of the sockeye population of Kuril L.

Table 31 shows the dynamics of the sexual composition of the sockeye smolts and the biomass of the food zooplankton during July–October in Kuril L. in the year preceding the downstream migration. Based on the data available to us, we calculated the second-order parabolic equation which we believe produced the closest extrapolation of the available group of points, the relationship is expressed by the following formula:

$$Y = 36.999 + 0.207x - 0.0007x^2,$$

where “*x*” – denotes the biomass of the food zooplankton in July–October in the year preceding the downstream migration (mg/m³), and “*Y*” – the proportion of females participating in the downstream migration (%).

Table 31. Sex composition of sockeye smolts and the biomass of food zooplankton in July–October in Kuril L. during the year prior to migration (Dubynin, Bugaev, 1988; with addenda), %

Migrating year	Ratio of migrants, %		Number of fish	Biomass of food zooplankton in year prior to migration mg/m ³
	Male	Female		
1976	52.3	47.7	132	-
1977	51.8	48.2	392	-
1978	45.0	55.0	242	-
1979	49.3	50.7	659	118.54
1980	50.5	49.5	321	92.33
1981	52.5	47.5	375	74.60
1982	48.3	51.7	464	118.77
1983	49.9	50.1	353	93.20
1984	47.1	52.9	666	119.70
1985	50.4	49.6	516	186.24
1986	44.6	55.4	381	125.00
1987	48.9	51.1	313	192.80
1988	47.3	52.7	383	195.68
1989	46.1	53.9	627	175.33
1990	53.1	46.9	196	54.68
1991	49.2	50.8	425	No data

The points characterizing individual years of downstream migration of sockeye smolts from Kuril L. (1985, 1987-1989) and belonging to the right branch of the parabola did not stand out from the others either in the incidence of yearling smolts, or in the temperature conditions.

The literature contains data on the possibility of sex reversal in juvenile sockeye at the early stages of postembryonic development, due to a variable intensity of feeding. This data was obtained under laboratory conditions. The authors attributed this phenomenon to the possible effect of androgenous hormones (the levels of which are quite high in crustaceans) on the endocrine system of young sockeye.

We do not exclude this possibility either, since the sockeye in Kuril L. feed mainly on crustacean zooplankton. However, we believe that sex reversal in the young of the Ozernaya R. sockeye is associated not only with the diet, but apparently with temperature conditions and possibly other environmental factors.

8.5. Feeding characteristics of juvenile sockeye in the Kamchatka R. waterwhed. Food competitors and predators

8.5.1. Spatial distribution of the threespine stickleback population in the Kamchatka R. watershed

The threespine stickleback, *Gasterosteus aculeatus*, is a widely distributed component of the lacustrine and fluvial ichthyofaunas of the Asian and American coasts of the North Pacific which is inhabited by Pacific salmon of the genus *Oncorhynchus*. Based on the number of lateral plates on the body, the following three morphs of the threespine stickleback are distinguished: *trachurus* in which a continuous row of 20-30 plates covers the whole body, fusing with the caudal keel; *semi-armatus* in which 10-20 plates are arranged in the anterior part of the body and a keel is present, but there is always a break between the plates and the keel; *leiurus* in which the body is glabrous, and 3-8 plates are present only in the anterior part of the body, the Palearctic and Nearctic seas are inhabited by the *trachurus* morph which migrates to the coastal areas and fresh waters during the breeding season. In freshwater lakes, we encounter monomorphic populations of each of the three morphs,

mixed populations with three morphs, or populations which include only *leiurus* and *trachurus* (Hagen, 1967; Ziuganov, 1983). However, small isolated lakes where there is no immigration from the sea are usually inhabited by monomorphic *leiurus* populations (Berg, 1948; Ziuganov, 1983).

At the present time, the freshwater threespine stickleback is regarded as a food competitor of young sockeye, which is equally detrimental to both species (Burgner et al., 1969; Markovtsev, 1972; O'Neil, Hyatt, 1987, etc.).

In the Kamchatka R. watershed, drastic increases in the abundance of the anadromous form of the threespine stickleback were noted at the end of the 1940s and the end of the 1970s–beginning of the 1980s. Based on the recommendations of the Kamchatka branch of TINRO, removals of this species were carried out in the Kamchatka R. watershed in 1979 through 1984, and they amounted to as much as 340 tons in 1983 (Lagunov, 1985); However, because of a decrease in the numbers of the stickleback in 1985, this practice was stopped and never resumed after that.

Two sympatric forms of *Gasterosteus aculeatus*, the freshwater *leiurus* with few plates and the anadromous *trachurus* with a large number of plates, have been discovered in Azabach L. (Ziuganov et al., 1987; Ziuganov, Bugaev, 1988; Bugaev, 1992), the largest foraging lake of the Kamchatka R. watershed where up to 50-70 % of all the juvenile sockeye of this river feed and grow (Bugaev, 1987).

Trawling in the pelagic zone of Azabach L. has shown that immatures of basically the freshwater (landlocked) form inhabited this area in June–August of 1980-1987; its absolute and relative abundance in the lake has increased significantly in recent years (Bugaev, 1988). In connection with this, we wonder whether the increase in the numbers of *leiurus* in Azabach L. is correlated to the decrease in the numbers of *trachurus* in the Kamchatka R. watershed.

The material for this particular study consisted of threespine stickleback caught in different parts of the Kamchatka R. watershed during 1985-1988 (fig. 3).

The spawning migration of *trachurus* in the Kamchatka R. lasts for quite a long time, 5-6 months, and it probably begins during the period when the river is still partly covered with ice. The fact that *trachurus* was encountered in the catches from the estuary of the Kamchatka R. at the end of April 1988 is an indication of this. The breakup in the lower reaches of the river in 1988 occurred at the very beginning of May (Bugaev, 1992a).

The largest catches (up to 500-600 per haul) in the estuary of the Kamchatka R. were noted from the middle of May to the middle of June, which obviously indicates that the migration of the anadromous stickleback peaks during this period. A noteworthy fact is that very significant fluctuations in abundance per haul are observed at short intervals in June. A study of the sexual composition of the catches showed that females predominated significantly in large hauls, and males predominated in small ones (Bugaev, 1992a).

The removals showed that the abandoned river channel (oxbow lake) above the village of Dolinovka, located about 495 km from the mouth of the Kamchatka R., was the upper boundary of the *trachurus* range in the Kamchatka R. watershed (table 32). While we encountered one specimen of *trachurus* here in 1986, we did not come across a single individual in 1988. Apparently, the anadromous form of the stickleback is kept from migrating upstream by the more rapid currents of the Kamchatka R. at the riffles near the village of Dolinovka, where they often reach a speed of 1.8-2.0 m/s and more (Vaskovsky, 1973).

If we disregard the catch per haul in the lakes of the lower Kamchatka R. (table 33), then we can say that the per haul catches of *trachurus* in 1988 decreased in direct proportion to the distance of the lake from the estuary of the Kamchatka R. on the Kurazherchnoye L.–Dolinovka stretch.

Tables 32 and 33 characterize the relative and absolute frequency of occurrence of the freshwater (*leiurus*) and anadromous (*trachurus*) threespine stickleback in the Kamchatka R. watershed, as we can see from these tables, the occurrence of *leiurus* and *trachurus* together is common for the lakes of the lower Kamchatka R. (lakes Nizovtsevo, Krasikovskoye, Azabach and Kursin), there is practically no *leiurus* in Kurazhechnoye L.; we came across three specimens of *leiurus*, two of them sexually mature ones, on 7 August 1986, and one immature specimen on 10 July 1988 (tables 32 and 33). On 3 August 1987, we caught three mature *trachurus* and numerous underyearling *trachurus* in Kharchinskoye L. (Yelovka R. watershed), but no adult or juvenile *leiurus* were encountered here. We did not encounter any *leiurus* in the “Ushkovskoye L.” limnokrene or in the “Lake Kulpik” oxbow lake either in 1986 or in 1988. We found no adult *leiurus* in the “Dedova Yurta” oxbow lake in either of these years, but we did catch 8 immature two-year-old *leiurus* in 1988. In the oxbow lake above the village of Tayozhny, we came across one mature two-year-old male *leiurus* in 1986, but we did not encounter any freshwater three-spine stickleback here in 1988. It is interesting to note that we encountered mainly immature *leiurus* in the oxbow lake above the village of Dolinovka and in the side channels of the Kamchatka R. near the village of Milkovo (tables 32 and 33).

We should note that the *leiurus* morph is systematically encountered in the vicinity of Milkovo in pits and small disjunct bodies of water which often are not connected with the Kamchatka R. For instance, we caught three 2-year-old *leiurus* with a dip net in one of such pits on 27 May 1986, and an underyearling *leiurus* in a disjunct pool next to it on 25 August 1987.

According to B. B. Vronsky's report, the threespine stickleback is not encountered at all in the upper reaches of the Kamchatka R. near the village of Pushchino (fig. 3); only the ninespine stickleback, *Pungitius pungitius*, is encountered there. The data in table 33 prove, to some extent, that the ninespine stickleback is encountered in the Kamchatka R. watershed (data presented without grouping into mature and immature individuals).

Based on an analysis of tables 32 and 33, one can say that there are two centres where populations of the freshwater form (*leiurus*) reproduce in the Kamchatka R. system, namely the upper reaches of the Kamchatka R. in the vicinity of the villages

Table 32. The frequency of occurrence of the morph *leiurus* and *trachurus* in the brood stock of threespine stickleback in the Kamchatka R. watershed, %

Catch region	3.08-7.08.19			7.07-16.07.1988		
	<i>Leiurus</i>	<i>Trachurus</i>	Number of fish	<i>Leiurus</i>	<i>Trachurus</i>	Number of fish
Branches of the Kamchatka R. (Pushchino village)	100.0	No data	15*	100.0	No	3**
Nameless oxbow lake of Kamchatka R. above the village of Dolinovka	90.0	10.0	10***	100.0	No	1
Nameless oxbow lake of Kamchatka R. above the village Tayeezhnyi	10.0	90.0	10	No	100.0	27
Dedova Yurta *	No	100.0	18	No	100.0	97
Kulpik L.	No	100.0	9	No	100.0	80
Ushkovskoye L.	No	100.0	520****	No	100.0	162
Kurazhechnoye L.	0.4	99.6	500*****	No	100.0	187
Nizovtsevo L.	–	–	–	52.7	47.3	165
Krasikovskoye L.	–	–	–	61.7	32.5	137
Azabach L.	39.3	60.7	107	39.4	60.6	241
Kursin L.	–	–	–	51.6	48.4	219
Mouth of the Kamchatka R.	–	–	–	No	100.0	408

*15 adults and 60 yearlings juvenile two year old *leiurus* were caught. Before 27.05.86 – 8 yearlings and immature two year old *leiurus* were caught.

**In lieu of data missing for 1988 are presented data collected in 25.08.87 where 68 underyearlings, 21 yearlings and 26 two year old *leiurus* were caught (of which there males displayed mating colours).

***9 adults and 28 yearling and juvenile two year old *leiurus* were caught.

****We collected carcasses of *trachurus* on the bottom, there were no *leiurus* spewciment among them.

***** *Trachurus* carcasses were and found on the shore, two adults and one yearling *leiurus* were caught in a beach seine.

Table 33. Catches of threespine and ninespine stickleback in a single sweep of a beach seine in the Kamchatka R. watershed in 1988, number of specimens

Catch region	Distance from mouth of Kamchatka R.	Data of catches	Catch number, specimens		
			Threespine stickleback		Ninespine stickleback
			<i>Trachurus</i>	<i>Leiurus</i>	
Nameless oxbow lake of Kamchatka R. above the village of Dolinovka	495	8.07	No	12.0 (97.2 % young)	8.3
Nameless oxbow lake of Kamchatka R. above the village Tayeezhnyi	430	8.07	13.5	No	0.5
Dedova Yurta *	420	8.07	32.7	2.7 (100 % young)	0.3
Kulpik L.	360	7.07	80.0	No	No
Ushkovskoye L.	220	9.07	163.0	No	No
Kurazhechnoye L.	120	10.07	270.0	1.0 (100 % young)	No
Nizotsevo L.	50	16.07	85.0	1030.0	27.0
Krasikovskoye L.	40	12.07	49.0	488.0 (73.7 % young)	481.0
Azabach L.	50	30.06-15.07	17.5	393.0 (93.3 % young)	107.5
Kursin L.	32	16.07	109.0	149.0 (6.7% young)	62.0

of Milkovo and Dolinovka, and the lakes of the lower part of the river watershed (lakes Nizovtsevo, Krasikovskoye, Azabach and Kursin).

Based on its morphometric characteristics, the *leiurus* morph of the upper Kamchatka R. differs from the same morph of the lower reaches of the river. Furthermore, *leiurus* individuals from the upper reaches of the Kamchatka R. are closer to the anadromous form of the threespine stickleback, than to the freshwater form of the lower Kamchatka R. in some of their characteristics. Certain morphometric characteristics point to sexual differences in *leiurus* and *trachurus* (Bugaev, 1992a).

A size comparison of the adult fish of these two forms of the threespine stickleback from the Kamchatka R. watershed on the basis of material of a single year has shown that the average size of *trachurus* is always greater than that of *leiurus*, and the females are always larger than the males. For example, the average size of *trachurus* males in lakes Nizovtsevo, Krasikovskoye, Azabach and Kursin in 1988 was 83.43 mm, and that of *leiurus* males 65.92 mm; the average size of the females was 89.84 and 77.63 mm respectively. We did not observe any consistent variations in the body size of fish from different lakes which were located at different distances from the mouth of the Kamchatka R. Nevertheless, one can say that *trachurus* individuals from the upper reaches of the Kamchatka R. on the Tayozhny–Kurazhechnoye L. stretch are somewhat larger than those from lakes Nizovtsevo, Krasikovskoye, Azabach and Kursin which are located in the lower part of the river watershed. For instance, the average size of *trachurus* males in 1988 was 86.62 mm in the upper reaches of the Kamchatka R., and 83.43 mm in its lower part; the average size of the females was 92.44 and 89.84 mm respectively. Based on the example of Azabach L. stickleback (data not included in this book), the average size of both forms in 1985–1986 and 1988 differed significantly, which points to the possibility of interannual fluctuation in the size of individual fish.

Females usually predominate in sample hauls of adult freshwater (*leiurus*) and anadromous (*trachurus*) threespine stickleback caught at spawning grounds, but we still have no data on the seasonal dynamics of their sex ratio.

Analysis of the age composition of adult fish at the spawning grounds has shown that most of the *trachurus* individuals (88.8 %) mature at age 3+, and the rest (11.2%) at age 4+. While studying the age composition of several hundred individuals, we came across three *trachurus* specimens which appeared to be of age 5+; However, since we were not certain of the exact age of these fish, we included them in the age 4+ group. In the *leiurus* morph, most of the individuals (82.8 %) also mature at age 3+, but the males also mature at age 2+ (6.1 %), and less commonly at age 4+ (1.2 %). We did not come across any *leiurus* females of age 2+, but we did encounter quite a few females of age 4+ (9.9 %). On the average, the smaller fish are younger, and the larger ones are older in both morphs. However, it is not always possible to correctly determine the age of adult stickleback by size alone, particularly in the older 3+ and 4+ age groups.

In Azabach L., individuals of the *trachurus* morph spawn somewhat earlier than *leiurus* (Ziuganov et al., 1987).

On the whole, the spawning of *trachurus* individuals in the Kamchatka R. watershed takes place earlier than the spawning of *leiurus*, and these differences are more obvious in lakes Nizovtsevo, Krasikovskoye and Kursin, than in Azabach L. The spawning of *trachurus* in Azabach L. lasts longer than in any of the other lakes that we have studied in the Kamchatka R. watershed (tables 32 and 33). This is probably due to the greater abundance of adult *trachurus* here, and also to the greater depth and area of this lake in comparison with all the others (Bugaev, 1992a).

Let us examine in greater detail the growth of the young of the freshwater form of the threespine stickleback in the Azabach L. watershed. As we can see from fig. 77, a two-peak distribution of body length is observed in the *leiurus* caught in the littoral zone two weeks after breakup (3 July 1985). Age determination showed that the first group of fish consisted of age 1+ individuals, and the second group age 2+ individuals. The presence of these groups was also observed in a sample taken later, on 23 July 1985, but the percentage of age 2+ individuals was much lower during this period. This may have been due to both the characteristics of the sample, and the migrations of the fish in the pelagic zone of the lake. On the same date, the mature *leiurus* caught in the same place formed a third size group. Determination of the age composition of the fish showed that this group consisted mainly of age 3+ individuals, but that age 2+ and 4+ fish were also present.

In 1986, the pattern of size distribution of immature *leiurus* at these spawning grounds was similar to that observed in 1985. For instance, on 29 June 1986, two weeks after breakup, the length distribution of the young again showed two size groups consisting of age 1+ and age 2+ fish respectively. Later, on 16 July 1986, the percentage of age 2+ individuals dropped significantly. As in 1985, the adult fish at this time formed a third group consisting mainly of age 3+ individuals.

Trawling on the lake on 17 July 1986 showed that immature individuals of age 2+ were present in the catches. Proceeding from these data, one can say that the decrease in the percentage of age 2+ individuals in the littoral catches of 16 July 1986 in comparison with the catches of 29 June 1986 was due to the migration of age 2+ individuals from the littoral zone to the pelagial.

Trawl catches of 23 July 1987 showed the presence of two size groups consisting of immature individuals mainly of ages 1+ and 2+, though older ones were encountered, some of which could have spawned in 1987, but at a later time. Removals in the pelagic zone on 18 June 1988 (several days after breakup) showed the presence of one group of fish consisting mainly of age 3+ individuals and occasionally age 2+ and 4+ individuals. Most of the 3+ and 4+ individuals were potential spawners and would spawn that year. Finally, the catches of 30 June 1988 in the littoral zone yielded mainly one age group of stickleback, 2+, and the adult fish consisted largely of age 3+ individuals. It can be assumed that the 3+ individuals had migrated from the pelagial to the littoral zone to spawn.

Analysis of fig. 77 shows that, despite the interannual similarity in the distribution of the young, significant changes in their distribution in the littoral and pelagic zones of Azabach L. can occur during certain years. This is probably related to both the abundance of *leiurus*, and the feeding and temperature conditions in the lake.

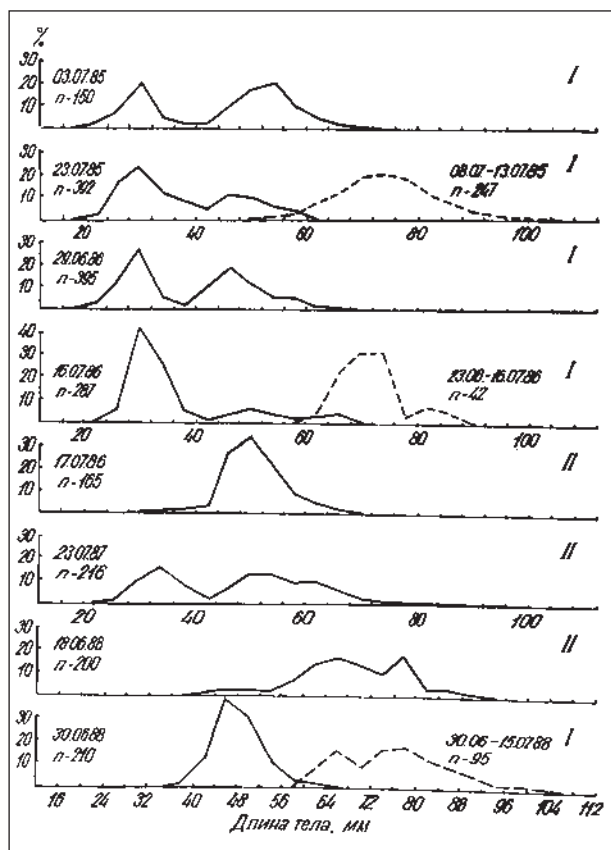


Fig. 77. Length of juveniles and spawners of the freshwater form of the threespine stickleback (*leirus*) in the Azabach L. watershed in 1985-1988. Y-axis – frequency of occurrence, %; X-axis – body length, mm.

I – off-shore catches with a fry trap net in the vicinity of Kultuchnyi beach in Timofeyevsky Bay; II – trawl catches on the lake (station No. 2).

Continuous line – juveniles and likely spawners of the year which have not begun to spawn (still in the pelagic zone); dotted line – adult fish spawning in the littoral zone of the lake.

Fig. 77 shows that, in the first approach during the first half of summer in Azabach L., *leirus* individuals up to 40 mm in length are generally considered as belonging to the 1+ age group, 41-60 mm fish to the 2+ age group, and 61 mm and larger fish to the 3+ age group. However, while the age of 1+ – 2+ individuals can be determined fairly accurately by their size, the age of likely three-year-olds is best determined by the otoliths, since age 4+ and occasionally age 2+ individuals can be encountered among these fish.

Let us now, on the basis of 1989 material, examine the seasonal linear growth of individuals of the *leirus* morph in the lake (fig. 78). As we can see from this diagram, large *leirus*, mostly of age 3+, which were to spawn that year, were encountered in the pelagic zone of the lake in the middle of June (combined data for stations 1, 2 and 3). At the beginning of July, the percentage of mature *leirus* dropped, and we began encountering masses of 30-42 mm yearlings in the pelagic zone. It is interesting to note that two-year-olds (43-60 mm) were scarce during this period.

By the beginning of the second and third 10-day periods of July, yearlings continued to abound in the catches, and we observed an increase in the percentage of two-year-olds which were nearly as large as the smallest three-year-olds.

In the middle–beginning of the third 10-day period of August, the catches began to yield under yearling *leirus* which clearly differed in size from the yearlings. Three clearly separate distributions could be traced; the first consisted entirely of underyearlings, the second of yearlings, and the third mainly of two-year-olds, but we also encountered three-year-olds which were probably going to spawn later that same year.

Underyearlings constituted the bulk of the catches at the beginning of September. Yearlings and two-year-olds were not as commonly encountered. At the beginning of the third 10-day period of September, underyearlings and yearlings constituted the bulk of the landings. At the end of September, basically only underyearlings were found in the catches. Underyearlings dominated at the end of the first ten days of October, but yearlings and two-year-olds were also encountered in significant numbers.

As indicated by our survey of the trawl catches of *leirus* during the summer of 1989, certain age groups of this morph of the threespine stickleback were periodically absent in the catches. We attribute this to the fact that we fished the surface waters, and some of the fish during this period could have been at depths inaccessible to our fishing gear. The seasonal vertical migrations of the threespine stickleback and other fish are determined by the vertical and horizontal distribution of the zooplankton in Azabach L. (Nikolayev, Bugaev, 1985; Nikolayev et al., 1989), as well as by the inter- and intraspecific food relationships of the fish in this lake.

In the case of the lake's fertilization, the question concerning the food relationships between the sockeye and its competitors will be one of the major ones when determining the probable effectiveness of fertilization.

8.5.2. Feeding habits of underyearling sockeye in the Kamchatka R. watershed

Our research has shown that the young of the early form of the sockeye in the upper tributaries of the Kamchatka R. migrate downstream to the sea mainly as underyearlings, while the young of the late form feed and grow in the spawning area

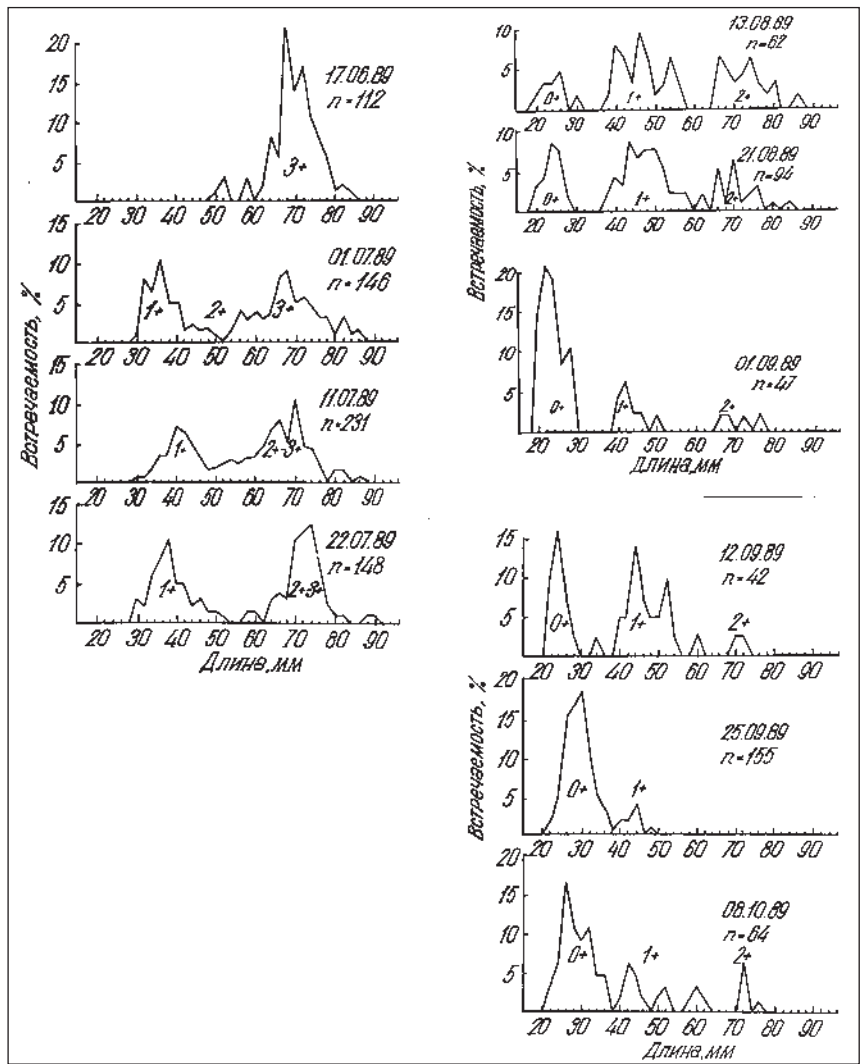


Fig. 78. Body length of the freshwater form of the threespine stickleback (*leiurus*) in the pelagic zone of Azabach L. in 1989 (combined data for stations 1-3). Y-axis – frequency of occurrence, %; X-axis – body length, mm. Figures on graphs denote predominant age in samples.

for a year. At the same time, the young fish from the tributaries of the middle and lower reaches (both seasonal races) enter Azabach L. in masses and Nerpichye L. in smaller numbers during the first year of foraging. In the process of catadromous migration, most of the underyearlings forage briefly in oxbow lakes, or abandoned river channels of the middle reaches of the river and in floodplain lakes of the lower reaches. The lake-spawned juveniles forage in lakes, for one year in lakes Kursin and Nerpichye, and two years in lakes Azabach and Dvukhyurtochnoye. Some of the underyearling sockeye (10-20 % according to our estimates) forage and overwinter in the floodplain and oxbow lakes of the Kamchatka R. watershed, as confirmed by our encounters of yearlings during the first half of summer (sections 8.3.1-8.3.3).

The mentioned types of foraging grounds of juvenile sockeye in the Kamchatka R. watershed are characterized by the specific nature of their abiotic and biotic conditions (water temperature, depth) and by the species composition of the food organisms (Kurenkov, 1967, 1967a, 1972; Simonovs, 1972a; Belousova, 1972, 1974; Bazarkina, 1983, 1986, 1989).

As shown earlier (section 8.3.1), the downstream migration of underyearling sockeye from the spawning grounds of the upper and middle part of the Kamchatka R. watershed takes place from the beginning of March up to the beginning of July.

Underyearling sockeye, migrating to the mouth of the Kamchatka R. or to foraging waters (primarily Azabach L.), must inevitably pass through the flood-plain lakes of the Kamakovskaya lowland, which are located between the Bolshaya Khapitsa and Yelovka rivers (fig. 2, 3). It is also possible for them to forage in other lakes and abandoned river channels in the middle reaches of the river. Having begun to forage while still at the spawning grounds, some of them migrate to the Kamchatka R.'s main channel, and some to the floodplain and oxbow lakes as the ice on them breaks up, where the foraging conditions are quite good prior to the high-water period (Kurenkov, 1967).

The maximum biomass of zooplankton in the floodplain lakes is noted at the beginning or in the middle of June, usually 10-15 days after breakup. The sequence in which the lake ice breaks up and the biomass of zooplankton increases can be traced from the area around the village of Milkovo (580 km) towards the mouth of the river (Kurenkov, 1967).

With the onset of the summer flood, particularly in the lakes of the middle part of the Kamakovskaya lowland. The lakes become flooded and their flowage increases at the end of June–beginning of July, which worsens foraging conditions (Kurenkov, 1967). In the lakes which partially cut into the original banks of the Kamchatka R. valley, the flowage is reduced and the effect of the flood on the reduction of zooplankton abundance is weaker. In low-flowage lakes, the abundance of the majority of zooplankton species decreases in the second half of August; in flow-through lakes, it increases. The patterns of

zooplankton development in the lakes of the Kamakovskaya lowland are typical of shallow lakes, and the biomass of the summer zooplankton in them is not high. On the whole, lakes of this type are unsuitable for the foraging of young sockeye (Kurenkov, 1967, 1978).

With the summer flooding of the floodplain lakes, the foraging conditions deteriorate, and some of the underyearlings migrate seaward. The thinning of the population apparently improves the foraging conditions of the young in the lakes to some extent. At the beginning of the downstream migration (in June), individuals with remnants of the yolk sac are encountered at the mouth of the Kamchatka R.; these young fish are very small, and do not have scales. Larger immature fish, nearly all of which have scales, migrate in July–beginning of August (table 17). One can assume that the underyearlings migrate towards the mouth of the Kamchatka R. in June, without staying in the floodplain lakes. On the other hand, the young that migrate downstream in August probably spend some time in the floodplain and oxbow lakes in the middle reaches of the river, and later migrate to its estuary only after the water level in the lakes drops. The number of underyearlings in the oxbow lakes or abandoned rivers channels of the middle reaches decreases considerably in the second half of summer.

The increase in the abundance of downstream migrants at the mouth of the Kamchatka R. in August coincides with the migration of young fish from the tributaries of its lower reaches (mainly from the Yelovka R.) to Azabach L. (Bugaev, 1981a), these underyearlings have scales, and are of the same size as the fish encountered in the estuary. The intensification of downstream migration during this period is due to the fact that, as early as the beginning of September, the biomass of zooplankton decreases and the foraging conditions deteriorate drastically in the floodplain lakes of the Kamchatka R. watershed because of the drop in water temperature (Kurenkov, 1967).

During the drop in water level, the young sockeye can remain in disjunct, partially disjunct, or other small bodies of water where, according to our observation, the temperature can go up to 24–25°C on some days during the summer months. In some cases, this can lead to total or partial mortality of the immature fish. At a water temperature of 24°C, young sockeye cease to grow, and the mortality rate increases (Brett et al., 1969). Our data on the rate of sclerite formation in underyearling sockeye also confirm the decrease in the growth rate of young sockeye in the Kamchatka R. watershed with higher than usual water temperatures (fig. 56).

The intensification of underyearling sockeye migration in August, when the water level is still fairly high, via the lakes of the Kamakovskaya lowland to Azabach L, and the mouth of the Kamchatka R. is ecologically justified. However, not all of the young fish that migrate towards the river's estuary proceed to the sea. Some migrate and remain in Nerpichye L. to feed and grow (Bugaev, 1984a).

Our investigations have shown that the index of fullness of underyearling sockeye in July–September in the different lakes of the Kamchatka R. watershed is extremely variable. For instance, the mean indexes of fullness on the same dates can differ by more than 50–100 ‰, and in mid August even by more than 400 ‰ (Bugaev, Nikolayeva, 1989).

Quality-wise, the food of juvenile sockeye in the Kamchatka R. watershed is quite varied; it consists of planktonic crustaceans, the pupae of chironomids, stoneflies, caddis flies and mayflies, as well as the imagoes of land insects (table 34).

The juveniles inhabiting lakes feed mainly on planktonic crustaceans. The food of underyearlings from small floodplain lakes consists mainly of *Daphnia cucullata*, and less commonly *Leptodora kindti*, *Heterocope appendiculata* and *Bosmina longirostris*. According to S. P. Belousova (1972, 1974), the juvenile sockeye in Azabach L. consume mostly *Cyclops scutifer* and *Daphnia galeata* during the summer–autumn period, which has also been confirmed by our own material (table 34, section 8.5.3). The young feed on planktonic crustaceans in the floodplain and oxbow lakes of the watershed only in summer (tables 34 and 35), during the prolific period of the latter's development (Kurenkov, 1967). Chironomids, stoneflies and land insects supplement the diet of underyearling sockeye considerably as the abundance of plankton diminishes. The proportion of amphi-biotic insects in the diet increases significantly during the mass emergence of the insects. The same change in the qualitative composition of the food consumed by the young of the sockeye was noted earlier (Belousova, 1974; Foerster, 1968). Young sockeye foraging in the vicinity of the spawning grounds or channels of the river watershed feed mainly on chironomids (table 34), as noted earlier by N. A. Simonova (1972a) and Rogers (1968).

A high frequency of occurrence of planktonic crustaceans (*Cyclops* sp.) was noted in the food consumed by young fish from Ushkovskoye L., which is not typical of the diet of fish that forage in spawning areas. This is due to the fact that the water level in this lake in summer rises drastically because of the flooding of the Kamchatka R.; this weakens the effect of the ground waters, increases the water temperature (Ostroumov, 1975b), and leads to the brief development of crustacean plankton which is readily consumed by the young of the sockeye.

Therefore, as indicated by our own material and the earlier results of other researchers (Krogus, Krokkin, 1956; Foerster, 1968; Burgner et al., 1969; Belousova, 1974; Smirnov, 1975; O'Neil, Hyatt, 1987; Burgner, 1991), young sockeye prefer to feed on plankton, consuming other organisms only when the latter is absent or in short supply.

According to I. I. Kurenkov (1978, section 7), the majority of Kamchatkan lakes are grouped, on the basis of the characteristics of their pelagial ecosystems, into two basic types, shallow (up to 13–18 m) and deep (over 13–18 m).

Most of the lakes of the Kamchatka R. watershed belong to the typically shallow group (e.g. oxbow lakes Dedova Yurta, Kulpik L., lake without a name above the village of Tayozhny; floodplain lakes Kurazhechnoye, Kobylkino, all the other lakes of the Kamakovskaya lowland; lakes Nizovtsevo, Krasikovskoye, etc.), and only two belong to the typically deep lakes (Azabach and Dvukhyurtochnoye), and one lake belongs to the intermediate type, but it is closer to the group of deep lakes (Kursin L.).

The pelagic zone of the small lakes is characterized by plankton species that undergo winter diapause. The pelagic

Table 34. The feeding spectrum of sockeye underyearlings in the Kamchatka R. watershed (ratio of stomach contents), %

Food composition	Spawning ground										Rivers (bellow spawning grounds)				Oxbow lakes and old side channels of Kamchatka R. valley		
	1		4		11		12		23		5		7				
	18.07.70	02.10.70	26.09.78	24.08.77	09.08.77	26.09.78	19.07.76	11.08.77	17.10.77	31.07.77	05.07.77	18.08.76					
Crustacea	20.3	2.6	-	-	41.7	-	16.4	5.6	+	87.1	97.3	72.4					
Ephemeroptera larvae	-	-	-	-	-	-	6.5	0.8	-	-	-	-					
Plecoptera larvae	-	12.5	0.2	-	-	-	-	-	4.1	-	-	-					
Coleoptera imago	-	-	-	-	-	-	-	0.8	1.4	-	-	-					
Trichoptera larvae	-	3.5	1.4	-	-	-	-	-	-	-	-	-					
Chironomidae larvae	54.3	70.7	14.5	40.9	12.4	25.6	40.2	1.6	17.9	0.7	0.5	2.9					
Chironomidae pupae	25.4	-	1.2	28.8	45.2	23.8	-	85.1	1.8	1.6	1.5	4.4					
Chironomidae imago	-	-	-	-	-	-	-	2.2	-	-	-	4.4					
Heleidae larvae	-	-	-	-	-	-	0.3	-	-	-	-	-					
Diptera larvae	-	-	12.6	2.6	-	-	-	0.6	-	-	-	-					
Terrestrial insects imago	-	-	7.3	20.3	-	-	19.5	3.3	25.5	1.6	0.7	3.6					
Araneinae imago	-	-	0.5	-	-	-	-	-	-	-	-	-					
Hydracarina larvae	-	1.8	-	-	-	-	-	-	0.1	-	-	-					
Pisces larvae	-	-	-	-	0.7	-	-	-	-	-	-	-					
Varia	-	8.9	62.3	7.4	-	50.6	17.1	-	49.2	9.0	-	12.3					
Total consumption index, ‰	128.4	43.7	155.0	113.4	271.5	85.9	89.5	268.5	31.1	74.8	140.9	134.2					
Empty stomachs, %	-	-	-	-	-	-	10.5	-	8.0	4.5	-	20.0					
Average body length, mm	35	56	47	46	63	73	45	53	75	65	60	61					
Number of fish	16	15	25	25	25	25	19	18	25	21	25	5					

Food composition	Oxbow lakes and old side channels of Kamchatka R. valley										Lakes along the lower part of the Kamchatka R.				
	10		14		15		16		17		20				
	25.05.78	19.06.77	19.07.77	31.07.77	20.08.76	20.08.77	02.09.76	03.09.76	16.10.79	12.08.77	13.08.77	09.09.76			
Crustacea	1.1	99.7	96.8	12.6	100	+	+	-	100	+	97.9	65.1			
Ephemeroptera larvae	-	-	-	-	-	-	-	-	-	-	-	-			
Plecoptera larvae	-	-	-	-	-	-	-	-	-	-	-	-			
Coleoptera imago	-	-	-	-	-	-	-	-	-	-	-	-			
Trichoptera larvae	-	-	-	-	-	-	1.5	-	-	-	-	-			
Chironomidae larvae	23.1	0.1	-	19.0	+	0.3	-	18.8	-	3.1	-	-			
Chironomidae pupae	59.6	0.2	3.2	66.7	-	54.9	-	0.2	-	75.1	0.2	5.1			
Chironomidae imago	2.3	-	-	-	-	-	-	-	-	-	-	-			
Heleidae larvae	-	-	-	-	-	-	-	-	-	-	-	-			
Diptera larvae	-	-	-	-	-	14.3	-	-	-	-	-	-			
Terrestrial insects imago	13.9	-	-	-	-	30.5	98.5	68.2	-	21.2	1.9	23.7			
Araneinae imago	-	-	-	-	-	-	-	-	-	-	-	1.3			
Hydracarina larvae	-	-	-	-	-	-	-	-	-	-	-	-			
Pisces larvae	-	-	-	-	-	-	-	-	-	-	-	4.8			
Varia	-	-	-	1.7	-	-	-	12.8	-	-	-	-			
Total consumption index, ‰	226.1	75.6	240.2	118.3	225.2	107.0	104.9	140.0	200.8	15.7	100.9	36.8			
Empty stomachs, %	5.6	-	-	-	-	-	-	-	-	24.0	4.2	61.8			
Average body length, mm	31	50	57	56	58	56	60	59	61	60	59	70			
Number of fish	18	25	26	6	25	5	25	18	25	25	25	34			

Note. Dates indicate the regions of data collection (as in fig. 3), the sign “+” – less 0.1 %.

Table 35. The ration of various species and groups of crustaceans in the food of sockeye underyearlings in the Kamchatka R. watershed (as a portion of food weight), %

Food composition	Spawning ground			Rivers (below spawning grounds)		Oxbow lakes and old side channels of Kamchatka R. valley		Oxbow lakes and old side channels of Kamchatka R. valley					Lakes along the lower part of the Kamchatka R.								
	1		12	13	23	5	7	10					14	16	18	17	20				
	18.07.1970	2.10.1970	18.08.1978	19.07.1976	11.08.1977	17.10.1977	31.07.1977	05.07.1977	18.08.1976	25.05.1978	19.06.1977	19.07.1977	31.07.1977	20.08.1976	20.08.1977	2.09.1976	16.10.1979	12.08.1977	13.08.1977	9.09.1976	
<i>Daphnia galeata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Daphnia cucullata</i>	-	-	-	-	-	-	-	78.0	11.6	-	-	12.6	8.2	-	-	-	-	-	80.3	-	21.9
<i>Bosmina longirostris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eurycerus lamellatus</i>	-	-	-	8.2	5.6	+	23.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chydorus sphaericus</i>	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4
<i>Leptodora kindtii</i>	17.4	1.3	-	-	-	-	-	18.8	3.6	2.4	20.7	-	19.5	-	-	-	-	-	16.7	-	-
<i>Heterocope appendiculata</i>	-	-	-	-	-	-	-	0.5	57.2	19.9	-	-	72.3	-	-	-	-	-	+	-	-
<i>Eurytemora kurenkovi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+
<i>Cyclops</i> sp.	2.9	1.3	41.2	-	-	-	18.6	-	-	+	-	-	-	+	-	-	-	-	0.9	-	40.5
<i>Cyclops scutifer</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acanthocyclops gigas</i>	-	-	-	7.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neomysis intermedia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3
Total Crustacea	20.3	2.6	41.2	16.4	5.6	+	87.1	97.3	72.4	1.1	99.7	96.8	12.6	100	+	100	+	97.9	-	65.1	

Note. Dates indicate the regions of data collection (as in fig. 3), the sign “+” – less 0.1 %.

zooplankton of the deep lakes consists of crustacean eupelagic forms which in winter only decrease in abundance and lag slightly in their development (Kurenkov, 1978). It therefore becomes clear that the forage base for juvenile sockeye in Azabach L., unlike that in oxbow and floodplain lakes, is more plentiful and stable throughout the year, which is probably one of the causes of the mass migration of underyearlings to this lake from the tributaries of the Kamchatka R. (Bugaev, 1981a, 1982).

Underyearling sockeye are encountered in the estuary of the Kamchatka R. from the beginning of June up to the end of August. The peak of their downstream migration is observed in the middle of June, its abatement in the middle of July, and its recurrent increase in August; the downstream migration comes to an end in September (Bugaev, Karpenko, 1983).

The feeding of underyearling sockeye at the mouth of the Kamchatka R. is characterized in table 36. The underyearlings apparently spend some time in the estuary, foraging in the zone where fresh and salt waters mix. The foraging conditions in June are more favourable, as the water level in the river is lower and the forage base is more abundant due to the intensive exchange of waters during the high and low tides in the estuarine zone. This is corroborated by the high percentage of brackish-water organisms in the diet of the sockeye (table 36). Marine organisms appear in the food bolus of the sockeye after the high-water peak, during the period of mass zooplankton development in the coastal waters of the Kamchatka Bay. For instance, the percentage of marine organisms in the food bolus on 10 July 1979 amounted to 36.1 % of its total mass, and Harpacticoida predominated among them.

Table 36. Food composition of sockeye underyearlings at the mouth of the Kamchatka R.

Food composition	1978			1979					
	28.07-1.08	05.08-6.08	20.08-21.08	02.06-7.06	15.06	20.06	1.07	10.07	10.08
<i>Podon leuckarti</i>	-	-	-	-	-	-	-	6.3/10	-
<i>Harpacticus</i> sp.	-	-	-	5.4/28	-	-	+20	29.8/70	-
<i>Ceniropagls currichi</i>	-	-	-	-	-	-	+10	-	-
<i>Lamprops korroensis</i>	-	-	-	12.2/28	3.8/13	-	-	2.1/10	-
Gammaridae gen. sp.	-	-	-	-	4.0/25	-	0.9/10	1.6/10	1.2/10
Ephemeroptera larvae	5.6/17	9.5/25	0.6/6	12.6/14	-	-	3.3/10	-	-
Plecoptera larvae	-	-	-	-	11.1/38	14.9/20	-	7.0/10	-
Chironomidae larvae	-	0.3/6	-	50.3/71	51.1/75	44.0/90	79.7/100	12.4/60	-
Diptera imago	64.7/100	89.4/94	97.2/94	11.5/43	30.0/75	34.0/50	16.1/50	39.8/80	95.6/100
Pisces larvae	29.7/33	-	-	-	-	-	-	1.0/10	-
Salmon eggs	-	-	-	8.0/28	-	-	-	-	-
Varia	-	0.8/6	2.2/6	-	-	7.1/10	-	-	3.2/10
Total consumption index, ‰	186.5	112.2	48.4	141.0	288.3	259.6	276.7	238.3	49.9
Empty stomachs, %	-	20	15	22	20	-	-	-	20
Average body length, mm	28-69	45-56	46-64	26-39	26-34	27-33	29-37	27-60	48-77
Number of fish	6	20	20	9	10	10	10	10	10

Note. Above the line is indicated the frequency of occurrence (in the food mass), %; below the line, the frequency of occurrence of food components, %, the sign "+" – less than 0.1.

During the high-water period, the underyearling sockeye in the river's estuary feed mainly on benthic organisms that float to the surface. During this period, the young sockeye pass through the estuary quite rapidly, and therefore marine and brackish-water organisms are not encountered in the food bolus. The food spectrum is similar in downstream-migrant sockeye in August as well. By this time, the emergence of insects is basically over, and the sockeye feeds mainly on their imagoes. Towards the end of August, the foraging conditions in the river deteriorate, as indicated by the low index of fullness observed in underyearling sockeye, the seaward migration of the young is comparatively quick; at sea, the foraging conditions in the littoral zone during this period are more favourable than in the river (Karpenko, 1979). During August 1978, the index of fullness in underyearling sockeye also dropped from 186.5 to 48.4 ‰. The change in the index of fullness of immature sockeye corresponds to the changes in the water level of the river (the higher the level, the higher the index of fullness), and depends largely on the volume of surfacing benthos, the main food of in the diet of underyearling sockeye (Bugaev, Karpenko, 1983).

8.5.3. Food relationships of fish foraging in the Azabach L. watershed

The survival of juvenile sockeye during the freshwater period is greatly influenced by their food competitors. The major food competitor of juvenile sockeye is the freshwater (landlocked) form of the threespine stickleback, *Gasterosteus aculeatus* (Burgner et al., 1969; O'Neil, Hyatt, 1987), and the less important competitor is the pond smelt, *Hypomesus olidus* (Burgner et al., 1969; Belousova, 1972).

In addition to the aboriginal juvenile sockeye of stock "A". individuals from the tributaries of the lower Kamchatka R, which migrated to the lake as under-yearlings (group "E") also forage in Azabach L.. Furthermore. young pond smelt migrate to this lake to forage, and the anadromous form of the threespine stickleback (*trachurus* morph) to spawn.

Since 1980, fishing in the Azabach L. watershed has been carried out with trawls, and it has been found (Bugaev, 1988) that the catches from the pelagic zone of the lake usually yield juvenile sockeye, mostly the freshwater form of the threespine stickleback (*leiurus* morph), the pond smelt, and only occasionally the ninespine stickleback (*Pungitius pungitius*) and immature coho salmon (*Oncorhynchus kisutch*), the arctic char, *Salvelinus alpinus* complex, is encountered in exceptional cases.

Over the past years, there has been a substantial increase in the proportion of the freshwater form of the threespine stickleback in the Azabach L. watershed; at the same time, the proportion of juvenile sockeye decreased (Bugaev, 1988; table 37). Apart from other causes, this is probably due to the intensification of intra- and interspecific food relationships between these species in Azabach L.

In this section, we present the results of our study on the food relationships of the fish in Azabach L. In connection with the possible artificial fertilization of the lake, the urgency of this research increases, as it (fertilization) will undoubtedly bring about changes in the composition of the lake's fish community.

Table 37. Trawl catch results in June–August in Asabach L. in 1980-1991

Year	Sockeye	Threespine stickleback		Pond smelt	Coho	Ninespine stickleback	Total
		<i>Leiurus</i>	<i>Trachurus</i>				
Station No. 2							
1980	<u>4.23</u> 77.60	<u>1.15</u> 21.10	No data No data	<u>0.07</u> 1.30	– –	No data No data	<u>5.45</u> 100
1984	<u>10.56</u> 53.80	<u>1.48</u> 7.50	No data No data	<u>7.60</u> 38.70	– –	No data No data	<u>19.64</u> 100
1985	<u>14.24</u> 78.70	<u>1.28</u> 7.1	– –	<u>2.52</u> 13.90	<u>0.06</u> 0.30	No data No data	<u>18.10</u> 100
1986	<u>1.83</u> 2.10	<u>85.43</u> 97.30	– –	<u>0.50</u> 0.60	– –	No data No data	<u>87.76</u> 100
1987	<u>8.82</u> 30.20	<u>17.88</u> 61.10	<u>0.30</u> 1.00	<u>2.18</u> 7.50	<u>0.07</u> 0.20	No data No data	<u>29.25</u> 100
1988	<u>2.00</u> 9.30	<u>16.89</u> 78.60	<u>1.21</u> 5.60	<u>1.40</u> 6.50	– –	No data No data	<u>21.50</u> 100
1989	<u>10.47</u> 51.00	<u>8.78</u> 42.80	<u>0.52</u> 2.50	<u>0.62</u> 3.90	– –	<u>0.14</u> 0.70	<u>20.53</u> 100
1990	<u>15.12</u> 26.00	<u>41.68</u> 71.70	<u>1.14</u> 2.00	<u>0.16</u> 0.30	– –	– –	<u>58.10</u> 100
1991	<u>3.87</u> 40.50	<u>3.95</u> 54.20	<u>1.23</u> 12.9	<u>0.43</u> 4.50	– –	<u>0.08</u> 0.80	<u>9.56</u> 100
Station No. 3							
1980	<u>7.03</u> 22.60	<u>2.50</u> 8.10	No data No data	<u>21.13</u> 68.10	<u>0.37</u> 1.20	No data No data	<u>31.03</u> 100
1984	<u>23.68</u> 22.60	<u>2.38</u> 2.30	No data No data	<u>78.55</u> 75.00	<u>0.17</u> 0.10	No data No data	<u>104.78</u> 100
1985	<u>7.04</u> 24.40	<u>2.84</u> 9.80	<u>0.6</u> 0.20	<u>18.76</u> 65.00	<u>0.16</u> 0.60	No data No data	<u>28.86</u> 100
1986	<u>1.03</u> 5.60	<u>17.47</u> 94.40	– –	– –	– –	No data No data	<u>18.50</u> 100
1987	<u>1.82</u> 6.40	<u>7.35</u> 25.70	<u>0.33</u> 1.10	<u>19.05</u> 66.60	<u>0.05</u> 0.20	No data No data	<u>28.60</u> 100
1988	<u>3.29</u> 12.00	<u>17.54</u> 63.60	<u>2.10</u> 7.60	<u>4.61</u> 16.70	<u>0.03</u> 0.10	No data No data	<u>27.57</u> 100
1989	<u>5.92</u> 32.00	<u>10.02</u> 54.20	<u>0.55</u> 3.00	<u>1.83</u> 9.90	<u>0.02</u> 0.10	<u>0.15</u> 0.80	<u>18.49</u> 100
1990	<u>1.84</u> 2.30	<u>69.56</u> 88.70	<u>2.56</u> 3.30	<u>1.58</u> 2.00	<u>0.02</u> +	<u>2.86</u> 3.70	<u>78.42</u> 100
1990	<u>1.18</u> 6.50	<u>11.35</u> 62.30	<u>1.35</u> 7.40	<u>3.85</u> 21.10	– –	<u>0.50</u> 2.70	<u>18.23</u> 100

Note. Upper value – mean catch per minute of trawling in June-August, specimens; lower value – frequency of occurrence, %. Until 1985 there no divisions made between the morphs *leiurus* and *trachurus* (No data). Due to low abundance of ninespine stickleback before 1989, this species did not calculated (No data). Sign "+" – less 0.01 %.

Feeding of juvenile sockeye

The feeding of young sockeye in the pelagic zone of Azabach L. in June–September is of a fairly diverse nature (tables 38-40).

The food spectrum of underyearling sockeye of group “E” (mean length 61 mm) after migration to the lake at the end of August, on 21 August 1989 (table 38), consists mainly of insect imagoes, predominantly the imagoes of Chironomidae (61.4 %) and Trichoptera (17.7 %) which occur with a frequency of 100 % and 61 % respectively. The number of these organisms per stomach averages 37.4 and 2.2 specimens. Planktonic crustaceans do not play a significant role during this period. Among the latter, we occasionally encounter male and female *Cyclops scutifer* (15 %), females being the predominant ones. The proportion of crustaceans in the food bolus does not exceed 8.3 %, and the average number per stomach is 101.5 specimens. The feeding intensity of group “E” underyearlings in August is relatively high, and the index of consumption is equal to 258.4 ‰. We do not have any data on the feeding of stock “A” underyearlings for this period.

Table 38. The feeding spectrum of sockeye underyearlings in Azabach L. in 1989, station No. 2 (T. N. Travina, T. L. Vvedensky, L. A. Bazarkina, V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	21.08.1989				25.09.1989				25.09.1989			
	Group “E”, age 0+				Stock “A”, age 0+				Group “E”, age 0+			
	1	2	3	4	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i>	15	101.5	41.8	8.3	86	479.9	104.1	48.9	100	632.0	65.1	58.7
N	–	–	–	–	57	25.1	0.2	0.1	33	64.0	0.1	0.2
I	–	–	–	–	57	52.6	2.4	0.7	–	–	–	–
II	–	–	–	–	86	91.4	6.1	2.5	67	56.0	1.1	1.3
III	–	–	–	–	29	41.1	4.3	2.5	100	128.0	4.9	4.7
Females VI	15	923	38.0	7.3	86	269.7	91.1	43.1	100	384.0	59.0	52.5
Males VI	15	9.2	3.8	1.0	–	–	–	–	–	–	–	–
<i>Daphnia galeata</i> , mm	–	–	–	–	86	543.6	69.2	29.1	100	688.5	25.5	27.2
0.45	–	–	–	–	57	41.1	1.6	0.8	100	75.3	1.4	1.2
0.50	–	–	–	–	86	134.8	7.7	3.2	100	96.0	2.2	1.9
0.55	–	–	–	–	86	80.0	6.2	2.4	67	117.3	3.0	3.4
0.60	–	–	–	–	–	–	–	–	33	128.0	4.8	4.1
0.65	–	–	–	–	86	63.7	10.5	4.3	67	37.3	1.5	1.5
0.70	–	–	–	–	57	50.3	5.8	2.8	33	42.7	1.4	2.1
0.75	–	–	–	–	–	–	–	–	33	53.3	3.5	3.1
0.80	–	–	–	–	71	80.0	12.0	6.3	67	85.3	4.9	5.7
0.85	–	–	–	–	86	59.4	16.6	5.4	33	53.3	2.8	4.2
0.90	–	–	–	–	42	20.6	5.9	2.2	–	–	–	–
0.95	–	–	–	–	14	13.7	2.9	1.7	–	–	–	–
<i>Leptodora kindt</i>	–	–	–	–	29	27.4	13.6	6.0	33	42.7	5.2	8.0
Chironomidae pupae	–	–	–	–	71	4.4	44.7	11.8	–	–	–	–
Chiiononudae imago	100	37.4	148.4	61.4	71	1.2	14.1	3.0	67	2.7	7.1	6.1
Insecta imago	100	18.1	25.9	12.0	–	–	–	–	–	–	–	–
Trichoptera pupae	8	0.1	0.7	0.6	–	–	–	–	–	–	–	–
Trichopteta imago	61	2.2	41.6	17.7	–	–	–	–	–	–	–	–
Nematoda	–	–	–	–	–	–	–	–	–	–	–	–
Hydrocarina	15	0.2	+	+	–	–	–	–	–	–	–	–
Misidae	8	0.2	+	+	14	0.9	7.0	1.2	–	–	–	–
Total consumption index, ‰ Empty stomachs, %	–	–	258.4	–	–	–	252.7	–	–	–	102.9	–
Average body length, mm	–	–	61.0	–	–	–	51.0	–	–	–	73.0	–
Number of fish	–	–	13	–	–	–	7	–	–	–	3	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1.

Significant changes occur in the feeding of underyearling sockeye on 25 September 1989 (table 38). The the feeding of both stock “A” (51 mm) and group “E” (73 mm) individuals is practically identical. Planktonic organisms, *Daphnia galeata* and *Cyclops scutifer*, become the main food organisms during this period; the latter play an especially important role. The percentage of the latter in the food bolus is 48.9 % in the stock “A” sockeye and 58.7 % in the group “E” sockeye (of the total mass), they are encountered at different stages of development, but females usually in greater numbers, 269.7 female specimens per stomach in stock “A” underyearlings, and 384 females per stomach in young fish entering the lake from other areas of the Kamchatka R.; the frequency of occurrence of these food organisms equals 86 % and 100 % respectively. Quite frequently (86-100 %), the fish stomachs also contain *Daphnia galeata* which vary in size from 0.45 to 0.95 mm, *Daphnia galeata* of 0.50 mm size are the most abundant in the stomachs of stock “A” underyearlings, and 0.55-0.60 mm individuals predominate in the stomachs of group “E” underyearlings. This is probably due to the fact that group “E” underyearlings are

Table 39. The feeding spectrum of sockeye yearling in Azabach L. in 1989, station No. 3
(T. N. Travina, T. L. Vvedenskay, L. A. Bazarkina, V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	11.07.89 г. – Stock “A”, age 1+				11.07.89 г. – Group “E”, age 1+			
	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i> (VI)	49	1046.1	100.3	94.6	50	490.6	38.4	82.3
<i>Daphnia galeata</i> (0.60 mm)	3	0.8	+	+	–	–	–	–
Chironomidae pupae	46	2.4	6.1	5.3	50	3.5	7.1	14.6
Chironomidae imago	3	+	0.1	0.1	–	–	–	–
Insecta imago	–	–	–	–	25	0.8	1.5	3.1
Total consumption index, ‰	–	–	106.5	–	–	–	47.0	–
Empty stomachs, %	–	–	51.0	–	–	–	50.0	–
Average body length, mm	–	–	70.0	–	–	–	76.0	–
Number of fish	–	–	39	–	–	–	8	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1.

Table 40. The feeding spectrum of sockeye yearling and two yearling in Azabach L. in 1990, station No. 2
(T. N. Travina, T. L. V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	Group “E”, age 1+				Stock “A”, age 1+				Stock “A”, age 2+			
	1	2	3	4	1	2	3	4	1	2	3	4
14.06.1990												
<i>Cyclops scutifer</i> (V-VI)	100	1856.0	85.6	78.7	87	1423.0	165.3	98.6	100	1459.0	63.7	66.1
<i>Daphnia galeata</i>	–	–	–	–	12	0.4	+	+	–	–	–	–
Chironomidae pupae	50	2.5	2.9	2.9	–	–	–	–	30	1.0	1.2	1.2
Chironomidae imago	100	16.0	19.3	18.4	18	0.7	2.7	1.4	100	26.0	47.1	31.4
Insecta imago	–	–	–	–	–	–	–	–	50	1.0	1.2	1.2
Total consumption index, ‰	–	–	107.8	–	–	–	168.0	–	–	–	113.2	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–	–	–	0.0	–
Average body length, mm	–	–	91.0	–	–	–	64.0	–	–	–	88.5	–
Number of fish	–	–	2	–	–	–	16	–	–	–	2	–
25.06.1990												
<i>Cyclops scutifer</i> (II-IV)*	39	442.0	13.1	5.5	58	874.7	39.2	16.2	33	8.3	0.1	0.2
<i>Cyclops scutifer</i> (V-VI)	94	3250.0	183.2	92.3	96	1926.0	183.5	82.0	100	15.1	67.0	97.6
<i>Daphnia galeata</i>	33	34.0	0.3	0.6	51	42.0	2.3	1.0	33	12.0	0.3	0.4
Chironomidae pupae	6	0.2	0.2	0.1	10	0.2	0.5	0.2	–	–	–	–
Chironomidae imago	33	1.5	2.1	1.2	14	0.2	0.4	0.2	33	1.0	1.3	1.8
Insecta imago	6	0.1	0.1	+	14	0.3	0.6	0.4	–	–	–	–
Plecoptera imago	6	0.1	7.8	+	–	–	–	–	–	–	–	–
Ephemeroptera imago	11	+	0.4	0.2	3	+	0.1	+	–	–	–	–
Total consumption index, ‰	–	–	207.8	–	–	–	226.6	–	–	–	68.7	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–	–	–	0.0	–
Average body length, mm	–	–	84.6	–	–	–	68.4	–	–	–	95.3	–
Number of fish	–	–	18	–	–	–	29	–	–	–	3	–
4.07.1990												
<i>Cyclops scutifer</i> (II-IV)*	–	–	–	–	20	132.0	3.9	13.7	–	–	–	–
<i>Cyclops scutifer</i> (V-VI)	50	1057.3	49.9	91.0	60	132.0	10.8	32.6	–	–	–	–
Chironomidae imago	100	4.0	6.1	9.0	100	7.6	16.7	49.0	–	–	–	–
Insecta imago	–	–	–	–	20	0.7	1.5	4.7	–	–	–	–
Total consumption index, ‰	–	–	56.0	–	–	–	32.9	–	–	–	–	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–	–	–	–	–
Average body length, mm	–	–	85.5	–	–	–	74.5	–	–	–	–	–
Number of fish	–	–	4	–	–	–	15	–	–	–	–	–
15.07.1990												
<i>Cyclops scutifer</i> (V-VI)	100	1670.0	148.8	92.7	50	16.0	2.3	21.5	–	–	–	–
Chironomidae imago	100	5.0	11.6	7.3	50	3.5	8.4	78.5	–	–	–	–
Total consumption index, ‰	–	–	160.4	–	–	–	10.7	–	–	–	–	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–	–	–	–	–
Average body length, mm	–	–	71.0	–	–	–	82.0	–	–	–	–	–
Number of fish	–	–	1	–	–	–	2	–	–	–	–	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1. *II-III stages mostly.

larger than those of stock "A". The percentage of *Daphnia galeata* in the food bolus is 29.1 % and 27.2 % (of the total mass) respectively. Apart from the above-mentioned organisms, mysids (Mysidae), *Leptodora kindti*, and the imagoes of chironomids and other insects are also encountered in the stomachs of the fish, but their role in the diet is insignificant.

Young sockeye of age 1+ feed largely on *Cyclops scutifer* in the middle of July (11 July 1989) (table 39), and only individuals at the 4th stage of development are encountered, 1046.1 specimens per stomach is found in stock "A" sockeye (70 mm), and only 490.6 specimens per stomach is found in group "E" sockeye (76 mm). The percentage of these organisms in the food bolus equals 94.6 % and 82.3 % (of the total mass) respectively.

In addition to *Cyclops scutifer*, pupae and imagoes of chironomids and other insects are consumed in small amounts by the young of the sockeye. The latter's intensity of feeding during this period is relatively low. The index of consumption is equal to 106.5 ‰ in the juvenile sockeye of stock "A", and does not exceed 47.0 ‰ in the yearlings of group "E".

On 14 June 1990 (table 40), stock "A" juvenile sockeye of age 1+ (64 mm) fed mainly on *Cyclops scutifer* at the 5-6th stages of development. The average number of these organisms per stomach amounted to 1423 specimens, and the percentage of them in the food bolus 98.6%. In addition to *Cyclops scutifer*, *Daphnia galeata* and chironomid imagoes were also noted in the diet of young Azabach L. sockeye, but they did not play a significant role in the middle of June, the index of consumption was 168.0 ‰.

On 25 June 1990, *Cyclops scutifer* at the 2nd-4th (mainly 2nd-3rd) stages of development, as well as *Daphnia galeata*, appeared in the food spectrum of stock "A" juvenile sockeye of age 1+ (68.4 mm), but *Cyclops scutifer* at the 5-6th stages continued to be the main component of their diet (82.0 %). The intensity of feeding increased at this time, the mean index of consumption going up to 226.6 ‰.

On 4 July 1990 (table 40), chironomid imagoes and *Cyclops scutifer* at the 5-6th (mostly 6th) stage of development began to predominate (49.0 % and 32.6 % of the total mass respectively) in the diet of stock "A" juvenile sockeye of age 1+ (74.5 mm), but the intensity of feeding declined drastically during this period, the index of consumption amounting to only 32.9 ‰.

On 15 July 1990, the food spectrum of stock "A" yearlings (82 mm) remained unchanged. As before, chironomid imagoes constituted the main component of the diet; their percentage in the food bolus increased to 78.5 %, but the index of fullness decreased even more and amounted to 10.7 ‰.

Analyzing the feeding behaviour of two-year-old sockeye of stock "A" (88.5 mm) prior to their seaward migration, we noted that, on 14 June 1990, *Cyclops scutifer* at the 5-6th stages of development were the main component of this group's diet, as in the yearlings of stock "A", and they also formed the greater part of the food bolus (66.2 %), though this was less than in the yearlings, the number of *Cyclops scutifer* per fish stomach was similar, 1459 specimens in two-year-olds and 1423 in yearlings. Besides *Cyclops scutifer*, chironomid imagoes were one of the major components of the diet of two-year-old juvenile sockeye, they constituted 31.4% of the food bolus. The index of consumption during this period was at 113.2 ‰.

On 25 June 1990 (table 40), the two-year-old sockeye of stock "A" (95.3 mm) continued to feed on *Cyclops scutifer*. The number of the latter per fish stomach amounted to 1505, which approximated the figure for the preceding period, but their weight in the food bolus constituted up to 97.6 %, as the percentage of chironomid imagoes had dropped to 1.3 % in comparison with the preceding period. The intensity of feeding decreased, and the index of consumption at this time was equal to 68.7 ‰.

Having examined the feeding behaviour of stock "A" yearlings and two-year-olds, let us now look at the feeding behaviour of group "E" sockeye of age 1+ prior to their seaward migration (table 40).

In the middle of June (14 June 1990), the yearlings of group "E" (91 mm), as in the Azabach L. sockeye, fed predominantly on *Cyclops scutifer*, but chironomid imagoes also made up a significant part of their diet; the two components made up 78.7 % and 18.4 % of the food bolus respectively. The index of consumption at this time was not very high (107.8 ‰).

On 25 June 1990, the food spectrum of the group "E" yearlings (84.6 mm) expanded, their stomachs were found to contain *Cyclops scutifer* at the 2nd-4th (mainly 2nd-3rd) and the 5-6th stages of development, *Daphnia galeata*, chironomid imagoes, etc. However, as before, *Cyclops scutifer* at the 5-6th stages were the main food component, constituting 92.3 % of the total weight of organisms in the food bolus. The intensity of feeding increased significantly, and the index of consumption went up to 207.8 ‰.

On 4 July 1990, the food spectrum in group "E" yearlings (85.5 mm) became narrower; *Cyclops scutifer* was the main component of their diet, but the amount of food being consumed decreased, as evidenced by the [low] indexes of consumption at the time (56.0 ‰).

On 15 July 1990, the intensity of feeding in group "E" yearlings (71 mm) increased, and the index of consumption went up to 160.4 ‰, but the food spectrum remained unchanged.

Unfortunately, S. P. Belousova's earlier data (1974) on the feeding of juvenile sockeye in Azabach L. do not compare favourably with our own data due to differences in age determination.

Feeding behaviour of the anadromous form of the threespine stickleback (*trachurus*)

The anadromous form of the threespine stickleback attains sexual maturity and migrates in masses to spawn in Azabach L. at age 3+, after which it dies. Prior to the seaward migration (in August–September), underyearling *trachurus* forage in the pelagic zone of the lake in large numbers.

At the beginning of September (1 September 1989), the anadromous threespine stickleback of age 0+ (27 mm) in Azabach L. feeds mainly on planktonic organisms, most commonly *Daphnia galeata* (84 %). The relative mass of the latter in the food bolus amounts to 84.6 %. *Chydorus sphaericus* are encountered occasionally (20 %), but they do not form more than 11.2 % of the total mass of the food bolus. The intensity of feeding of this species is very low, the index of consumption amounting to only 6.8 ‰ (Appendix, table 18).

On 25 September 1989, the feeding activity of underyearling *trachurus* (31 mm) increased, and the index of consumption more than tripled (22.8 ‰). During this period, the stickleback feeds mainly on detritus; the frequency of occurrence of the latter is 76 %, and it forms 79.6 % of the total weight in the food bolus. Almost every fish stomach contains *Cyclops scutifer*, mostly their nauplii (56 %) and individuals at the 1st stage of development; their weight in the fish stomachs constitutes 7.7 and 6.3 % respectively. The fish stomachs were found to contain small quantities of *Daphnia galeata* and predaceous copepods (*Ergasilus* sp.) (Appendix, table 18).

In the middle of June (14 June 1990). *Cyclops scutifer* were the main food component in the stomachs of three-year-old (90.8 mm) and four-year-old (97.8 mm) *trachurus*; their relative weight in the food bolus amounted to 78.9 % and 84.7 % respectively. An interesting fact is that the stomachs of the 3-year-old *trachurus* were found to contain the remains of juvenile salmon (not threespine stickleback), which, during this period, were probably from underyearling sockeye. The index of consumption was 449.0 ‰ in the 3-year-olds, and 315.1 ‰ in the 4-year-olds (Appendix, table 19).

On 15 July 1990, the food spectrum of both 3-year-old (88.5 mm) and 4-year-old (95.3 mm) *trachurus* changed drastically. At this time, the 3-year-olds began to feed intensively on the eggs of sticklebacks, both unfertilized eggs and those with embryos at the stage of eye pigmentation. The relative mass of these eggs in the food bolus amounted to 62.6 %. The number of eggs per stomach averaged 20.8. In addition to this, the food bolus consisted 17.0 % of insect imagoes and 19.3 % of *Gammarus lacustris*. The larger four-year-olds fed mostly on *Gammarus lacustris* during the same period (57.3% of the food bolus by weight). Compared with the previous month, the intensity of feeding declined substantially; the index of consumption was 99.5 ‰ in the three-year-olds, and 78.3 ‰ in the four-year-olds (Appendix, table 19).

In conclusion, let us examine the feeding behaviour of *trachurus* in the littoral zone of Azabach L. (Timofeyevsky Bay).

The food spectrum of adult *trachurus* on 13 July 1987 in the littoral zone of Azabach L. (Timofeyevsky Bay) was quite diverse. *Gammarus lacustris* were most commonly encountered (62 %) in the stomachs of the fish (90.0 mm); they measured 13–27 (average 17.2) mm in length, and made up 18.2 % of the food bolus. The frequent occurrence of *Gammarus lacustris* in the stomachs of adult *trachurus* on the spawning grounds of the Azabach L. watershed has been noted earlier (Ziuganov et al., 1987). Fish is rarely encountered (12 %) in the stomachs of *trachurus*, but its weight in the food bolus can be the highest (57 %). The fish remains encountered in *trachurus* stomachs were from the ninespine stickleback (6 %) and underyearling sockeye (6 %). Stickleback eggs are an important component of the *trachurus* diet; they make up 17.3 % of the food bolus by weight, and occur with a frequency of 19 %. Of the planktonic organisms. *Cyclops scutifer* are the most frequently encountered (38 %); the number of these organisms found in the fish stomachs averaged 31, and their weight in the food bolus was equal to 1.2 %. The intensity of feeding of the anadromous stickleback was quite high, and the index of fullness amounted to 169 ‰. Fish with empty stomachs were not encountered (data not tabled in this book).

Feeding behaviour of the freshwater form of the threespine stickleback (*leiurus*)

Most of the freshwater (landlocked) threespine stickleback in Azabach L. attains sexual maturity at age 3+. The feeding behaviour of *leiurus* individuals of different age differs significantly.

At the beginning of September (1 September 1989), underyearling threespine stickleback (23 mm) feed mainly on *Daphnia galeata*. The latter occur frequently (72 %) in the stomachs of these fish, and form the bulk of the food bolus (94.1 %). In addition to *Daphnia galeata*, *Chydorus sphaericus* (12 %) and rotifers (Rotatoria) (20 %) are sometimes encountered, but these do not play a major role in the diet of the underyearlings. The intensity of feeding at this time is not high, and the index of consumption amounts to only 8.5 ‰ (Appendix, table 20).

On 8 October 1989, the feeding behaviour of underyearling *leiurus* (31 mm) changed significantly. The index of consumption increased by two orders of magnitude to 689.7 ‰, their diet consisted mainly of *Cyclops scutifer*; the latter was encountered with a frequency of 100 %, and formed the bulk of the food bolus (96.3 %). The index of consumption for these crustaceans amounted to 666.7 ‰, with 2826.2 specimens encountered per fish stomach. The *Cyclops scutifer* found in the stomachs of the yearlings consisted of nauplii and individuals at the 1st–3rd stages (mostly 1st stage) of development. *Daphnia galeata* were encountered in small quantities (average 36.2 specimens) in the stomachs of underyearlings, they varied in size, but 0.65 and 0.80 mm individuals prevailed.

The feeding behaviour of older *leiurus* in summer (June–August) changes significantly.

In the middle of June (17 June 1989), 2-year-old (69 mm) and 3-year-old *leiurus* fed on *Cyclops scutifer*, including individuals at the 4–5th stages and males at the 6th stage of development. The number of *Cyclops scutifer* per stomach amounted to 4270.5 in 2-year-old *leiurus*, and 3836.6 in 3-year-olds. *Cyclops scutifer* at the 5th stage of development dominated in numbers and percentage of the total mass of the food bolus. The index of consumption was quite high, 458.3 ‰ in stickleback of age 2+, and 319.6 ‰ in age 3+ (Appendix, table 21).

On 11 July 1989, the freshwater threespine stickleback continued to feed mainly on *Cyclops scutifer*. Individuals at the 5th and 6th stages of development were encountered with the latter predominating. The number of *Cyclops scutifer* per stomach

amounted to 862.7 in stickleback of age 1+ (44 mm), and 3126.8 in age 2+ (67 mm); the relative mass of these crustaceans in the food bolus amounted to 99.6 and 98.8 % respectively. The pupae and imagoes of chironomids and other insects were occasionally encountered. Compared with the previous month, the intensity of feeding rose, and the index of consumption reached 554.0 ‰ in yearlings and 532.4 ‰ in two-year-olds.

On 22 July 1989, the feeding behaviour of different age groups of the threespine stickleback remained practically unchanged. *Cyclops scutifer* continued to be the main component in the food spectrum, the females of this species playing an exclusive role. The number of these crustaceans per stomach amounted to 146.4 in the 1+ age group (38 mm), 102.8 in fish of age 2+ (73 mm), and 673.3 in 3+ individuals (82 mm). The intensity of feeding was practically the same in yearlings and two-year-old fish, and the index of consumption was 200.8 and 182.9 ‰; it was considerably lower (80.6 ‰) in 3-year-old individuals (Appendix, table 21).

Significant changes occurred in the feeding behaviour of the different age groups of the threespine stickleback on 21 August 1989. The intensity of feeding declined substantially, to 35.9 ‰ in yearlings (48 mm) and to 22.0 ‰ in two-year-olds (72 mm). The stickleback fed on insects during this period. The imagoes of chironomids (74.5 %) and other insects (21.9 %) prevailed in the food bolus of the yearlings, and chironomid imagoes (51.3 %) and pupae (27.1 %) in two-year-old individuals. Planktonic organisms made up 3.6 % of the food bolus in stickleback of age 1+, and 11.2% in age 2+ individuals.

Analyzing the feeding behaviour of the freshwater threespine stickleback in 1990, one notes that, on 14 June 1990, *leiurus* yearlings (33.1 mm) consumed mainly *Cyclops scutifer* at the 5th and 6th stages of development, which occurred in the fish stomachs with a frequency of 100 % and made up 97.5 % of the total weight in the food bolus. In addition to *Cyclops scutifer*, *Daphnia galeata* were encountered quite frequently in 50% of the cases, but they did not play an important part in the diet of these fish. The intensity of feeding in *leiurus* of age 1+ at this time was very high, the index of consumption per stomach averaging 424.9 ‰ (Appendix, table 22).

On 25 June 1990, *Cyclops scutifer* at the 2nd-4th (mainly 2nd-3rd) stages of development dominated in the food bolus of yearling *leiurus* (33.4 mm). With a 100 % frequency of occurrence, they formed the bulk of the stomach contents (99.0 %). When the yearling *leiurus* began feeding on younger age groups of *Cyclops scutifer*, the index of consumption decreased by one-half to 262 ‰, though the number of organisms per stomach increased to 468 at the time.

On 4 July 1990, the food spectrum changed both in quality, and quantity. For instance, in the July 4th sample, yearling *leiurus* (37.2 mm) consumed *Cyclops scutifer* at the 2nd-4th (mainly 2nd and 3rd) stages of development with a frequency of 40 %, and individuals at the 5th and 6th stages with a frequency of 60 %; a high frequency of occurrence of rotifers (60 %) and a lower frequency of *Daphnia galeata* (30 %) was observed. *Cyclops scutifer* at the 5th and 6th stages made up 77.4 % of the food bolus, and individuals at the 2nd-4th (mainly 2nd and 3rd) stages of development 10.9 %. For instance, one fish stomach averaged 147 *Cyclops scutifer* at the 5th and 6th stages, and 47 at the 2nd-4th (mainly 2nd and 3rd) stages of development. Rotifers played a definite role in the diet of yearling *leiurus*, numbering more than 200 per stomach; However, because of their small size, they made up not more than 0.9 % of the food bolus by weight. In addition to the above, the stomachs of yearling *leiurus* were found to contain chironomid pupae and imagoes, insect larvae and algae. The intensity of feeding decreased at this time, and the index of consumption averaged 164.2 ‰ (Appendix, table 22).

On 15 July 1990, the intensity of feeding in yearling *leiurus* (32.6 mm) dropped significantly and the index of consumption was only 17.4 ‰, due to the fact that *leiurus* of this age had almost completely begun feeding on rotifers (frequency of occurrence 75 %) and *Bosmina* sp. (35 %). However, due to the small size of these organisms, their weight in the food bolus amounted to only 16.6 and 2.8 % respectively.

On 17 August 1990, adult *Daphnia galeata* and *Cyclops scutifer*, mainly female individuals, became the main components in the diet of yearling *leiurus* (40 mm). The number of *Daphnia galeata* per stomach amounted to 136, and the number of *Cyclops scutifer* 68, the intensity of feeding increased, and the index of consumption was 185.6 ‰ during this period (Appendix, table 22).

Examining the feeding behaviour of two-year-old *leiurus*, one notes that, on 14 June 1990, individuals measuring 56.2 mm in length fed mainly on *Cyclops scutifer* at the 5th and 6th stages of development, which formed the bulk of the food bolus (up to 100 %). The index of consumption amounted to 1438.6 ‰, and the number of *Cyclops scutifer* per stomach averaged 6893.

On 27 July 1990, two-year-old *leiurus* (54.7 mm) fed on the young age groups of *Cyclops scutifer* which occurred with a frequency of 79 %, but individuals at the 5th and 6th stages of development dominated in numbers and weight percentage in the food bolus of the fish. The intensity of feeding fell drastically, and the index of consumption dropped to 186.3 ‰. *Daphnia galeata* and chironomid pupae and imagoes were encountered occasionally (Appendix, table 22).

On 4 July 1990, the food spectrum of two-year-old *leiurus* (54.5 mm) changed somewhat, *Cyclops scutifer* at the 5th and 6th stages of development continued to be the main component of their diet, but at the same time, chironomid imagoes began to appear more frequently in the stomachs of the fish (in 94 % of the cases), forming 33.0 % of the total weight in the food bolus. *Daphnia galeata* and insect larvae and imagoes were encountered now and then. The intensity of feeding at this time remained practically unchanged, and the index of consumption was 121.0 ‰.

On 15 July 1990, the number of *Cyclops scutifer* per stomach in *leiurus* individuals measuring 59.5 mm in length dropped sharply to 184, but the percentage of them in the food bolus remained extremely high (93.5 %). At the same time, the role of *Daphnia galeata* began to increase; the frequency of this species increased to 72 %, but because so very few of them (about 15) were found in the stomachs, their percentage in the food bolus was only a mere 4.3 %. The intensity of feeding during this period declined even further to 38.7 ‰ (Appendix, table 22).

On 17 August 1990, the feeding behaviour of two-year-old *leiurus* (60.8 mm) changed significantly as the food spectrum expanded. *Daphnia*, chironomid imagoes, imagoes of flying insects and *Cyclops scutifer* became the main components of their diet, with *Daphnia* constituting the bulk of the food bolus (84.7 %) and averaging 865 specimens per stomach. The intensity of feeding began to increase once again, and the index of consumption reached 136.5 ‰.

Analysis of the feeding habits of three-year-old *leiurus* (75.5 mm) showed that, as in the younger age groups, the main components of their diet in the middle of June were *Cyclops scutifer* at the 5th and 6th stages of development with a 100 % frequency of occurrence and a 99.8 % mass in the food bolus. The index of consumption amounted to 922.7 ‰, with the number of individuals per stomach at 10.458. *Daphnia*, chironomid larvae and imagoes, and nematodes (Nematoda) were encountered now and then (Appendix, table 22).

On 25 June 1990, the intensity of feeding of three-year-old *leiurus* (73.4 mm) dropped off significantly, the index of consumption amounting to 280.5 ‰, as before, *Cyclops scutifer* at the 5th and 6th stages of development were the main component in the food bolus, but the number of these crustaceans per stomach fell to 2353. *Cyclops scutifer* at the 2nd-4th (mainly 2nd and 3rd) stages did not play a major role at this time, constituting only 7.5 % of the food bolus. *Gammarus* made up only 5.5 %, and chironomid imagoes and *Daphnia* not more than 0.9 % of the total mass of organisms in the food bolus.

On 4 July 1990, chironomid imagoes and *Cyclops scutifer* became the main component of the diet of three-year-old *leiurus* (77.3 mm) (100 % and 75 % respectively), with chironomid imagoes constituting 51.1 % of the total weight in the food bolus. The intensity of feeding at this time diminished somewhat, and the index of consumption at the beginning of July was 172.8 ‰ (Appendix, table 22).

On 15 July 1990, three-year-old *leiurus* (76.8 mm) began feeding actively on *Cyclops scutifer* at the 5th and 6th (mainly 6th) stages of development; these made up 95.3 % of the total weight in the food bolus, *Daphnia* became the second food component with a 70 % frequency of occurrence, but their weight in the food bolus amounted to only 2.0 %. The index of consumption averaged 141.1 ‰.

On 17 August 1990, as they continued to feed on *Cyclops scutifer* at the 6th stage of development, three-year-old *leiurus* (70.2 mm) began feeding on the imagoes of flying insects, as well as underyearlings and yearlings of the threespine stickleback. The intensity of feeding did not change, and the index of consumption averaged 143.8 ‰ (Appendix, table 22).

In conclusion, let us examine the feeding behaviour of *leiurus* in the littoral zone of Azabach L. (data not tabled in this book). Having analyzed our material, we did not note any significant differences in the feeding behaviour of *leiurus* individuals from different parts of the littoral zone of Azabach L. (in the vicinity of the Lotnaya, Bushuyka, Lamutka, Snovodovskaya and Ponomarskaya rivers).

Chironomids and crustaceans were the principal food of the freshwater form of the threespine stickleback in the littoral zone of this lake in July–September 1970. Fish of different sizes displayed significantly different feeding behaviour. Smaller individuals (31.0 mm) fed mainly on chironomid larvae and imagoes (62.7 %). Crustaceans took second place in the food spectrum, the mass of *Gammarus*, Cumacea and Ostracoda in the fish stomachs being equal and totalling 29.8 %. Benthopelagic plankters (*Chydorus sphaericus* and *Biapertura affinis*) were encountered quite frequently (40 %) in the food bolus. The number of these organisms in the stomach averaged 4.2. Pelagic zooplankters were a rare occurrence (10 %) in the diet of these fish, and the number of organisms per stomach was also relatively low (0.6 specimens). Altogether, the pelagic and benthopelagic zooplankton made up 7.5 % of the total weight of the food bolus. The index of fullness was fairly high, 241 ‰ (L. V. Kokhmenko, KoTINRO archives).

The larger stickleback (58 mm) fed primarily on *Gammarus* (63.4 %), as indicated earlier for adult *leiurus* of Azabach L. (Ziuganov et al., 1987). Chironomid larvae and pupae were the most frequently occurring organisms (66.0 %); at the same time, their weight in the food bolus amounted to 28.8 %. The presence of pelagic zooplankters in the food spectrum should also be noted, they comprised an insignificant part of the food bolus (4.9 %) in comparison with other components, but they averaged about 30 specimens per stomach. The index of fullness amounted to 119.0 ‰ which is nearly half the level noted in small stickleback (L.V. Kokhmenko, KoTINRO archives).

In the side channel of Azabach L. (near the Dyakonovskaya R.), 58-62 mm *leiurus* fed mainly on *Gammarus* (64.3 %), chironomid larvae (22.7 %) and chironomid pupae (11.5 % of the total mass in the food bolus) during August. Littoral zooplankters (mainly *Chydorus sphaericus*) were encountered quite frequently (40 %) in the stomachs of these fish. The number of these organisms per stomach averaged 12, and their weight in the food bolus amounted to 1.1% (L.V. Kokhmenko, KoTINRO archives).

Feeding behaviour of the ninespine stickleback

On 21 August 1989, two-year-old ninespine stickleback (60 mm) fed on organisms found in the littoral zone, these fish did not forage in the pelagic zone at this time. The food spectrum confirmed this; the latter consisted mainly of chironomid larvae (90.2 % of the total weight) belonging exclusively to the species *Chironomus annularis*. These larvae inhabited the shallow waters, and were never found in plankton samples. *Sergentia coracina* (Wulker, 1961) was the only species of chironomid larvae encountered in the pelagic zone. These larvae were noted in the diet of pelagic fish of Dalneye L. by T. L. Vedenskaya (unpublished data). In addition to larvae, the stomachs of ninespine stickleback were found to contain small quantities of chironomid pupae (3.7 %), *Gammarus* (3.4 %) and other organisms, which comprised a fairly small part of the

total weight in the food bolus, but they were representatives of the littoral zone. The intensity of feeding of the ninespine stickleback was high at this time, and the index of consumption amounted to 338.7 ‰ (Appendix, table 23).

On 12 September 1989, chironomid pupae dominated in the diet of yearling ninespine stickleback (51 mm), they made up 94.8 % of the total weight of organisms in the food bolus. Chironomid larvae were encountered quite frequently (50 %), but they were not an important part of the diet (4.3 % of the total weight). The larvae were represented only by *Cladotanytarsus* sp. Planktonic organisms were encountered now and then, but their mass in the food bolus did not exceed 0.9 %. The index of consumption dropped to 77.7 ‰ in comparison with the previous months.

Analyzing the feeding behaviour of the ninespine stickleback in 1990, one notes that, on 25 September 1990, age 1+ individuals (34.8 mm) fed on *Bosmina* sp., ostracods, *Chydorus sphaericus* and chironomid larvae, organisms which inhabit the zone at the very surface of the bottom. Furthermore, 40 % of all the stomachs examined were empty, and the index of fullness was very low (21.2 ‰). All this indicates that the ninespine stickleback does not forage in the pelagic zone at this time (Appendix, table 23).

In Azabach L., the ninespine stickleback lives mostly in the shallow waters of bays and inlets. In the near-shore part of the littoral zone, it stays with the threespine stickleback. Like the latter, it probably spawns in July–August, but since the threespine stickleback dominates in numbers, the reproductive success of the ninespine stickleback is lower because of this (Ketele, Verheyen. 1985).

In summer (August 1970), the ninespine stickleback (54.0 mm) in the littoral zone of the lake (in the vicinity of the Ponomarskaya R.) fed mainly on stoneflies (*Capnia* sp.) (50.3 % of the total mass of the food bolus), which were also the most frequently encountered in the stomachs of the fish (57 %). Chironomid larvae and pupae also played a significant part in the diet of this species of fish; their weight and frequency of occurrence amounted to 11.9–17.5 % and 40–52 % respectively. The ninespine stickleback fed less actively on crustaceans (7.4 % of the total weight of the food bolus). The latter included an abundance of Cumacea and ostracods (L. V. Kokhmenko, KoTINRO archives).

During the same period, in August 1970, the feeding of the ninespine stickleback (44 mm) in the Azabachye side channel (near the Dyakonovskaya R.) was quite different. These fish consumed mainly *Gammarus* (47 %), chironomid pupae (35.7 %) and littoral plankton (10.3 % of the total mass of the food bolus). *Biapertura affinis* were the most foraged planktonic organisms (10.1 %) (L. V. Kokhmenko, KoTINRO archives).

Feeding behaviour of the pond smelt

Underyearling pond smelt (43 mm) in the pelagic zone of the lake in the middle of August (13 August 1989) consume mainly *Cyclops scutifer*, which are encountered in the food bolus of all the fish. The number of these crustaceans per stomach averages 770.6, their relative mass in the food bolus equals 97.6 %. *Daphnia* (0.50–0.90 mm long) are encountered quite frequently (71 %) in the stomachs of these fish. With the numbers per stomach averaging 31.7 specimens, the percentage of *Daphnia* in the food bolus does not exceed 2.2 %. *Leptodora* is encountered occasionally (7 %) in the food bolus, but its importance in the food spectrum is minimal (0.2 %), the index of consumption in underyearling pond smelt reaches 542.3 ‰ at this time (Appendix, table 24).

Analyzing the feeding behaviour of two-year-old pond smelt (97 mm), one notes that, on 22 July 1989, *Cyclops scutifer* was the major component of the diet of this age group. These crustaceans made up 55 % of the food bolus, and averaged 104.6 specimens per stomach with a frequency of occurrence not greater than 14 %. Chironomid imagoes and pupae were encountered quite frequently (71 and 43 % respectively), and their relative weight in the food bolus amounted to 30.7 % and 8.2 %. The consumption of insect larvae by the pond smelt was lower, i.e. with a 29 % frequency of occurrence, insect larvae made up only 6.1 % of the food bolus, the feeding rate of two-year-old pond smelt at this time is low, and the index of consumption equals 9.4 ‰.

On 21 August 1989, the feeding rate of two-year-old pond smelt (102 mm) increased significantly in comparison with the previous months (to 150.9 ‰), due to more active consumption of *Cyclops scutifer*. These crustaceans were found in the stomachs of all the fish, the number of them per stomach reaching a high of 2221.3 specimens, they made up 91.7 % of the food bolus with the index of consumption equal to 138.5 ‰. In addition to *Cyclops scutifer*, the stomachs frequently contained the imagoes of chironomids (83 %) and other insects (66 %), the numbers of which amounted to 10.2 and 1.8 specimens per stomach respectively (Appendix, table 24).

Our study of the feeding behaviour of the pond smelt in 1990 showed that, on 15 July 1990, two-year-old pond smelt (93 mm) fed predominantly on chironomid imagoes and pupae which made up 77.3 and 19.4 % of the food bolus respectively. The feeding rate at this time was not high, and the index of consumption was 34.5 ‰ (Appendix, table 25).

On 17 August 1990, *Cyclops scutifer* at the 5th and 6th stages of development became the principal component of the diet of one-year-old and two-year-old pond smelt (80.6 mm). The number of *Cyclops scutifer* encountered per stomach was 4041, and their relative weight in the food bolus was 96.5 %. *Daphnia* were also encountered quite frequently (72%) with the average number per stomach equal to 273.5 specimens, but they made up only 3.5 % of the food bolus. During this month, the feeding rate increased sharply, and the index of consumption peaked at 358.1 ‰.

On 25 September 1990, *Daphnia* began to prevail in the food spectrum of one- and two-year-old individuals (84.1 mm), constituting 57.1% of the food bolus. In addition to *Daphnia*, the stomachs of the fish often contained *Cyclops scutifer* at the 1st–6th (predominantly 2nd and 3rd) stages of development, which made up 37.5 % of the food bolus. *Cyclops scutifer* at

the 5th and 6th stages were encountered less frequently, and constituted not more than 1 % of the food bolus. The index of consumption once again dropped to 12.9 ‰ (Appendix, table 25).

Let us now examine the feeding behaviour of the pond smelt in the littoral zone of the lake (Timofeyevsky Bay). For instance, on 27 June 1988, yearling pond smelt (56 mm) fed mainly on *Cyclops scutife*, most frequently (55 %) on individuals at the 5th stage of development, which made up 94.8 % of the food bolus. The number of these crustaceans per stomach averaged 356 specimens. The feeding rate was quite high, and the index of consumption was 91.6 ‰.

In July (11 July 1987), the feeding behaviour of yearling pond smelt (60 mm) changed significantly. The consumption of *Cyclops scutifer* decreased several-fold, and the importance of chironomids increased. The weight of the latter in the food bolus amounted to 75.7 %, and all the stages of metamorphosis were encountered, but imagoes dominated, constituting 52.9 % of the total mass of the food bolus. The index of consumption in July fell to 37.2 ‰ (tabled data on the feeding of pond smelt in the littoral zone of the lake are not presented in this book).

Discussion of data on the food relationships of fish in Azabach L.

There is a multitude of methods by which the food relationships of fish can be established. Here, on the basis of the material available to us, we determined the degree of food similarity (FS) (Manual..., 1961; Methodological Handbook..., 1974).

In July 1989, the food similarity between the immature sockeye of stock "A" and group "E" on the one hand and the freshwater (landlocked) threespine stickleback of age 1+ and 2+ reached a high level (table 41). Tense food relations such as these emerge because of a preference for the the same organisms. In this particular case, young sockeye and the stickleback consume mainly *Cyclops scutifer* in July, and both feed exclusively on 6th-instar individuals during this period.

In August 1989, we determined the degree of food similarity between under-yearling sockeye of group "E" and freshwater threespine stickleback of age 1+ and 2+ (table 41). We found that the most tense food relations emerged between underyearling sockeye and yearling threespine stickleback, the degree of food similarity running to 76.7 %. Somewhat weaker food relations were noted between underyearling sockeye and two-year-old stickleback, the degree of food similarity between them amounting to 59.6 %. Mainly chironomid imagoes were the common food items at this time. The consumption of planktonic organisms declined sharply, and their role in the diet diminished considerably.

Table 41. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 1989, %

Data	Treespine stickleback, morph, age	Sockeye, group "E", age 0+	Sockeye, stock "A", age 1+	Sockeye, group "E", age 1+
11.07	<i>Leiurus</i> , age 1+	—	92.1	82.5
11.07	<i>Leiurus</i> , age 2+	—	95.0	82.8
21.08	<i>Leiurus</i> , age 1+	76.7	—	—
21.08	<i>Leiurus</i> , age 2+	59.6	—	—

In the middle of June 1990, the young of the sockeye and all the age groups of the freshwater and anadromous forms of the threespine stickleback fed mainly on 5th- and 6th-instar *Cyclops*. The degree of food similarity at this time was quite high (table 42). The threespine stickleback foraged more actively than the juvenile sockeye during this period.

Table 42. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 14 June 1990, %

Species, stock, group, morph, age	Sockeye			Treespine stickleback, <i>leiurus</i>			Treespine stickleback, <i>trachurus</i>	
	"A", age 1+	"E", age 1+	"A", age 2+	Age 1+	Age 2+	Age 3+	Age 3+	Age 4+
Sockeye "A", age 1+	—	80.1	67.6	97.5	98.6	98.6	79.2	86.1
Sockeye "E", age 1+	80.1	—	85.8	79.4	78.7	78.7	78.9	88.7
Sockeye "A", age 2+	67.6	85.8	—	66.8	66.2	66.2	66.4	74.5
<i>Leiurus</i> , age 1+	97.5	79.4	66.8	—	97.5	97.6	78.9	85.4
<i>Leiurus</i> , age 2+	98.6	78.7	66.2	95.7	—	99.8	78.9	84.7
<i>Leiurus</i> , age 3+	98.6	78.7	66.2	97.6	99.8	—	78.9	84.7
<i>Trachurus</i> , age 3+	79.2	78.9	66.4	78.9	78.9	78.9	—	79.2
<i>Trachurus</i> , age 4+	86.1	88.7	74.5	85.4	84.7	84.7	79.2	—

At the end of June, the degree of food similarity between juvenile sockeye and two- and three-year-old freshwater threespine stickleback remained practically unchanged (table 43), whereas the FS between juvenile sockeye and yearling threespine stickleback dropped sharply, as they began feeding actively on 2nd- and 3rd-instar *Cyclops* during this period. The index of fullness in yearling sockeye increased.

At the beginning of July, the FS diminished somewhat due to the fact that the food spectrum of young sockeye and of the threespine stickleback broadened and changed (table 44). Nevertheless, they continued to be each other's major food competitors.

In the middle of July, neither the pond smelt, nor the anadromous threespine stickleback is a food competitor for either the young of the sockeye, or the freshwater form of the threespine stickleback. The FS in this case does not exceed even 10 %.

Table 43. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 25 June 1990, %

Species, stock, group, morph, age	Sockeye			Treespine stickleback, <i>leiurus</i>		
	"E", age 1+	"A", age 1+	"A", age 2+	Age 1+	Age 2+	Age 3+
Sockeye "E", age 1+	–	88.5	94.2	6.5	81.1	92.4
Sockeye "A", age 1+	88.5	–	82.9	17.2	91.4	89.8
Sockeye "A", age 1+	94.2	82.9	–	1.7	75.7	87.2
<i>Leiurus</i> , age 1+	6.5	17.2	1.2	–	25.2	8.4
<i>Leiurus</i> , age 2+	81.1	91.4	75.7	25.2	–	83.1
<i>Leiurus</i> , age 3+	92.4	89.8	87.2	8.4	83.1	–

Table 44. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 04 July 1990, %

Species, stock, group, morph, age	Sockeye		Treespine stickleback, <i>leiurus</i>		
	"E", age 1+	"A", age 1+	Age 1+	Age 2+	Age 3+
Sockeye "E", age 1+	–	41.6	81.0	71.1	56.8
Sockeye "A", age 1+	41.6	–	47.0	68.5	81.5
<i>Leiurus</i> , age 1+	81.0	47.0	–	67.7	51.4
<i>Leiurus</i> , age 2+	71.1	68.5	67.7	–	80.7
<i>Leiurus</i> , age 3+	56.8	81.5	51.4	80.7	–

Sixth-instar *Cyclops* are the cause of the major competition between the young of the sockeye and all the age groups of the threespine stickleback. However, we should keep in mind that the FS during this period is somewhat lower than in the preceding ones, but it still remains quite high (table 45).

Table 45. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 15 July 1990, %

Species, group, morph, age	Sockeye	Treespine stickleback, <i>leiurus</i>			Treespine stickleback, <i>trachurus</i>		Pond smelt
	"A", age 1+	Age 1+	Age 2+	Age 3+	Age 3+	Age 4+	Age 2+
Sockeye "A", age 1+	–	53.3	89.8	88.3	1.0	6.2	12.5
<i>Leiurus</i> , age 1+	53.3	–	57.8	55.6	0.0	5.5	3.4
<i>Leiurus</i> , age 2+	89.8	57.8	–	96.3	1.0	2.7	3.2
<i>Leiurus</i> , age 3+	88.3	55.6	96.3	–	1.4	2.9	3.0
<i>Trachurus</i> , age 3+	1.0	0.0	1.0	1.4	–	29.6	1.0
<i>Trachurus</i> , age 4+	6.2	5.5	2.7	2.9	29.6	–	6.8
Pond smelt, age 2+	12.5	3.4	3.2	3.0	1.0	6.8	–

In the middle of August, the degree of food similarity between the pond smelt and the yearlings and three-year-olds of the freshwater form of the threespine stickleback increased (table 46), due to the fact that the pond smelt began to feed actively on *Cyclops* and *Daphnia* during this period. The degree of food similarity between the yearlings and two-year-olds of the freshwater threespine stickleback remained at the same level as in June and July. We should note that *Daphnia* were the main component in the diet of yearling and two-year-old *leiurus* at this time, and 5th- and 6th-instar *Cyclops* were the main food of pond smelt.

Table 46. Degree of feed similarity in fish of various ages in the pelagic zone of Azabach L. in 17 August 1990, %

Species, morph, age	Treespine stickleback, <i>leiurus</i>			Pond smelt, Age 1+ and age 2+
	Age 1+	Age 2+	Age 3+	
<i>Leiurus</i> , age 1+	–	65.3	18.7	40.2
<i>Leiurus</i> , age 2+	65.3	–	15.7	5.5
<i>Leiurus</i> , age 3+	18.7	15.7	–	18.7
Smelt, age 1+ and age 2+	40.2	5.5	18.7	–

Our study of the food relations of the fish that forage in the pelagic zone of Azabach L. has already enabled us to draw certain conclusion regarding the factors that cause changes in the abundance of some species of fish in the watersheds of Azabach L. and the Kamchatka R.

It is not excluded that the recently observed increase in the numbers of *leiurus* in Azabach L. (Bugaev, 1988; table 37) is associated with the specialized *trachurus* fishery that was carried on in the lower reaches of the Kamchatka R. in 1979 through 1984 (Lagunov, 1985), and then stopped in 1985 because of overexploitation. Prior to overfishing, *trachurus* spawned in Azabach L. on a very large scale. Underyearling *trachurus* migrate seaward from Azabach L. in masses at the end of August through September. Analysis of the degree of food similarity between underyearling *leiurus* and *trachurus* has shown that it

amounted to 90.2 % in this lake watershed at the beginning of September 1989 mainly because of *Daphnia* and, to a smaller degree, *Chydorus*. At the end of September–beginning of October, the degree of food similarity between underyearling *leiurus* and *trachurus* in Azabach L. declined sharply to a mere 11.7 %, but by this time practically all of the underyearling *trachurus* had migrated seaward from the lake.

We assume that before the specialized *trachurus* fishery was started, the high abundance of underyearling *trachurus*, which emerged earlier than underyearling *leiurus*, suppressed and limited the increase in *leiurus* numbers through food competition during the first summer. This promoted more favorable foraging conditions for the young of the sockeye. The sharp increase in the abundance of *leiurus* (observed by us since 1984), which coincided with the overcrowding of spawning grounds in the Azabach L. watershed in 1982-1985 (Bugaev, 1986b), could have been one of the causes of the decline in the present abundance of group “E” sockeye which, based on long-term averages, had once constituted more than 40 % of all the sockeye of the Kamchatka R. The increase in *leiurus* numbers did not have the same catastrophic effect on the abundance of stock “A” sockeye because the abundance of the latter is restricted by the area of the spawning grounds in the Azabach L. watershed (Bugaev, 1986b).

Later, as recommendations on bio-amelioration measures are developed, more profound and detailed research into the ecosystem of the Kamchatka R. will become necessary.

Nevertheless, in order to reduce the incidence of *leiurus* in the Azabach L. watershed, we can already recommend to interested organizations the method of experimental fishing of immature and adult *leiurus* and pond smelt with fine-mesh seines off shore in the littoral zone of the lake. The frequency of occurrence of immature sockeye in these catches is extremely low, usually less than 0.1-1 % of the total catch. The yield of *leiurus* (mainly immature individuals) per haul of a 10-metre seine in June–July amounts to 2000-4000 in some places.

8.5.4. Predators of the sockeye in the Azabach L. watershed

The feeding behaviour of arctic char of the *Salvelinus alpinus* complex in the Azabach L. watershed has been researched by L. V. Kokhmenko (1970, 1972).

Based on their feeding habits, the char in the lake can be grouped into predators of the first order (benthophagous) and predators of the second order (fish-eaters), or the predaceous char. Second-order predators with a small percentage of benthos feeding are also encountered. Char that feed exclusively on fish are more abundant than benthophagous ones in the Azabach L. watershed. Of the total number of fish examined, 76 % were predaceous, and 22.4 % benthophagous. Only 1.6 % of the fish were mixed feeders (Kokhmenko, 1970).

The predaceous char in the lake feed predominantly on pond smelt and three-spine stickleback; young sockeye are foraged less and in small quantities (table 47). On the other hand, young sockeye are an important food of predaceous char in the side channel of Azabach L. (40 % of the total quantity of food, 64.4 % by weight). The other fish (pond smelt and threespine stickleback) make up 60 % of the quantity and 35.4 % of the weight of the food bolus (table 48).

Table 47. *The food composition of arctic char stomachs in Azabach L. (Kokhmenko, 1970)*

Feeding components	Frequency of occurrence, %;	Number of organisms in one stomach		Weight of organisms in one stomach	
		Number of fish	%	Grammes	%
Sockeye	9.5	0.3	6.5	1.0	7.1
Pond smelt	41.0	1.5	32.6	8.7	61.7
Treespine stickleback	45.6	2.4	52.2	3.9	27.7
Ninespine stickleback	6.9	0.4	8.7	0.5	3.5
Number of fish		621			
Body length, cm		25.5-62.5 (average – 40.0)			

Table 48. *The food composition of arctic char stomachs in the stream flowing from Azabach L. to the Kamchatka R. (Kokhmenko, 1970)*

Feeding components	Frequency of occurrence, %;	Number of organisms in one stomach		Weight of organisms in one stomach	
		Number of fish	%	Grammes	%
Sockeye	36	3.5	40	9.1	64.6
Pond smelt	37	1.9	22	4.5	32.0
Treespine stickleback	15	1.5	16	0.3	2.1
Ninespine stickleback	18	1.9	22	0.2	1.3
Number of fish		1155			
Body length, cm		11.8-52.0 (average – 34.0)			

The composition of the food consumed by the predaceous char in the lake is basically invariable. The few changes that are observed may be due to a difference in sampling time and to fluctuations in prey abundance.

Depending on the season, the species composition of the forage fish of this form remains almost constant, the changes occurring only in the ratio of individual species and the size of the prey. The predators feed on threespine stickleback throughout the year, and on pond smelt nearly all the time. Juvenile sockeye were found in their stomachs in February, July, August and September (Kokhmenko, 1970).

In the side channel of Azabach L., the seasonal change in the feeding behaviour of the predaceous char is more noticeable than in the lake itself. In winter, they feed mainly on mature pond smelt migrating to the lake, and in March occasionally on immature individuals of the species as well. In May, the predaceous char in the river's estuary feed mainly on threespine stickleback, but pond smelt and juvenile sockeye are also included in their diet. In July, August and part of September, the predaceous char feed on underyearling pond smelt and sockeye (Kokhmenko, 1970).

As the size of the fish increases in a population of predaceous char, so does the average size of the prey in the majority of cases (Kokhmenko, 1972).

Having determined the population of fish-eating char to be the predators of juvenile sockeye in the Azabach L. watershed, we can say that the char in the lake itself sooner plays a positive role by consuming the potential food competitors of young sockeye. During the period of research (1964-1967), 621 char stomachs were found to contain 181 juvenile sockeye, i.e. an average 0.3 specimens per stomach, and at the same time 1.5 pond smelt and 2.4 threespine stickleback per stomach. Char are more perceptibly detrimental to the young of the sockeye in the side channel of Azabach L. From 1964 to 1967, the stomachs of 1155 char from the side channel were found to contain 4060 juvenile salmon (an average 3.5 specimens per predator). An interesting fact to note is that juvenile coho salmon are very rarely encountered in the stomachs of char, though this species of salmon is quite plentiful in both the lake and the river (Kokhmenko, 1970).

The abundance of char in the Kamchatka R. watershed (including Azabach L.) fluctuates periodically, as indicated by the dynamics of the Kamchatka R. char catches recorded by the Ust-Kamchatsk Fish Cannery. For instance, since 1963, the largest catches of Kamchatka R. char (330-550 tons) were observed in 1968, 1976-1977 and 1986, and the smallest ones (40-100 tons) in 1964, 1973, 1983 and 1990.

In her research work, L. V. Kokhmenko (197, 1972) did not separate the freshwater and anadromous forms of the threespine stickleback, which should be taken into account when analyzing her data. There have been no recent investigations on the effect of predaceous char on the young of the sockeye in the Azabach L. watershed.

8.6. Feeding habits of juvenile sockeye in Kuril L.

According to V. A. Dubynin's data from trawl catches (personal communication), the catches from the Kuril L. watershed contained strictly juvenile sockeye. Over the long period of time since 1977, only several occurrences of threespine stickleback in a trawl catches have been reported, but it is not known whether they belonged to the freshwater form or the anadromous form. V. A. Dubynin's special research conducted at our request in 1987-1988 showed that individuals of the freshwater form of the threespine stickleback (*leiurus* morph) could be found (in small numbers) at the outfall of the Ozernaya R. All of these facts taken together lead us to believe that predominantly only intraspecific food competition exists in the young of the sockeye in the Kuril L. watershed (due to the rare occurrence of other species of fish), which is quite different from the situation in Azabach L.

The feeding behaviour of juvenile sockeye in the Kuril L. watershed, compared with other biological aspects of this species, has not been researched well enough. In the past, A. I. Synkova (1951) studied the feeding behavior of under-yearling sockeye in the littoral zone of the lake, and later (in the mid 1970's), I. A. Nosova (KoTINRO archives) processed some data on the feeding habits of juvenile sockeye in the pelagic zone of the lake in 1976-1977.

In 1992, the research on the feeding habits of juvenile sockeye in the Kuril L. watershed was continued by T. L. Vvedenskaya. The first results of this research, based on V. A. Dubynin's trawl data for 1990-1992, have been included in our book. Trawling was carried out in the vicinity of Severnaya Bay (fig. 4). Due to the rare occurrence of two-year-old sockeye in the August-October catches in Kuril L., the feeding behaviour of only the most abundant age groups (under-yearlings and yearlings) will be examined in this section of the book. The research covers the period from August to October, which is the main period of growth of the young sockeye remaining in Kuril L. till the following year (Bugaev, Dubynin, 1991).

The food spectrum of juvenile sockeye of different age groups in the pelagic zone of Kuril L. is relatively narrow. The appearance of new organisms in the diet of the sockeye is timed to the seasonal changes in the composition of the zooplankton in the pelagic zone of the lake. Besides, the vegetative period in amphibiotic insects is followed by metamorphosis, which also affects the feeding behaviour of the sockeye. The consumption of different organisms by the sockeye throughout the season and from year to year differs significantly, and age-related changes are also observed (tables 49, 50, 51).

In 1990 (table 49), juvenile sockeye in September-October fed exclusively on *Cyclops* and *Daphnia*, underyearlings showing a preference for *Daphnia*, and yearlings for *Cyclops* in September and *Daphnia* in October. The feeding activity fluctuated from 60.8 to 161.7 ‰. The consumption of crustaceans by underyearlings and yearlings was high in September (161.7 and 72.5 ‰), and would drop in October to 63.7 and 60.8 ‰ respectively. The yearlings fed less actively. We should point out that the warming up of the water in 1990 was greater than in the years that followed.

The feeding behaviour of juvenile sockeye was totally different in 1991 (table 50). The underyearlings showed a preference for amphibiotic insects in August, and for *Cyclops* in the months that followed. The yearlings fed mainly on *Cyclops* in

August through October. In addition to these organisms, juvenile sock-eye salmon of different age groups consumed *Daphnia* in October; this organism made up 38.0-44.5 % of the food bolus in 0+ and 1+ individuals respectively. The amount of food consumed by the sockeye in 1991 also differed somewhat. The feeding activity of underyearlings increased sharply by October, the index of consumption amounting to 293.5 ‰. In October, the feeding activity declined slightly, but remained quite high (212.6 ‰). The dynamics of the feeding activity in yearling sockeye varied. The consumption of food gradually increased from 43.2 ‰ in August to 220.9 ‰ in October.

The feeding behaviour of the sockeye in 1992 is shown in table 51. Underyearlings and yearlings consumed *Cyclops* more activity in August and September. The role of the second most important food component, *Daphnia*, varied. It played an insignificant part (6.9 ‰) in the diet of older immature fish (yearlings), the consumption of *Daphnia* by underyearlings increased in September, amounting to 34.8 ‰ of the food bolus. The feeding activity of the sockeye in August was higher in yearlings (183.1 ‰), while the index of consumption in underyearlings did not exceed 94.9 ‰. In September, the index of food consumption was practically identical in all the juvenile sockeye, and amounted to 106.5-116.1 ‰.

Table 49. The pelagic feeding spectrum of young sockeye in Kuril L. in 1990 (T. L. Vvedenskaya, V. F. Bugaev and V. A. Dubynin – KotINRO archives)

Feeding components	Age, 0+				Age, 1+			
	1	2	3	4	1	2	3	4
September								
<i>Cyclops scutifer</i>	79	724.6	56.7	35.3	93	1921.4	40.8	58.6
I	–	–	–	–	7	8.5	+	0.1
II	3	2.1	0.2	+	13	6.9	0.2	0.1
III	3	4.6	0.6	0.2	13	26.1	1.0	0.9
IV	3	5.5	1.2	0.4	13	24.5	1.6	1.1
V	3	2.9	1.0	0.3	13	3.7	0.4	0.3
Female VI	3	0.8	0.3	0.1	7	1.0	0.2	0.1
Male VI	3	0.8	0.5	0.2	13	6.9	0.6	0.6
Underemined stage	76	707.9	52.9	34.1	80	1843.8	36.8	55.4
<i>Daphnia longiremis</i> , mm	92	572.0	105.0	64.7	93	525.8	28.3	36.7
0.35-0.40	3	0.4	+	+	–	–	–	–
0.42-0.48	–	–	–	–	7	2.1	+	+
0.50-0.52	3	1.7	+	+	7	2.1	+	+
0.58-0.70	13	17.7	2.3	1.4	7	10.7	0.8	0.5
0.72-0.85	16	162.9	40.4	24.9	7	1.0	0.1	0.1
0.88-1.08	16	42.5	18.8	11.3	7	2.1	0.5	0.4
1.10-1.30	8	3.4	2.6	1.7	–	–	–	–
1.32-1.52	3	0.4	0.6	0.4	–	–	–	–
Undetermined stage	68	343.0	40.3	25.0	87	509.8	26.9	35.7
Insecta imago	–	–	–	–	13	1.7	3.4	4.7
Nematoda	3	+	+	+	–	–	–	–
Total consumption index, ‰	–	–	161.7	–	–	–	72.5	–
Empty stomachs, %	–	–	7.9	–	–	–	6.7	–
Average body length, mm	–	–	51.6	–	–	–	78.5	–
Number of fish	–	–	38	–	–	–	15	–
October								
<i>Cyclops scutifer</i>	32	16.2	0.8	1.3	69	291.2	15.5	12.6
IV	–	–	–	–	6	3.0	0.1	+
V	–	–	–	–	6	0.9	+	+
Female VI	–	–	–	+	6	2.0	0.2	0.1
Male VI	–	–	–	–	6	2.0	0.1	+
Undetermined stage	32	16.2	0.8	1.3	62	283.2	15.1	12.5
<i>Daphnia longiremis</i> , mm	68	655.6	62.4	98.4	94	864.0	42.2	83.3
0.58-0.70	4	1.1	+	0.2	6	13.0	0.4	0.3
0.72-0.85	4	1.8	0.2	0.5	6	65.0	4.1	2.9
0.88-1.08	4	0.2	+	+	6	39.0	4.2	3.1
1.10-1.30	–	–	–	–	6	13.0	2.7	2.0
Undetermined stage	64	652.6	62.2	97.7	88	734.0	30.8	75.0
Chironomidae larvae	4	+	0.4	0.4	–	–	–	–
<i>Bosmina</i> sp.	4	0.6	+	+	–	–	–	–
Insecta imago	–	–	–	–	6	2.0	3.1	4.1
Total consumption index, ‰	–	–	63.7	–	–	–	60.84	–
Empty stomachs, %	–	–	32.0	–	–	–	6.3	–
Average body length, mm	–	–	58.6	–	–	–	80.5	–
Number of fish	–	–	25	–	–	–	16	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1.

On the basis of the above information, one can conclude that *Cyclops* and *Daphnia* constitute the bulk of the food consumed by the young of the sockeye in Kuril L. in August–October, either the first or the second species being the dominant one during the same months from year to year. We did not observe any clear alternation in the consumption of *Daphnia* and *Cyclops* during 1990-1992, as we did in the sockeye of Azabach L. (Belousova, 1974).

As a result of hydroacoustic surveys in Kuril L., it was established (Nikolayev, 1990) that, in the pelagic zone of the lake in summer, the young of the sockeye are distributed in the 0-50 m layer during the dark hours. This coincides with the diel vertical migrations of *Cyclops* (Nosova, 1968, 1972).

Table 50. *The pelagic feeding spectrum of young sockeye in Kuril L. in 1991*
(T. L. Vvedenskaya, V. F. Bugaev and V. A. Dubynin – KoTINRO archives)

Feeding components	Age, 0+				Age, 1+			
	1	2	3	4	1	2	3	4
August								
<i>Cyclops scutifer</i>	50	16.0	2.0	2.3	73	846.8	22.7	40.9
N	–	–	–	–	9	0.9	+	+
I	50	4.0	2.0	0.3	27	44.7	0.7	1.7
II	50	4.0	0.3	0.4	36	113.8	3.0	6.6
III	50	4.0	0.6	0.6	32	30.4	1.1	2.8
IV	50	4.0	0.9	1.0	9	4.4	0.2	0.6
V	50	–	–	–	4	0.7	+	0.2
Undetermined stage	–	–	–	–	61	651.9	17.7	29.0
<i>Daphnia longiremis</i> , mm	50	28.0	4.5	5.3	59	103.4	6.2	11.8
0.50-0.52	–	–	–	–	4	0.2	+	+
0.58-0.70	–	–	–	–	4	4.4	0.3	0.7
0.72-0.85	–	–	–	–	4	2.9	0.2	0.8
Undetermined stage	50	28.0	4.5	5.3	54	96.0	5.7	103
<i>Bosmina</i> sp.	20	1.2	1.5	+	–	–	–	–
Chironomidae pupae	50	0.5	12.5	10.9	18	0.5	3.5	10.6
Chironomidae imago	–	–	–	–	32	0.8	4.6	14.5
Trichoptera pupae	50	0.5	62.5	72.6	–	–	–	–
Insecta imago	50	0.5	6.3	7.4	32	0.9	6.2	22.2
Hydracarina	–	–	–	–	4	+	+	+
Total consumption index, ‰	–	–	89.0	–	–	–	43.2	–
Empty stomachs, %	–	–	0.0	–	–	–	21.4	–
Average body length, mm	–	–	41.0	–	–	–	67.1	–
Number of fish	–	–	2	–	–	–	22	–
September								
<i>Cyclops scutifer</i>	86	2796.3	267.8	91.4	92	5398.0	144.3	82.6
I-II	57	1822.1	120.4	39.0	79	1546.7	27.1	13.9
III	71	439.5	45.2	17.7	85	1538.0	35.4	20.7
IV	50	252.2	49.2	15.7	85	1351.4	47.2	28.0
V	14	110.0	37.3	10.9	67	326.6	17.8	10.7
Female VI	7	9.1	3.2	1.5	10	19.7	2.2	1.1
Undetermined stage	36	163.4	12.5	6.6	72	615.7	14.6	8.2
<i>Daphnia longiremis</i> , mm	43	58.1	7.1	2.8	51	185.5	7.5	4.6
0.88-1.08	–	–	–	–	2	+	+	+
1.10-1.30	–	–	–	–	2	+	+	+
1.32-1.5	–	–	–	–	2	+	+	+
Undetermined stage	43	58.1	7.1	2.8	49	185.5	7.5	4.6
Chironomidae larvae	–	–	–	–	2	+	+	+
Chironomidae pupae	14	9.4	15.9	4.8	13	0.4	0.7	0.5
Chironomidae imago	14	0.3	2.7	1.0	5	+	0.1	+
Insecta imago	–	–	–	–	2	0.5	3.3	2.9
Hydracarina	–	–	–	–	5	0.2	+	+
Pisces	–	–	–	–	2	–	10.4	9.4
Total consumption index, ‰	–	–	293.5	–	–	–	166.44	–
Empty stomachs, %	–	–	0.0	–	–	–	2.6	–
Average body length, mm	–	–	42.5	–	–	–	76.0	–
Number of fish	–	–	14	–	–	–	39	–

Feeding components	Age, 0+				Age, 1+			
	1	2	3	4	1	2	3	4
October								
<i>Cyclops scutifer</i>	80	1300.0	123.4	58.3	83	3770.7	115.7	56.4
I	45	704.0	2.4	1.1	67	138.7	1.5	0.6
II	65	411.2	23.8	10.3	83	373.3	9.0	2.6
III	60	308.8	27.5	12.1	83	1301.4	32.3	14.1
IV	60	270.4	32.6	16.4	83	1125.3	35.3	18.8
V	55	94.4	16.5	9.1	83	624.0	28.8	16.5
Female VI	10	12.2	5.2	3.1	17	42.7	2.4	1.9
Male VI	25	17.6	3.3	1.9	17	5.3	0.9	0.2
Undetermined stage	40	108.0	12.1	4.3	33	160.0	5.5	1.7
<i>Daphnia longiremis</i> , mm	80	415.0	87.6	41.5	83	1413.4	102.0	38.0
0.42-0.48	15	6.4	0.3	0.1	33	96.0	0.9	0.5
0.50-0.52	15	8.8	0.5	0.3	17	42.7	0.7	0.4
0.58-0.70	30	73.6	10.8	4.7	33	426.7	17.7	7.5
0.72-0.85	50	134.4	35.8	16.8	67	650.7	54.5	22.4
0.88-1.08	30	55.1	23.2	12.0	33	101.3	24.3	6.0
Undetermined stage	55	136.8	17.0	7.6	33	36.0	3.9	1.2
Chironomidae pupae	5	+	1.2	0.2	–	–	–	–
Chironomidae imago	5	+	0.4	0.2	17	1.2	0.6	1.0
Insecta imago	–	–	–	–	17	4.7	2.6	4.6
Hydracarina	–	–	–	–	17	0.7	+	+
Total consumption index, ‰	–	–	212.6	–	–	–	220.9	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–
Average body length, mm	–	–	48.5	–	–	–	78.2	–
Number of fish	–	–	20	–	–	–	6	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1.

Table 51. The pelagic feeding spectrum of young sockeye in Kuril L. in 1992
(T. L. Vvedenskaya, V. F. Bugaev and V. A. Dubynin – KoTINRO archives)

Feeding components	Age, 0+				Age, 1+			
	1	2	3	4	1	2	3	4
August								
<i>Cyclops scutifer</i>	45	256.7	51.0	68.7	79	2941.1	169.4	97.5
I	–	–	–	–	15	10.9	0.2	+
II	9	1.1	+	0.1	38	68.1	10.0	2.0
III	27	29.4	3.1	4.6	71	649.0	25.2	61.1
IV	45	159.8	29.6	38.6	76	1488.5	80.1	19.9
V	36	66.4	18.3	25.4	65	605.3	47.6	12.8
Female VI	–	–	–	–	9	9.4	1.4	0.3
Male VI	–	–	–	–	12	15.5	1.4	0.3
Undetermined stage	–	–	–	–	15	94.4	3.5	0.3
<i>Daphnia longiremis</i> , mm	18	12.4	24.0	7.9	32	17.9	1.8	0.3
0.35-0.40	–	–	–	–	3	0.9	+	+
0.42-0.48	9	1.5	0.4	0.1	–	–	–	–
0.50-0.52	9	0.7	0.3	+	6	1.0	+	+
0.58-0.70	–	–	–	–	9	3.3	0.3	0.1
0.72-0.85	9	2.9	1.1	1.5	9	1.5	0.3	+
0.88-1.08	9	7.3	22.2	6.3	9	0.5	0.3	+
1.10-1.30	–	–	–	–	3	0.2	0.2	+
Trichoptera pupae	9	+	13.6	15.6	44	10.5	0.7	0.2
<i>Bosmina</i> sp.	9	1.3	0.2	+	–	–	–	–
Insecta imago	9	0.3	6.1	7.8	29	1.4	11.7	2.2
Chironomidae imago	–	–	–	–	3	+	0.2	+
Total consumption index, ‰	–	–	94.9	–	–	–	183.1	–
Empty stomachs, %	–	–	45.0	–	–	–	11.8	–
Average body length, mm	–	–	45.4	–	–	–	66.0	–
Number of fish	–	–	11	–	–	–	34	–

Feeding components	Age, 0+				Age, 1+			
	1	2	3	4	1	2	3	4
September								
<i>Cyclops scutifer</i>	67	460.8	60.5	64.0	100	2552.0	110.2	93.1
I	33	67.3	4.0	3.8	50	40.0	0.3	0.4
II	33	88.0	5.9	3.3	25	16.0	0.4	0.2
III	50	123.0	16.6	16.9	100	624.0	13.7	13.6
IV	42	101.7	19.4	21.6	100	1112.0	40.8	37.4
V	42	33.0	9.0	11.1	100	720.0	50.4	38.4
Female VI	8	0.3	0.2	0.2	50	24.0	3.5	2.2
Male VI	8	2.7	0.8	1.0	25	16.0	1.7	«.9
Undetermined stage	17	44.7	4.6	6.1	–	–	–	–
<i>Daphnia longiremis</i> , mm	50	86.1	44.8	34.9	75	88.0	5.9	6.9
0.50-0.52	8	2.7	0.2	0.3	–	–	–	–
0.58-0.70	8	2.7	0.8	0.6	–	–	–	–
0.72-0.85	17	10.8	5.0	4.7	–	–	–	–
0.88-1.08	17	13.3	12.8	10.2	–	–	–	–
Undetermined stage	25	56.7	26.0	19.1	75	88.0	5.9	6.9
Chironomidae larvae	8	+	+	1.2	–	–	–	–
Total consumption index, ‰	–	–	106.5	–	–	–	116.1	–
Empty stomachs, %	–	–	33.0	–	–	–	0.0	–
Average body length, mm	–	–	46.8	–	–	–	78.2	–
Number of fish	–	–	12	–	–	–	4	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %, the sign “+” signifies less than 0.1.

Active diel vertical migrations are observed in all the age groups of *Cyclops* (except nauplii and copepodites I). Copepodites III and IV are characterized by large near-surface nocturnal concentrations; the nocturnal surfacing is brief, and occurs around midnight in all the groups. The largest concentrations are noted at depths of 0-10 m (Nosova, 1968, 1972).

In our material, the stomachs of juvenile sockeye of different age groups were found to contain an abundance of copepodites III and IV mixed in with *Cyclops* in the food bolus. In the older juveniles (1+), larger individuals of the 4th and 5th instars, and sometimes even mature female and male *Cyclops*, predominated in the majority of cases. The year 1991 was an exception; 2nd-instar *Cyclops* predominated in the stomachs of yearlings in August (55.8 %), and in underyearlings in September (45.8 %), which can be attributed to the delayed development of zooplankton due to the low water temperatures that year. Earlier, I. A. Nosova (personal communication) also noted the more active consumption of mature females and 3rd–5th-instar copepodites of *Cyclops* by the young of the sockeye.

The degree of food similarity between the different age groups of young sockeye follows a similar seasonal pattern from year to year. In August, it is quite low, and varies from 25.2 to 37.7 % during different years. Such a low degree of food similarity can be attributed to a more diverse diet, for in addition to *Cyclops* and *Daphnia*, juvenile sockeye during this period feed quite actively on adult amphibiotic insects which are undergoing metamorphosis at the time.

In the following months, their diet becomes more uniform, altering the mechanism of interrelations. In September, the degree of food similarity increases to 54.9-61.9 %, and in October reaches 73.7-76.3 %. During this period, juvenile sockeye feed exclusively on *Cyclops* and *Daphnia*. In October, underyearling and yearling sockeye feed more actively on third- and fourth-instar *Cyclops* and mainly 0.35 mm *Daphnia*.

8.7. Interannual variability in the growth of the sockeye, depending on the feeding and temperature conditions at the foraging grounds (structural analysis of fish scales)

The most important factor in the growth of young sockeye prior to the seaward migration is the interannual variability of the growth rate as determined by the conditions of their habitat (Foerster, 1944; Krogius, 1961; Johnson, 1965; Burgner et al., 1969; Goodlad et al., 1974; Bugaev, 1983a; Dubynin, 1986; Graynoth, 1987; Burgner, 1987; Kyle et al., 1988; Bugaev et al., 1989; Bugaev, 1989; etc.), which determines the future survival of the young at sea (Ricker, 1962; Koenings, Barket, 1987a; Koenings et al., 1993).

As our years of research have shown (Bugaev, 1981, 1983a, 1984b; Bugaev et al., 1989; Bugaev, Dubynin, 1991, etc.), the structure of the fish scales characterizes the growth of juvenile sockeye in greater detail than the changes in their size and weight characteristics.

There are indications (Vaganov, 1978) that the biotic and abiotic conditions of a body of water affect the formation of fish scales in different ways, i.e. the availability of food has a greater effect on the number of sclerites, while the temperature of

the water has a greater effect on the formation of the spaces between the sclerites. In connection with this, we are tempted to use the scale structure as an indicator of the foraging conditions of the fish.

In addition to this, analysis of the interannual variability of scale structure in sockeye helps us to identify more accurately the fish of some stocks in sea catches.

Before we set out to analyze the interannual variability of the scale structure of sockeye from lakes Azabach and Kuril, let us examine the correlation between body size and scale structure in the juvenile sockeye from these lakes. This will enable us, wherever possible, to translate the scale characteristics of the young to linear size.

8.7.1. Correlation between body size and scale structure in juvenile sockeye

We are quite aware of the correlations between the body size of fish and the characteristics of their scales, bones and otoliths as a whole (Bryuzgin, 1969), but these correlations have not been fully determined for Pacific salmon of the genus *Oncorhynchus*.

In their classic work devoted to the study of the sockeye of the Frazer R. (British Columbia). Clutter and Whitesel (1956) note a very strong correlation between the body size of juvenile sockeye and the number of sclerites that form on their scales ($r=0.998$). We are very tempted to put this strong correlation to practical use, keeping in mind, of course, that sockeye populations may have different regression curves, therefore, it is best check this correlation in each individual case.

To plot the correlation between the size of the young and their scale structure, Clutter and Whitesel (1956) used juveniles from 50 to 150 mm in length (mixed material) for their analysis, i.e. individuals of different age groups with a different number of ZAS (zones of adjacent sclerites) on their scales.

In our opinion, the correlation between the size of smolts and the structure of their scales, plotted for individual age groups (or the number of ZAS), is of great importance to the reconstruction of smolt size based on the scales of adult sockeye.

As our investigations have shown (see section 8.7.2), the growth of juvenile sockeye in Azabach L. varies from year to year, depending on the level of the forage base, the abundance of immature sockeye in the lake and the temperature of the water. As a result, juvenile sockeye grow better and are larger by the end of the growing season or the freshwater period during certain years, and grow at a slower rate and are smaller during others. Taking this fact into account, we examined samples taken in 1979-1980 (downstream migrants from the lake were large) and in 1984-1987 (downstream migrants from the same lake were smaller) separately.

Table 52 contains the coefficients of rank correlation and the equations of linear regression for the total number of sclerites on the scales depending on the length of the fish, and with the grouping of all individuals according to the number of ZAS for all the years studied and according to the periods 1979-1980 and 1984-1987. Analysis of this table shows that, in all the cases, high reliable coefficients of rank correlation are observed between the length of the juveniles and the number of sclerites on their scales, the highest ones being noted in individuals without ZAS as compared with those having one or two ZAS.

Table 52. *The significance of coefficients of rank correlations in the analysis of sockeye young body length and the total number of sclerites in the scales of young Azabach L. sockeye*

Number ZAS	Coefficients of rank correlation, reliability, number of mean value pairs, regressive equation	
	1979-1987	
Without ZAS	$r_s = 0.967, P < 0.01, n = 29, Y = 0.223x - 7.36$	
One ZAS	$r_s = 0.849, P < 0.01, n = 49, Y = 0.14x - 2.07$	
Two ZAS	$r_s = 0.936, P < 0.01, n = 66; Y = 0.188x - 3.58$	
	1979-1980	1984-1987
Without ZAS	$r_s = 0.956, P < 0.01, n = 13;$ $Y = 0.254x - 8.94$	$r_s = 0.929, P < 0.01, n = 16;$ $Y = 0.198x - 6.14$
One ZAS	$r_s = 0.865, P < 0.01, n = 20;$ $Y = 0.126x - 0.73$	$r_s = 0.875, P < 0.01, n = 29;$ $Y = 0.210x - 5.79$
Two ZAS	$r_s = 0.801, P < 0.01, n = 27;$ $Y = 0.158x - 0.56$	$r_s = 0.851, P < 0.01, n = 39;$ $Y = 0.172x - 2.49$

Note. "x" – body length according to Smith, mm; "Y" – total number of sclerites in scales; "n" – number of mean value pairs.

When comparing the coefficients of rank correlation for the period 1979-1987, we note that these values are minimal in fish with one ZAS in all the cases (table 52, fig. 79). However, when we classify this material according to the period of good growth (large juveniles) and poor growth (small juveniles), we observe a gradual decrease in the coefficients of rank correlation from the samples of individuals with no ZAS to the samples of individuals with two ZAS.

The correlation between the scale structure and body size of the young during the years of good and poor growth varies (table 52). In connection with this, when we proceed to reconstruct body size from the structure of the scales, we must take into account the growth rate of juveniles at that particular time in Azabach L. The lines of regression in juveniles without ZAS, with one ZAS and with two ZAS on their scales for the years of good and poor growth vary significantly in slope, and intersect (graph not presented in this book).

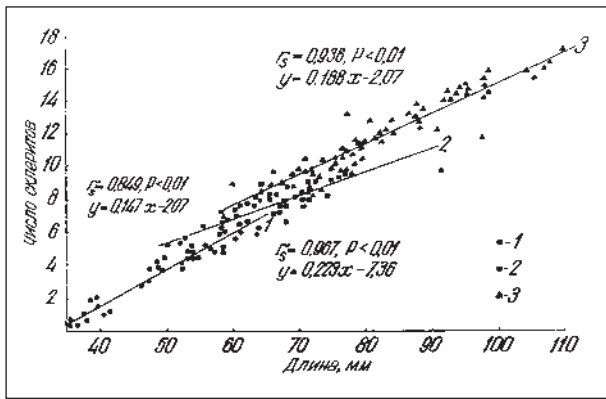


Fig. 79. Correlation between the mean length of individuals and the average number of sclerites on the scales of sockeye smolts and foraging juveniles in the Azabach L. watershed, based on 1979-1987 material. **Y-axis – number of sclerites; X-axis – body length, mm.**

1 – without ZAS, 2 – with one ZAS, 3 – with two ZAS.

Analysis of the closeness of the relationship between the body length of juveniles and the number of sclerites on their scales, without classification of individuals according to the number of ZAS, has shown that the coefficients of correlation for 1979-1980 and 1984-1987 were equal to $r = 0.973$ ($r_s = 0.971$) and $r = 0.966$ ($r_s = 0.959$) respectively, which closely approximates the data of Clutter and Whitesel (1956), according to which the coefficient of rank correlation between the body length and the total number of sclerites is equal to $r = 0.991$. In all the cases, the above coefficients of correlation and the coefficient of rank correlation had a confidence level of $P < 0.01$. The higher coefficients of correlation presented by Clutter and Whitesel (1956) can be attributed to the wider range of the mean values of body length in their juveniles in comparison with our material, and also to the fact that these researchers took scale samples from a more precise point on the body of the fish (between the dorsal and the fatty fin above the lateral line) than we did in our own samples (Pravdin, 1966).

In conclusion we would like to note that both the sockeye of stock “A” and the sockeye of group “E” probably have their own characteristics of linear growth and scale structure of the young, but so far we have not researched this.

A study of the correlation between the body size and scale structure in juvenile sockeye of Kuril L. has shown (fig. 80) that the overall coefficient of rank correlation (for all the age groups) is $r_s = 0.830$ ($P < 0.01$, $n = 139$). Our coefficients of rank correlation are much lower than those obtained by Clutter and Whitesel (1956), which can be attributed, as in the case of the Azabach L. sockeye, to the narrower range of variation in these indices, as well as to the fact that scale initiation in Kuril L., sockeye has its own specificity. We note that the coefficients of rank correlation in the sockeye of Kuril L. increase from the yearlings to the three-year-olds.

In our opinion, the observed differences may be due to the fact that the sockeye of this lake are characterized by exceptionally prolonged and late spawning, which begins at the end of July and lasts up to the beginning of February. This leads to extremely prolonged emergence of sockeye alevins from the nest (from March to September) and, consequently, a later appearance in the pelagic zone (Yegorova, 1970, 1970a). As a result, some of our samples may have contained juveniles that overwintered in the lake without scales, i.e. individuals that missed an annulus. The possibility of this happening is corroborated by the occurrence of fish with 2-3 sclerites in the first annual zone of the scales, particularly during the years of high abundance and poorer foraging conditions in the lake.

Having the most representative material for the 2+ age group, we present (fig. 80) separate data on the correlation between the size of smolts and the number of sclerites on their scales during the years of good and poor growth (sizes greater and smaller than the mean long-term value). As we can see (fig. 80), the points on the graph for the years of poor growth of the young are distributed somewhat separately. The lines of regression for each group of points (not shown on the graph) practically overlap each other, and do not disturb the general dependence for 2+ individuals. Age groups 1+ and 3+ are not very well represented in our material; we do have some data on the good and poor years of growth for age group 3+, but only data on the good years for age group 1+ (during the years of poor growth, yearlings do not usually take part in the downstream migration).

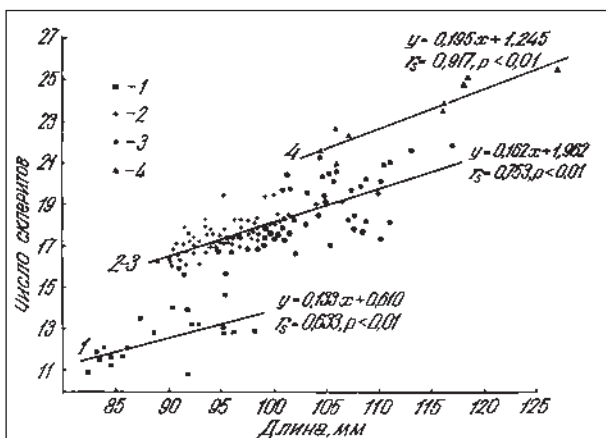


Fig. 80. Correlation between the mean length of individuals and the average number of sclerites on the scales of sockeye smolts in Kuril L. (based on 1975-1987 material). **Y-axis – number of sclerites; X-axis – body length, mm.**

1 – yearlings; 2 – two-year-olds (length and weight of body below long-term average); 3 – two-year-olds (length and weight above long-term average); 4 – three-year-olds.

As our analysis has shown, the correlation between the size of the juveniles and the structure of their scales in the sockeye from lakes Azabach and Kuril has its own characteristics, despite a number of similarities.

8.7.2. Growth of juvenile sockeye in Azabach L. (Kamchatka R.)

At the present time, we are extensively using a method for identifying mature fish from Azabach L. (stock "A") and from the tributaries of the lower Kamchatka R. (group "E") in the landings of our own fishery (Bugaev, 1986a), and have been working on methods for identifying the immature fish of stock "A" and group "E" during the foraging period in the Azabach L. watershed (Bugaev, Bazarkin, 1987; Butorina, Shedko, 1988; Kovalyov, 1988; Dubynin, Bugaev, 1988).

Though we have established the changes that occur during the freshwater growth of the Azabach L. stock of sockeye from year to year, and particularly in relation to the abundance of parents (Bugaev, 1983a), the claim that the stock "A" sockeye is not characterized by growth variability dependent on living conditions (Konovalov et al., 1971; Konovalov, 1980) is still accepted by some researchers of this lake's sockeye (Ostrovsky, 1987, 1987a, 1988; Kovalyov, 1988, 1989, 1990), and these researchers do not take the interannual variability of growth into consideration in their work.

We now have material that enables us, for the first time, to determine the growth of juvenile sockeye in Azabach L. in relation to the conditions in this lake, which is the subject of this section of the book. Research of this nature makes it possible to predict the sizes of smolts that migrate from this lake, and to improve the method of forecasting the abundance of Kamchatka R. sockeye (Bugaev, 1987a).

Smolts of stock "A" and group "E" were identified by a method used earlier (Bugaev, Bazarkin, 1987; Dubynin, Bugaev, 1988). When we compared the scale characteristics of stock "A" smolts that migrated downstream in 1979, 1980 and 1984-1988, which were identified in the catches of sockeye smolts at the outlet of the side channel from Azabach L. (table 53), with the scale characteristics of stock "A" adults of the same year-classes (table 54), we noted that the scales from the same growth zones were somewhat similar. For instance, during the first year of growth, Spearman's coefficient of rank correlation between the number of sclerites in adult fish and in smolts was $r_s=0.571$ ($P>0.05$), in the second year $r_s=0.881$ ($P<0.01$), and in the year of the smolts' seaward migration (marginal zone of scales) $r_s=0.691$ ($P<0.05$) (8 year-classes in all the cases). However, when the scale characteristics of group "E" smolts that migrated downstream the same years as stock "A" smolts were compared with the scale characteristics of stock "A" adult fish, the coefficient of rank correlation was $r_s=0.214$ ($P>0.05$) during the first year, $r_s=0.857$ ($P<0.05$) during the second year, and $r_s=0.738$ ($P>0.05$) during the year of the smolts' downstream migration (8 year-classes in all the cases). As we have already noted (Bugaev, 1981a), the first zone of scale growth in group "E" individuals is formed prior to the migration of this group's underyearlings to Azabach L. To this we can attribute the lower correlation between the number of sclerites in the first growth zone in group "E" individuals in comparison with the young of stock "A" and the first year of growth of stock "A" adults ($r_s=0.214$ and $r_s=0.571$ respectively). The strong correlations of the characteristics of scales from other growth zones of group "E" (except the first) with the corresponding scale characteristics of stock "A" adults can be attributed to the fact that the juveniles of stock "A" and group "E" forage in the lake together after the migration of the underyearlings to the lake.

The overwhelming majority (89.2-96.2 %) of the sockeye smolts that migrate downstream from Azabach L. have two zones of adjacent sclerites (ZAS) on their scales (Dubynin, Bugaev, 1988), and belong both to stock "A" and to group "E". The individuals of stock "A" are two-year-olds, and those of group "E" are yearlings; the first ZAS in the latter is a supplementary structure, and it is formed as a result of the migration of underyearlings to the lake (Bugaev, 1981a, 1983c, 1986; Bugaev, Bazarkin, 1987).

The abundance of immature sockeye that forage annually in Azabach L. is not determined on a regular basis for the time being, though occasional surveys are carried out with the help of hydroacoustic devices (Nikolayev, Bugaev, 1985; Nikolayev et al., 1989).

We know from the literature (Ricker, 1954; Burgner et al., 1969) that a certain correlation exists between the abundance of spawned out adults and the abundance of foraging immature sockeye and smolts, which enables us, in the cases where we have no data on the abundance of juveniles, to utilize (as an indicator of interannual abundance) the information available on the abundance of spawned out adult sockeye.

When analyzing the effect of abundance on growth in the sockeye, we derived the relative value of the interannual abundance of individuals foraging in the Azabach L. watershed at the same time by means of the formula

$$N=Na+Ne+Na1,$$

where "N" denotes the total abundance of adult fish, the offspring of which forage in Azabach L. at the same time (thou. specimens); "Na" – the abundance of adult fish that spawned out in the Azabach L. watershed in the year preceding a particular year of foraging, which arbitrarily reflects the abundance of stock "A" underyearlings in the lake (thou. specimens); "Ne" – the abundance of adult fish that spawned out in the breeding area of group "E" in the year preceding a particular year of foraging, which arbitrarily reflects the abundance of group "E" underyearlings in the lake (thou. specimens); and "Na1" – the abundance of adult fish that spawned out in the Azabach L. watershed two years prior to a particular year of foraging, which arbitrarily reflects the abundance of stock "A" yearlings in the lake (thou. specimens).

Table 53 contains the scale characteristics of stock "A" and group "E" smolts that migrated from Azabach L. in 1979-1980 and during 1984-1991. As we can see from this table, the sockeye smolts during these periods underwent significant changes in the number of sclerites in some growth zones and, consequently, in the total number of sclerites on the scales,

Table 53. Number of scale sclerites of sockeye smolts migrating from Azabach L. in 1979-1991

Migration year	Stock "A", age 2+ (two ZAS)						Number of fish
	First year		Second year		Migration year		
	Range	Average	Range	Average	Range	Average	
1979	4-10	6.46 ± 0.12	5-13	8.61 ± 0.17	-1-5	0.87 ± 0.17	125
1980	3-9	6.50 ± 0.19	4-10	7.54 ± 0.24	-1-2	-0.11 ± 0.16	56
1981	–	–	–	–	–	–	–
1982	–	–	–	–	–	–	–
1983	–	–	–	–	–	–	–
1984	2-8	4.82 ± 0.12	4-11	7.39 ± 0.17	-1-3	-0.21 ± 0.15	82
1985	3-8	5.04 ± 0.13	4-9	5.60 ± 0.14	-1-4	0.75 ± 0.19	68
1986	3-8	5.67 ± 0.50	4-8	6.22 ± 0.40	-1-1	-0.33 ± 0.22	9
1987	2-7	4.13 ± 0.16	4-8	5.73 ± 0.14	-1-6	2.16 ± 0.28	55
1988	2-7	4.88 ± 0.08	4-11	7.12 ± 0.11	-1-7	3.60 ± 0.12	125
1989	4-10	6.21 ± 0.10	5-14	9.32 ± 0.14	-1-3	1.10 ± 0.09	144
1990	3-11	7.33 ± 0.17	5-12	7.95 ± 0.15	-1-3	1.45 ± 0.15	83
1991	4-10	6.72 ± 0.12	5-14	9.02 ± 0.17	-1-4	1.19 ± 0.10	122
Migration year	Group "E", age 1+ (two ZAS)						Number of fish
	First year (zone 1)		First year (zone 2)		Migration year		
	Range	Average	Range	Average	Range	Average	
1979	3-10	6.00 ± 0.11	4-12	8.28 ± 0.14	-1-6	1.38 ± 0.15	166
1980	3-11	6.18 ± 0.11	3-13	7.49 ± 0.15	-1-3	0.24 ± 0.11	122
1981	–	–	–	–	–	–	–
1982	–	–	–	–	–	–	–
1983	–	–	–	–	–	–	–
1984	2-9	4.36 ± 0.17	3-10	5.87 ± 0.19	-1-5	0.40 ± 0.21	70
1985	2-8	4.96 ± 0.14	2-8	4.79 ± 0.13	-1-4	0.84 ± 0.16	94
1986	3-10	5.21 ± 0.26	3-8	5.23 ± 0.22	-1-2	0.54 ± 0.13	39
1987	2-9	4.93 ± 0.14	2-7	3.86 ± 0.12	-1-8	2.00 ± 0.18	94
1988	3-9	5.34 ± 0.16	2-10	5.60 ± 0.19	-1-7	2.71 ± 0.23	87
1989	2-8	4.95 ± 0.18	2-9	5.63 ± 0.18	-1-4	1.61 ± 0.16	59
1990	2-10	5.58 ± 0.19	3-11	5.83 ± 0.23	-1-4	1.32 ± 0.13	65
1991	2-10	5.60 ± 0.15	2-12	5.01 ± 0.16	-1-5	1.90 ± 0.11	163

Note. "–1" – without annulus.

Table 54. Number of scale sclerites in adult sockeye in the fresh water zone of Azabach L. (at age 2.3 mostly)*

Spawning year	First year		Second year		Migration year		Number of fish
	Range	Average	Range	Average	Range	Average	
1963	2-9	5.78 ± 0.19	3-13	5.97 ± 0.24	0-6	2.06 ± 0.17	65
1964	–	–	–	–	–	–	–
1965	3-10	6.34 ± 0.19	4-12	8.14 ± 0.21	0-6	2.37 ± 0.25	59
1966	–	–	–	–	–	–	–
1967	4-10	6.17 ± 0.24	3-12	7.57 ± 0.37	0-8	2.81 ± 0.26	42
1968	1-9	5.59 ± 0.24	6-12	9.16 ± 0.26	0-4	1.05 ± 0.19	37
1969	2-9	6.18 ± 0.15	5-13	7.75 ± 0.16	0-3	0.91 ± 0.09	76
1970	4-9	6.39 ± 0.16	5-12	7.34 ± 0.15	0-4	1.30 ± 0.11	79
1971	3-11	5.40 ± 0.12	4-10	6.84 ± 0.13	0-6	2.52 ± 0.16	93
1972	2-9	5.80 ± 0.12	3-10	6.40 ± 0.13	0-7	2.19 ± 0.13	121
1973	3-9	5.86 ± 0.14	3-10	6.92 ± 0.19	0-7	3.74 ± 0.19	73
1974	2-10	5.71 ± 0.21	6-14	8.65 ± 0.25	0-6	2.59 ± 0.24	49
1975	2-12	6.89 ± 0.29	3-16	10.29 ± 0.31	0-6	1.38 ± 0.15	65
1976	3-11	7.43 ± 0.31	3-13	9.60 ± 0.38	0-5	1.57 ± 0.22	35
1977	1-12	7.49 ± 0.23	5-15	10.49 ± 0.16	0-5	0.90 ± 0.14	78
1978	2-10	5.78 ± 0.22	4-12	8.29 ± 0.26	0-11	1.39 ± 0.29	51
1979	3-10	6.23 ± 0.18	5-17	8.96 ± 0.30	0-5	1.41 ± 0.18	69
1980	4-10	6.20 ± 0.15	3-15	9.81 ± 0.23	0-6	2.28 ± 0.14	80
1981	5-14	8.56 ± 0.27	4-15	10.25 ± 0.35	0-4	1.60 ± 0.20	48
1982	4-12	7.49 ± 0.21	4-13	8.88 ± 0.31	0-8	2.70 ± 0.28	43
1983	3-10	6.65 ± 0.17	5-16	7.63 ± 0.23	0-9	1.72 ± 0.19	75
1984	3-11	6.67 ± 0.15	5-14	9.59 ± 0.18	0-10	1.54 ± 0.15	94
1985	5-10	7.22 ± 0.12	5-13	8.96 ± 0.21	0-6	2.09 ± 0.15	74
1986	4-10	6.85 ± 0.15	4-12	6.51 ± 0.20	0-5	2.49 ± 0.15	74
1987	4-10	6.26 ± 0.10	4-11	7.47 ± 0.13	0-6	2.65 ± 0.12	106
1988	3-8	5.63 ± 0.10	4-10	6.42 ± 0.13	0-4	1.84 ± 0.10	122
1989	2-9	5.17 ± 0.09	3-10	5.47 ± 0.11	0-7	3.24 ± 0.13	148
1990	3-8	5.25 ± 0.10	4-8	6.09 ± 0.11	0-6	3.46 ± 0.15	89
1991	2-10	5.11 ± 0.10	4-15	7.32 ± 0.12	0-8	4.46 ± 0.14	170

Note. In some cases, while collecting scales by the Clutter-Whitesel method (1956), scale characteristics were brought close to those resulting from collection by the Pravdin method (1966). *In some years, up to a maximum of 8-10 % of cases, there were specimens having two ZAS; one of which was supplementary (at age 1.3)

which was the result of the interannual variability in the size of the smolts migrating from the lake (Dubynin, Bugaev, 1988; Bugaev, 1989; Bugaev, Dubynin, 1991). In the sockeye of the freshwater period, we note a strong positive correlation between body size and the total number of sclerites on the scales (Clutter, Whitesel, 1956; Bugaev et al., 1989; see section 8.7.1).

Our analysis of the correlation between the average abundance of *Cyclops* (by months) and the number of sclerites in the growth zones of the scales of smolts has shown that the correlation between these indices in stock “A” sockeye is generally stronger than in group “E” individuals (table 55). The highest coefficients of rank correlation in stock “A” smolts are noted in September–October during the first year of growth ($r_s=0.786$, $P<0.05$), in September ($r_s=0.881$, $P<0.01$) and November ($r_s=0.857$, $P<0.05$) during the second year, and in October and November during the year of downstream migration ($r_s=0.750$, $P>0.05$), after the downstream migration of juvenile sockeye from the lake.

In group “E” smolts (table 55), the highest coefficients of rank correlation are noted in June during the first year of growth prior to the migration of underyearlings to the lake (first zone of growth) ($r_s=0.500$, $P>0.05$), in August during the first year of growth following the migration of underyearlings to the lake (second zone of growth) ($r_s=0.667$, $P>0.05$), in August ($r_s=0.821$, $P<0.05$) and October ($r_s=0.821$, $P<0.05$) during the year of downstream migration, following the downstream migration of the juvenile sockeye.

The problem of analyzing the correlation between the average abundance of *Cyclops* and the number of sclerites in the zones of scale growth in sockeye smolts migrating from Azabach L. becomes more complex due to the fact that, in addition to juvenile sockeye of stock “A” and group “E”, two forms of the three-spine stickleback (*Gasterosteus aculeatus*), the anadromous form (*trachurus* morph) and the freshwater (landlocked) form (*leiurus* morph), as well as the pond smelt (*Hypomesus olidus*) and the ninespine stickleback (*Pungitius pungitius*) also forage in the same lake; these species are the food competitors of young sockeye, and their abundance varies considerably from year to year (Bugaev, 1988).

Table 55. The significance of coefficients of rank correlations in the analysis sockeye smolt (at age 2+) sclerites and the mean abundance of *Cyclops scutifer* in the summer fall foraging period of 1982-1990 in Azabach L.

Growth year	June		July		August	
	Stock “A”	Group “E”	Stock “A”	Group “E”	Stock “A”	Group “E”
First	$r_s = 0.619$ –	$r_s = 500$, $r_s = 0.61$	$r_s = 0.524$ –	$r_s = 0.309$, $r_s = 0.619$	$r_s = 0.571$ –	$r_s = 0.071$, $r_s = 0.667$
Second	$r_s = 0.833^*$, $a = 0.000038$, $b = 6.52$	– – –	$r_s = 0.833^*$, $a = 0.000111$, $b = 6.10$	– – –	$r_s = 0.762^*$, $a = 0.000041$, $b = 6.85$	– – –
Migrating year	$r_s = 0.643$ – –	$r_s = 0.679$ – –	$r_s = 0.643$ – –	$r_s = 0.714$ – –	$r_s = 0.750$ – –	$r_s = 0.821^*$, $a = 0.000032$, $b = 0.81$
<i>Continued, Table 55</i>						
Growth year	September		October		November	
	Stock “A”	Group “E”	Stock “A”	Group “E”	Stock “A”	Group “E”
First	$r_s = 0.786^*$, $a = 0.000013$, $b = 5.05$	$r_s = 0.286$, $r_s = 0.500$ –	$r_s = 0.786^*$, $a = 0.000013$, $b = 4.61$	$r_s = 0.238$, $r_s = 0.548$ –	$r_s = 0.738^*$, $a = 0.000014$, $b = 4.73$	$r_s = 0.333$, $r_s = 0.524$ –
Second	$r_s = 0.881^{**}$, $a = 0.000015$, $b = 6.52$	– – –	$r_s = 0.809^{**}$, $a = 0.000015$, $b = 6.13$	– – –	$r_s = 0.857^*$, $a = 0.000017$, $b = 6.27$	– – –
Migration year	$r_s = 0.714$ – –	$r_s = 0.750$ – –	$r_s = 0.750$ – –	$r_s = 0.821^*$, $a = 0.000012$, $b = 0.24$	$r_s = 0.750$ – –	$r_s = 0.786^*$, $a = 0.000012$, $b = 0.40$

Note. For specimens of group “E” the upper figure during the first year of growth represent the first zone of scale growth (growth prior to the migration to Azabach L.), the lower figure represents the second growth zone (growth in Azabach L.). In the first and second growth years there were 8 years of observation while migration years were observed for 7 years. One star “*” indicates situations where $p<0.05$; two stars “**” where $P<0.01$; “a” and “b” indicate regressive equation coefficients $Y=ax + b$, where “x” – abundance of *Cyclops scurifer*, with per m^3 ; “Y” – number of sclerites.

According to the data available to us (table 74), the feeding behaviour of the foraging juveniles and smolts of the sockeye differs during the years of high *Cyclops* abundance (large smolts) and low *Cyclops* abundance (small smolts) in the lake. When *Cyclops* are abundant, the sockeye feed predominantly on these organisms, eating up the largest instars; during the lean years, they feed mainly on the pupae of chironomids and the imagoes of flying insects.

The data in table 55 show that, in group “E” smolts, the strongest correlations between the abundance of *Cyclops* and the annual increments in all the zones of scale growth occur sooner than in stock “A” individuals, which points to a certain discreteness of the foraging grounds of stock “A” and group “E” juveniles in the lake.

Judging by the results of trawl and seine catches in Azabach L., stock "A" individuals are inclined to stay in the pelagic zone of the lake; in the second half of summer through autumn, they keep to the deeper levels of this zone, and do not surface in large numbers (in trawl catches in the 0-1 m layer, group "E" individuals predominate, even during the years when stock "A" individuals are more abundant in the lake).

Analysis of the number of gill rakers in adult sockeye has shown that stock "A" individuals have more gill rakers than group "E" individuals on the average, which leads to the assumption that stock "A" individuals are more planktophagous than group "E" individuals (fig. 41).

As a whole, the correlation between the scale structure of stock "A" sockeye and the abundance of *Cyclops* in the lake is stronger than in group "E" individuals. This also confirms that the individuals of stock "A" are more planktophagous than those of group "E".

Data on the abundance of *Cyclops* for each month has been available to us since 1981, and data on the abundance of *Cyclops* in October since 1979. The use of these data enables us to increase the number of points on the graph when estimating the correlations between abundance and scale characteristics both in smolts and in mature fish.

As we can see from tables 56 and 81, strong correlations between the number of sclerites and the abundance of *Cyclops* in October are noted during the first and the second year of growth both for the scales of smolts and the scales of adult fish. The coefficients of rank correlation are quite high (though unreliable) for the marginal zone of the scales in smolts, whereas they are low and also unreliable in the marginal zone of the freshwater part of the scales in mature fish.

Table 56. The significance of coefficients of rank correlation in the analysis of the number of sockeye scale sclerites (smolts and adults) and the mean abundance of *Cyclops scutifer* in October in Azabach L., 1979-1990

Growth year	Stock "A" (smolts)	Group "E" (smolts)	Stock "A" (adults)
First	$r_s = 0.786^*$, $n = 8$ $a = 0.000013$, $b = 4.61$	$r_s = 0.283$, $n = 9$; $r_s = 0.533$, $P > 0.05$, $n = 9$	$r_s = 0.867^{**}$, $n = 9$ $a = 0.000019$, $b = 4.79$
Second	$r_s = 0.783^*$, $n = 9$; $a = 0.000015$, $b = 6.17$	– –	$r_s = 0.855^{**}$, $n = 10$ $a = 0.000016$, $b = 6.18$
Migrating year	$r_s = 0.617$, $n = 9$	$r_s = 0.617$, $n = 9$	$r_s = 0.264$, $n = 11$

Note. For specimens of group "E" the upper figure during the first year of growth represent the first zone of scale growth (growth prior to the migration to Azabach L.), the lower figure represents the second growth zone (growth in Azabach L.). Notes as per table 55.

As we have already mentioned, a correlation between the characteristics of the freshwater zone of the scales of Azabach L. adult sockeye and the abundance of stock "A" and group "E" adults whose offspring forage together in the Azabach L. watershed has already been shown on the basis of the data for 1963-1979 (Bugaev, 1983a).

As we analyze the changes in the scale structure of stock "A" and group "E" smolts in relation to the abundance of spawners (which arbitrarily reflect the inter-annual abundance of foraging juveniles in the lake, see section "Material and Method"), we note a significant negative correlation between the number of sclerites and the number of spawners in stock "A" smolts during the first and second years (table 57). With an increase in the abundance of spawners and, consequently, the abundance of foraging juveniles in the lake, the growing conditions of the young deteriorate, and vice versa.

Table 57. The significance of coefficients of rank correlation in the analysis of the number of sockeye scale sclerites (smolts and adults) and the abundance of brood stock in Azabach L. and streams along the lower Kamchatka R. from which sockeye underyearlings migrate to forage in Azabach L.

Growth year	Stock "A" (smolts)	Group "E" (smolts)	Stock "A" (adult)
First	$r_s = -0.709^*$, $n = 10$; $a = -0.0020$, $b = 7.07$	$r_s = -0.297$, $n = 10$; $r_s = -0.249$, $n = 10$	$r_s = -0.727^*$, $n = 11$ $a = 0.0019$, $b = 7.51$
Second	$r_s = -0.806^{**}$, $n = 10$ $a = -0.0026$, $b = 9.22$	– –	$r_s = -0.618^*$, $n = 11$; $a = -0.0031$, $b = 9.75$
Migrating year	$r_s = -0.697^*$, $n = 9$; $a = -0.0015$, $b = 1.97$	$r_s = -0.600$, $n = 9$ –	$r_s = -0.409$, $n = 11$ –

Note. For specimens of group "E" the upper figure during the first year of growth represent the first zone of scale growth (growth prior to the migration to Azabach L.), the lower figure represents the second growth zone (growth in Azabach L.). One star "*" indicates situations where $p < 0.05$; two stars "**" where $P < 0.01$; "a" and "b" indicate regressive equation coefficients $Y = ax + b$, where "x" – brood stock abundance, in thou.of units; "Y" – number of sclerites.

A similar correlation is also observed for the number of sclerites in stock "A" spawners during the first and second year of growth (table 57). This type of correlation is practically nonexistent in group "E" smolts during the first year of life (in the first and second growth zones), but a negative correlation between these characteristics is observed in the marginal zone of the scales in stock "A" and group "E" smolts. In mature fish, a very weak (unreliable) negative correlation with the abundance of spawners is observed for the marginal zone of the freshwater part of the scales.

Fig. 81 illustrates some of the data presented in table 57, as we can see from the diagram, the line of regression of the correlation between the number of sclerites and the abundance of spawners in mature fish during the first year extends slightly above the same line in smolts, which is probably due to the elimination of the smaller juveniles after their seaward migration. During the second year, the differences between the lines of regression in smolts and mature fish are smaller.

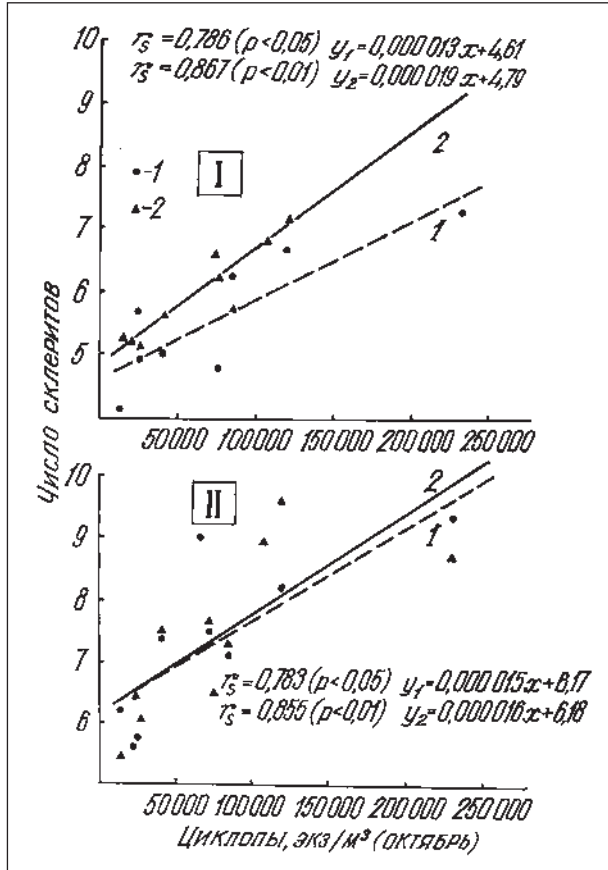


Fig. 81. Variation in the number of sclerites on the scales of stock "A" sockeye during the first and second years of growth, depending on the average abundance of *Cyclops scutifer* in Azabach L. in October. Y-axis – number of sclerites; X-axis – abundance of *Cyclops scutifer*, specimens/m³. I – first years of growth, II – second year of growth; 1 – smolts (age 2+), 2 – adults (age 2.3).

We also analyzed the rank correlations between the number of sclerites in the growth zones of the scales of stock "A" and group "E" sockeye and the average monthly abundance of *Daphnia galeata* for the June–November period (table 58). Our analysis showed the highest correlations ($r_s = 0.707-0.809$) for the second year of growth of stock "A" individuals in July–September, which for August ($r_s = 0.809$) and September ($r_s = 0.719$) were statistically reliable ($P < 0.05$; years of ob-

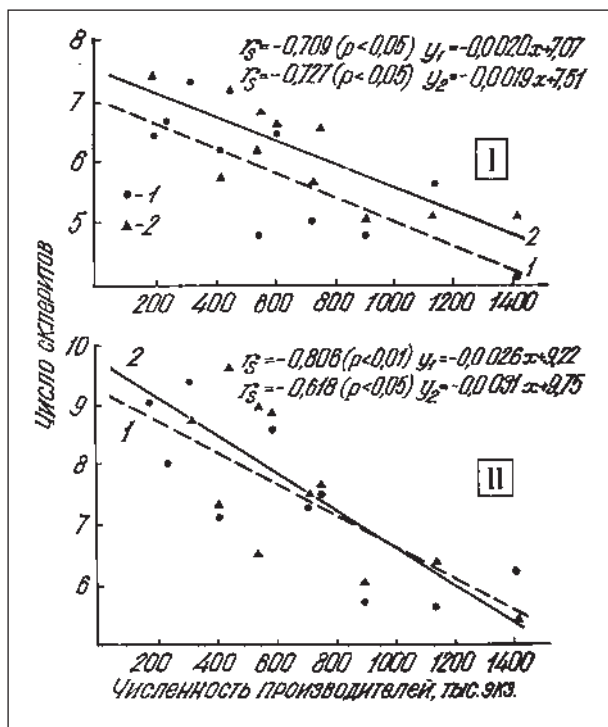


Fig. 82. Variation in the number of sclerites on the scales of stock "A" sockeye during the first and second years of growth, depending on the average abundance of sockeye parent spawners in Azabach L. and the tributaries in the lower reaches of the Kamchatka R. Y-axis – number of sclerites; X-axis – abundance of spawners, thou. specimens. I – first year of growth, II – second year of growth; 1 – smolts (age 2+), 2 – adults (age 2.3).

servation equal to 8). In all the rest of the cases, the correlations were weaker and unreliable. These facts indicate that the growth of juvenile sockeye in Azabach L. is less dependent on the abundance of *Daphnia* than on the abundance of *Cyclops* in this lake.

The rank correlations between the average monthly abundance of *Cyclops* and *Daphnia* for the period 1981-1990 were significant during certain months. For instance, the coefficients of rank correlation were $r_s=0.589$ ($P>0.05$) in June, $r_s=0.755$ ($P<0.05$) in July, $r_s=0.758$ ($P<0.05$) in August, $r_s=0.815$ ($P<0.01$) in September, $r_s=0.261$ ($P>0.05$) in October and $r_s=0.529$ ($P>0.05$) in November for an observation period equal to 10 years. In Kuril L., the monthly values of *Cyclops* and *Daphnia* abundance practically do not correlate with each other; in 1973 through 1989, the coefficients of rank correlation varied from -0.191 to 0.248 ($P>0.05$) (Bugaev, Dubynin, Milovskaya, 1995).

Table 58. The significance of coefficients of rank correlations in the analysis sockeye smolt sclerites and the mean abundance of *Daphnia galeata* in the summer fall foraging period of 1982-1990 in Azabach L.

Growth year	June		July		August	
	Stock "A"	Group "E"	Stock "A"	Group "E"	Stock "A"	Group "E"
First	$r_s = -0.412$ –	$r_s = 0.577$, $r_s = -0.247$	$r_s = 0.342$ –	$r_s = 0.098$, $r_s = 0.146$	$r_s = 0.548$ –	$r_s = 0.048$, $r_s = 0.309$
Second	$r_s = 0.412$ – –	– – –	$r_s = 0.707$ – –	– – –	$r_s = 0.809^*$, $a = -0.00024$, $b = 6.77$	– – –
Migrating year	$r_s = 0.204$	$r_s = 0.000$	$r_s = 0.342$	$r_s = 0.306$	$r_s = 0.429$	$r_s = 0.393$
Growth year	September		October		November	
	Stock "A"	Group "E"	Stock "A"	Group "E"	Stock "A"	Group "E"
First	$r_s = 0.527$	$r_s = -0.227$, $r_s = 0.575$	$r_s = 0.262$	$r_s = -0.476$, $r_s = -0.024$	$r_s = 0.595$	$r_s = -0.286$, $r_s = 0.167$
Second	$r_s = 0.719^*$, $a = 0.00014$, $b = 6.82$	– – –	$r_s = 0.262$ – –	– – –	$r_s = 0.381$ – –	– – –
Migrating year	$r_s = 0.414$	$r_s = 0.487$	$r_s = 0.357$	$r_s = 0.286$	$r_s = 0.393$	$r_s = 0.429$

Note. For specimens of group "E" the upper figure during the first year of growth represent the first zone of scale growth (growth prior to the migration to Azabach L.), the lower figure represents the second growth zone (growth in Azabach L.). In the first and second growth years there were 8 years of observation while migration years were observed for 7 years. One star "*" indicates situations where $P<0.05$; "a" and "b" indicate regressive equation coefficients $Y=ax + b$, where "x" – abundance of *Daphnia galeata*, units per m^3 ; "Y" – number of sclerites.

Analysis of the relationship between the water temperature in Azabach L. at the 0, 5, 10, 15, 20 and 30 m levels (in June, July, August, September, October and November) and the number of sclerites in the zones of scale growth in smolts (264 coefficients of rank correlation estimated) showed that these relationships were the most significant in stock "A" individuals for the temperatures in August (table 59), and in group "E" for the temperatures in November–October.

We noted a very strong correlation between the number of sclerites in second-year individuals of stock "A" and the water temperature at a depth of 10 m in August (table 59, fig. 83); a strong correlation with the water temperature at a depth of 15 m was also noted ($r_s=0.790$, $P<0.05$; observation period $n=8$ years). During the year of downstream migration, we noted a negative correlation ($r_s=-0.766$, $P<0.05$) with the water temperature at a depth of 0 m, and a positive correlation ($r_s=0.786$, $P<0.05$) with the temperature at a depth of 10 m (in both cases, the observation period was equal to 8 years).

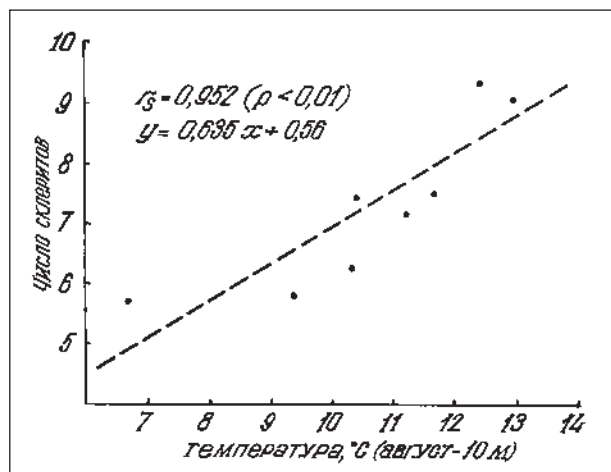


Fig. 83. Variation in the number of sclerites during the second year of scale growth in sockeye of stock "A", depending on the water temperature in Azabach L. at a depth of 10 m in August. Y-axis – number of sclerites; X-axis – water temperature at a depth of 10 m in August, °C.

Very high coefficients of rank correlation were noted between the water temperatures at depths of 0, 5, 10, 15 and 20 m in November and the increase in the number of sclerites in the first zone of scale growth in group “E” (when the young had not yet migrated to the lake). The coefficients of rank correlation were $r_s = -0.929$ at 0 m, $r_s = -0.922$ at 5 m, $r_s = -0.929$ at 10 m, $r_s = -0.946$ at 15 m (fig. 84), and $r_s = -0.880$ at 20 m ($P < 0.01$ and observation period $n = 8$ years in all the cases). Slightly lower coefficients of rank correlation were noted between the increment in the same zone of scale growth in group “E” individuals and the October water temperatures at depths of 0, 5, 10 and 15 m; they were $r_s = -0.826$, $r_s = -0.905$, $r_s = -0.857$ and $r_s = -0.809$ respectively ($P < 0.01$ for the 5 m level, and $P < 0.05$ for the rest; observation period $n = 8$ years).

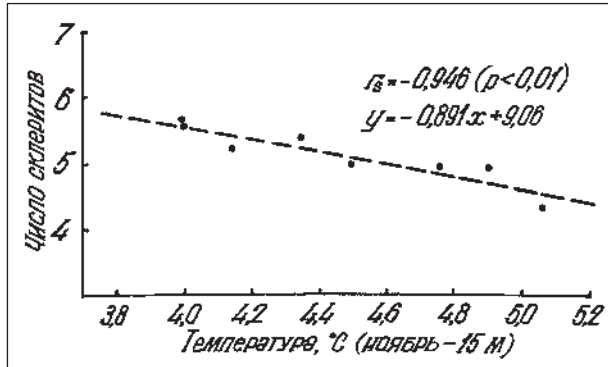


Fig. 84. Variation in the number of sclerites in the first zone of scale growth in sockeye of group “E”, depending on the water temperature in Azabach L. at a depth of 15 m in November. Y-axis – number of sclerites; X-axis – water temperature at a depth of 15 m in November, °C.

Table 59. The significance of coefficients of rank correlations in the analysis sockeye smolt sclerites and water temperature by horizons in Azabach L. in August 1982-1991

Horizon, m	Growth year	Stock “A”	Group “E”
0	First	$r_s = -0.143$	$r_s = -0.333$,
	“_”	–	$r_s = -0.071$
	Second	$r_s = -0.333$	–
	Migrating year	$r_s = -0.762^*$, a = -0.600, b = 10.59	$r_s = -0.595$
5	First	$r_s = 0.476$	$r_s = 0.214$,
	“_”	–	$r_s = 0.238$
	Second	$r_s = 0.309$	–
	Migrating year	$r_s = 0.024$	$r_s = 0.143$
10	First	$r_s = 0.667$	$r_s = 0.524$,
	“_”	–	$r_s = 0.452$
	Second	$r_s = 0.952^{**}$, a = 0.635, b = 0.56	–
	Migrating year	$r_s = 0.786^*$, a = 0.453, b = -3.68	$r_s = 0.667$
15	First	$r_s = 0.204$	$r_s = 0.239$
	“_”	–	$r_s = 0.311$
	Second	$r_s = 0.790^*$, a = 0.839, b = 0.80	–
	Migrating year	$r_s = 0.527$	$r_s = 0.407$
20	First	$r_s = -0.643$	$r_s = 0.143$,
	“_”	–	$r_s = 0.095$
	Second	$r_s = 0.191$	–
	Migrating year	$r_s = -0.214$	$r_s = -0.238$
30	First	$r_s = -0.671$	$r_s = -0.132$
	“_”	–	$r_s = -0.263$
	Second	$r_s = -0.072$	–
	Migrating year	$r_s = -0.371$	$r_s = -0.515$

Note. For specimens of group “E” the upper figure during the first year of growth represent the first zone of scale growth (growth prior to the migration to Azabach L.), the lower figure represents the second growth zone (growth in Azabach L.). In the first and second growth years there were 8 years of observation while migration years were observed for 7 years. One star “*” indicates situations where $p < 0.05$; two stars “**” where $P < 0.01$; “a” and “b” indicate regressive equation coefficients $Y = ax + b$, where “x” – water temperature, °C; “Y” – number of sclerites.

Another noteworthy rank correlation was the one observed in group “E” individuals between the water temperature at a depth of 30 m in June and the number of sclerites in the second growth zone (after the migration of juveniles to the lake); it was $r_s = -0.786$ ($P < 0.05$; observation period $n = 8$ years; $Y = -1.421x + 11.15$, where “x” denotes the water temperature at a depth of 30 m, and “Y” the number of sclerites in the second growth zone).

Finally, a rank correlation of $r_s = 0.762$ ($P < 0.05$) was noted for stock “A” individuals between the September water temperature at a depth of 15 m and the number of sclerites in the second year of growth ($Y = 0.902x - 0.68$, where “x” denotes the water temperature at a depth of 15 m in September, and “Y” the number of sclerites in the second year of growth).

Due to the short observation series on sockeye smolts migrating from Azabach L., we are unable at this time to analyze the growth of juvenile sockeye in relation to the abundance of *Cyclops* and *Daphnia*, with classification based on water temperatures in the lake into warm and cold years of growth as we have done for the sockeye of Kuril L. (Bugaev et al., 1989). This will become possible not sooner than 8-10 years from now.

Analysis of the correlation between the abundance of *Cyclops* in Azabach L. in October and the number of sclerites in the growth zones of the central part of the scales in sockeye spawners of age 2.3 (table 54) caught during 1963-1991 (individuals of age 2.2 caught in 1991 were included for extension of the observation series) showed (table 60) that, during the growing season of 1958 through 1979, the correlations were statistically reliable in stock “A” individuals during the first and second years of growth, though the coefficients of rank correlation were quite low in the first year.

Analysis of the growth of the same individuals for the periods 1958-1969 and 1979-1989 showed that the rank correlations were high in the second year of growth during both periods, but were high in the first year of growth only during 1979-1989 (table 60). No correlations were noted between the increase in the marginal zone of the scale and the abundance of *Cyclops* in either of these periods (table 60). There may be several reasons for the absence of correlations in the first year of growth during 1958-1969, but it is impossible to determine the main one at the present time. It may have something to do with the foraging and temperature conditions in the lake, the numbers of the sockeye and its food competitors, and also the quality of our initial data on the scales of sockeye spawners from Azabach L. During 1963-1974, we used archival data on the scales of spawners, and in some cases the scale sampling method could not be ascertained, and this could have had some bearing on the number of sclerites recorded in the first year of growth (Bugaev, 1983a; Bugaev, 1989).

Table 60. The significance of coefficients of rank correlations in the analysis the number of sclerites in the freshwater zone of adult sockeye aged 2.3 years from “A” stock and the mean abundance of *Cyclops scutifer* in October of 1958-1989 in Azabach L.

Growth year	Foraging year		
	1958-1989	1958-1969	1979-1989
First	$r_s = 0.487^*$, $n = 19$ $a = 0.0000027$, $b = 5.74$	$r_s = 0.018$, $n = 10$ —	$r_s = 0.867^{**}$, $n = 9$ $a = 0.000019$, $b = 4.79$
Second	$r_s = 0.821^{**}$, $n = 19$ $a = 0.000011$, $b = 6.46$	$r_s = 0.817^*$, $n = 9$; $a = 0.000008$, $b = 6.57$	$r_s = 0.855^{**}$, $n = 10$ $a = 0.000016$, $b = 6.18$
Migrating year	$r_s = 0.125$, $n = 19$ —	$r_s = 0.024$; $P > 0.05$, $n = 8$	$r_s = 0.264$, $n = 11$ —

Note. To increase the number of observations, adult sockeye aged 2.2 were included for 1991. Notes as per table 55.

Table 61. The significance of coefficients of rank correlations in the analysis of the number of sclerites in scales of adult sockeye in the freshwater zone, aged 2.3 years of stock “A” and the mean abundance of parents sockeye in Azabach L, and streams along the lower Kamchatka R., from which sockeye underyearlings migrate to forage in Azabach L.

Growth year	Foraging year		
	1958-1989	1958-1969	1979-1989
First	$r_s = -0.347$, $n = 28$ —	$r_s = -0.098$, $n = 17$ —	$r_s = -0.727^*$, $n = 11$, $a = -0.0019$, $b = 7.51$
Second	$r_s = -0.470^*$; $n = 28$; $a = 0.0026$, $b = 9.46$	$r_s = -0.331$; $n = 17$ —	$r_s = -0.618^*$; $n = 11$; $a = -6.0031$; $b = 9.75$
Migrating year	$r_s = 0.259$, $n = 28$ —	$r_s = 0.351$; $n = 17$ —	$r_s = -0.409$; $n = 11$ —

Note. To increase the number of observations, adult sockeye aged 2.2 were included for 1991. Notes as per table 57.

Analysis of the scale structure of stock “A” sockeye spawners depending on the abundance of parent fish (table 61) that spawned out in Azabach L. and the tributaries of the lower Kamchatka R. during 1956-1990 showed a fairly weak reliable correlation only in the second year of growth for the period 1958-1989. However, the correlations for 1977-1989 were quite strong both in the first, and in the second year of growth, as compared with the extremely weak correlations for the growing season during 1958-1978. As in the previous case (table 60), we are still unable to determine the cause of these differences

for the individual periods.

With our strong correlations between the abundance of *Cyclops* in October and the number of sclerites in second-year stock "A" sockeye (table 60), we are tempted to reconstruct, on the basis of the number of sclerites, the abundance of *Cyclops* in October for the period 1970-1978 by means of the correlation formula for the 1958-1989 period. This is, $Y = 44858x - 243997$ ($r_s = 0.821$, $n = 19$, $P < 0.01$), where "x" denotes the number of sclerites in the second year of growth, and "Y" the number of *Cyclops* in October. However, the reliability of the results obtained by this formula should be determined experimentally by analyzing the fluctuations in the abundance of sockeye in Azabach L. over a number of years.

This analysis of the correlation between the foraging and temperature conditions and the growth of stock "A" and group "E" sockeye migrating from Azabach L. has unquestionably demonstrated the effect of environmental factors on the growth of this lake's sockeye. It has also been shown that the sockeye feeding and growing in Azabach L. has the same environment-dependent growth characteristics as the sockeye from other bodies of water in Asia, North America and New Zealand (Foerster, 1944; Krogus, 1961; Johnson, 1965; Burgner et al., 1968; Goodlad et al., 1974; Dubynin, 1986; Burgner, 1987; Graynoth, 1987; Kyle et al., 1988; Bugaev et al., 1989; Bugaev, 1989, and others).

Fig. 85 illustrates the interannual variability of the freshwater zone of the scales in the Azabach L. stock of sockeye spawners, the interannual variability of the scales in yearlings of the same stock is shown in fig. 65.

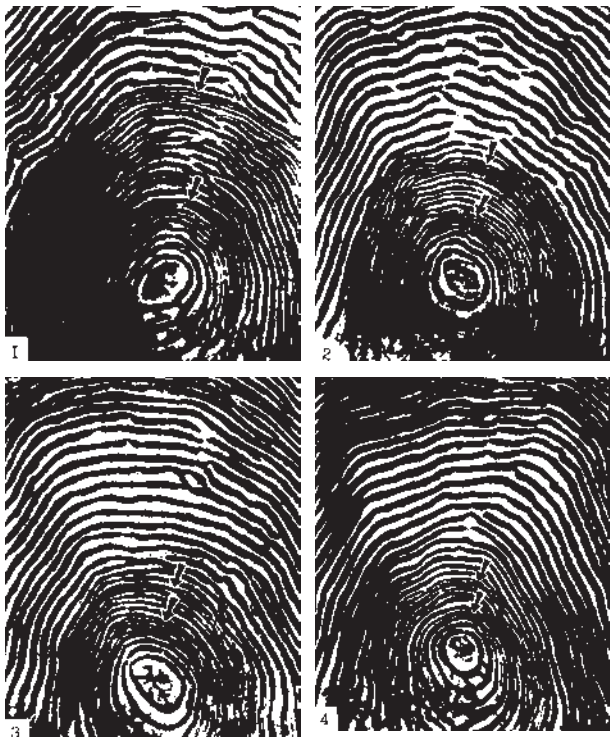


Fig. 85. Interannual variability in the structure of the central part of the scales in sockeye spawners of Azabach L. (mouth of the Bushuyka R.). Arrows mark ZAS – annuli.
 1-5 July 1981, AC=660 mm, male, age 2.3; 2 – 30 June 1985, AC=570 mm, female, age 2.3;
 3-1 July 1986, AC=655 mm, male, age 2.3; 4 – July 1986, AC=575 mm, female, age 2.3.

8.7.3. Growth of juvenile sockeye in Kuril L. (Ozernaya R.)

To increase the reproductive level of the Ozernaya R. sockeye, Kuril L. has been subjected to systematic artificial fertilization since 1981, which has already effected an increase in the abundance of spawning runs of mature fish to the mouth of the Ozernaya R. during 1985-1991.

As we know (Kurenkov, 1975; Bugaev, 1986b; Manzer, 1976; Stockner, Hyatt, 1984), artificial and natural fertilization (by volcanic ash during the eruption of volcanoes) of waters foraged by juvenile sockeye usually increases their productivity drastically. At the same time, we should keep in mind that it is necessary to correct the standard fishery forecasts of sockeye abundance, since the relationships on which the forecasting methods are based prior to fertilization are disrupted after fertilization (Stockner, Hyatt, 1984). Experience has shown that it does not pay to forecast the abundance of sockeye runs after fertilization. This fact has also been pointed out by researchers from other countries (Stockner, Hyatt, 1984).

We were tempted to use the scale structure of the Kuril L. sockeye as an indicator for the evaluation of their foraging conditions, which may help to improve the method of forecasting the abundance of this sockeye stock over the one being used at the present time (with smolt size as the indicator).

In the process of their work on a theoretical model of salmonid growth, modern researchers (Brett, 1983; Elliot, 1975) supported the view that at least three factors, i.e. food availability, body size and temperature, should be used as the major independent variables to construct any model. Food availability in a natural environment serves as the principal limiting factor which regulates the growth rate of fish during the growing season. Furthermore, in a natural environment, we can clearly trace the dependence of the growth rate on the temperatures of the season and its apparent decline with age and body size

(Nikolsky, 1974, 1974a; Mina, Klevezal, 1976; Brett, 1983).

As we have shown earlier, the growth rate and size of juvenile sockeye is closely related to the structure of their scales. Therefore, in our research of this species, we are able to foresee the growth of the fish, but in greater detail, since the various structural elements of the scales, i.e. the number of scerites and the distance between them, are differently affected by environmental changes (Vaganov, 1978).

Our analysis of the correlation between the number of sclerites in the zones of scale growth (tables 62, 63) and the mean abundance of *Cyclops* in May–June, June–July, July–August, etc. has shown (table 64) the strongest correlations to be in July–September (2.2) and August–November (2.3) in the first year of growth, and in August–October in both age groups in the second year of growth. All of this points to the fact that the second half of summer and autumn are the main period of growth for the sockeye in this lake.

Table 62. Number of scale sclerites in adult sockeye in the fresh water zone of Ozernaya R. (Kuril L.) (at age 2.2, two ZAS)

Spawning year	First year		Second year		Migrating year		Distance between sclerites		Number of fish
	Range	Average	Range	Average	Range	Average	First year	First year	
							Average	Average	
1964	3-10	5.03 ± 0.24	4-12	8.00 ± 0.29	0-4	1.25 ± 0.17	1.92	2.09	40
1965	3-7	4.88 ± 0.22	7-12	8.75 ± 0.28	1-6	3.71 ± 0.22	2.16	2.38	24
1966	2-12	6.24 ± 0.16	6-15	10.34 ± 0.15	0-7	1.86 ± 0.13	2.44	2.39	90
1967	5-10	7.57 ± 0.16	6-12	8.31 ± 0.17	0-7	2.41 ± 0.12	2.56	2.48	54
1968	4-7	5.43 ± 0.17	7-12	9.18 ± 0.27	0-3	0.93 ± 0.19	2.53	2.39	28
1969	2-11	5.36 ± 0.46	4-12	8.05 ± 0.47	1-7	2.86 ± 0.29	2.09	2.11	22
1970	2-10	5.57 ± 0.38	5-13	9.40 ± 0.34	0-6	2.03 ± 0.22	1.99	2.39	35
1971	3-10	5.14 ± 10.23	6-12	9.19 ± 0.25	0-7	1.95 ± 0.19	2.16	2.15	42
1972	3-10	5.69 ± 0.21	5-13	8.57 ± 0.28	1-7	2.78 ± 0.16	2.67	2.35	49
1973	3-9	5.94 ± 0.36	6-13	9.11 ± 0.46	0-7	3.33 ± 0.33	2.53	2.44	18
1974	5-11	8.05 ± 0.25	6-14	10.73 ± 0.29	2-7	3.16 ± 0.19	2.73	2.61	37
1975	3-11	7.09 ± 0.15	7-12	9.39 ± 0.14	0-7	2.73 ± 0.13	2.87	2.65	80
1976	4-9	6.15 ± 0.13	8-14	11.23 ± 0.15	1-5	2.97 ± 0.10	2.49	2.75	79
1977	4-10	6.91 ± 0.31	4-14	10.22 ± 0.45	0-5	2.74 ± 0.23	2.99	2.81	23
1978	4-11	6.24 ± 0.25	7-16	12.20 ± 0.29	0-6	2.95 ± 0.18	2.70	2.82	41
1979	5-12	8.54 ± 0.18	4-14	9.89 ± 0.24	0-5	2.11 ± 0.12	2.86	2.57	70
1980	3-9	5.55 ± 0.16	6-15	11.75 ± 0.21	0-5	2.33 ± 0.12	2.29	2.83	60
1981	5-11	7.97 ± 0.24	7-17	9.62 ± 0.32	0-4	0.90 ± 0.14	2.87	2.57	39
1982	3-11	6.96 ± 0.29	5-13	7.62 ± 0.32	2-6	3.84 ± 0.12	2.66	2.49	51
1983	3-8	5.45 ± 0.25	7-14	9.77 ± 0.34	1-4	3.09 ± 0.19	2.06	2.26	22
1984	3-8	5.42 ± 0.46	7-13	9.50 ± 0.78	1-3	1.84 ± 0.31	2.35	2.63	12
1985	4-11	7.42 ± 0.33	4-12	9.10 ± 0.30	0-4	2.42 ± 0.17	2.47	2.49	31
1986	4-12	7.41 ± 0.24	7-17	11.97 ± 0.28	0-4	2.17 ± 0.12	2.62	2.53	59
1987	4-12	8.85 ± 0.34	6-14	9.23 ± 0.32	0-2	1.35 ± 0.32	2.94	2.63	26
1988	7-12	8.69 ± 0.20	5-12	8.90 ± 0.27	0-4	2.79 ± 0.15	2.77	2.42	39
1989	4-11	6.54 ± 0.29	6-14	11.80 ± 0.25	0-3	1.63 ± 0.14	2.44	2.58	41
1990	6-11	8.98 ± 0.10	7-13	9.71 ± 0.19	0-4	1.10 ± 0.14	2.66	2.41	49
1991	4-11	7.33 ± 0.24	7-15	10.85 ± 0.25	1-4	2.54 ± 0.14	2.58	2.16	41

Note. Scales collected by Clutter-Whitesel method (1956).

As we can see (table 64), the coefficients of rank correlation between the number of sclerites and the abundance of *Cyclops* are higher in the second year, than in the first. In our opinion, this can be attributed to the fact that the emergence of underyearlings in the pelagic zone of the Kuril L. watershed takes a very long time due to the prolonged spawning of the parents (Yegorova, 1970, 1970a), and many of them begin feeding on plankton after the young of other age groups have resumed their seasonal growth following the autumn–winter diapause.

We did not take the 1977 year-class into account when calculating the strength of the correlation, since these individuals displayed drastic growth deviations from the general relationship. Despite the high overall abundance of *Cyclops* in August–October, sockeye growth in 1979 was the worst for the entire period of our research. Analysis of the *Cyclops* population showed that the amount of copepodite plankton consumed by the fish in 1979 was much lower than in the other years due to the low consumption of 3rd- and 4th-instar copepodites by the young fish. Taking this into consideration, we did not analyze the growth of the underyearlings foraging in the lake in 1979 (spawned in 1978). The year 1979 was excluded from the study in all the cases where the effect of environmental factors on the formation of the scale structure of sockeye was examined (Bugaev et al., 1989).

Analysis of the correlation between the average number of sclerites in the growth zones of the central part of the scales in age 2.2 and 2.3 sockeye spawners and the water temperature at 0, 10, 20, 30, 40 and 50 m in Kuril L. during the spring–autumn (May–November) of 1959–1984 (168 coefficients of rank correlation determined) showed only one reliable correlation with the water temperature at 40 m in age 2.2 sockeye in August in the second year of growth ($r_s = -0.515$, $P < 0.05$, $n = 17$), and one reliable correlation with the temperature at 20 m in age 2.2 individuals in September in the first year of growth ($r_s = 0.530$, $P < 0.05$, $n = 17$).

Table 63. Number of scale sclerites in adult sockeye in the fresh water zone of Ozernaya R. (Kuril L.) (at age 2.3, two ZAS)

Spawning year	First year		Second year		Migrating year		Distance between sclerites		Number of fish
	Range	Average	Range	Average	Range	Average	First year	Second year	
							Average	Average	
1964	2-8	4.58 ± 0.17	4-13	7.47 ± 0.30	0-6	2.05 ± 0.17	1.95	2.09	64
1965	2-7	4.52 ± 0.18	6-11	8.03 ± 0.25	0-5	1.81 ± 0.23	2.24	2.26	31
1966	3-10	5.52 ± 0.13	4-15	8.84 ± 0.16	0-9	2.89 ± 0.15	2.11	2.21	142
1967	2-10	6.17 ± 0.12	5-14	10.21 ± 0.13	0-4	1.84 ± 0.08	2.35	2.45	140
1968	2-8	5.48 ± 0.19	6-13	8.75 ± 0.20	0-5	2.39 ± 0.15	2.51	2.44	56
1969	3-10	5.37 ± 0.13	4-13	9.34 ± 0.16	0-8	1.61 ± 0.17	2.23	2.21	108
1970	3-9	5.50 ± 0.43	7-11	9.08 ± 0.36	0-6	2.58 ± 0.46	2.02	2.07	12
1971	2-9	4.53 ± 0.23	5-12	9.44 ± 0.24	0-5	2.56 ± 0.19	2.24	2.33	57
1972	3-10	5.14 ± 0.23	6-12	9.19 ± 0.25	0-7	1.95 ± 0.19	2.16	2.15	42
1973	3-10	5.69 ± 0.21	5-13	8.57 ± 0.28	1-7	2.78 ± 0.16	2.67	2.35	49
1974	2-11	5.02 ± 0.14	4-15	11.88 ± 0.17	1-7	3.67 ± 0.10	2.04	2.43	100
1975	4-12	7.64 ± 0.19	8-14	11.20 ± 0.18	0-4	2.22 ± 0.12	2.88	2.80	74
1976	4-11	7.25 ± 0.13	7-13	9.74 ± 0.18	0-5	2.58 ± 0.12	2.70	2.59	65
1977	3-10	6.51 ± 0.17	5-16	11.19 ± 0.25	0-9	2.81 ± 0.18	2.73	2.75	70
1978	3-11	6.79 ± 0.19	7-15	11.17 ± 0.21	0-6	2.67 ± 0.13	2.81	2.72	75
1979	4-14	7.68 ± 0.26	6-17	12.32 ± 0.27	0-4	2.41 ± 0.12	2.66	2.81	59
1980	4-12	7.88 ± 0.19	5-15	10.22 ± 0.12	0-5	2.10 ± 0.11	2.79	2.60	98
1981	3-10	5.44 ± 0.19	7-16	11.85 ± 0.22	0-5	2.26 ± 0.12	2.27	2.81	62
1982	4-11	7.68 ± 0.21	6-12	9.10 ± 0.22	0-5	1.12 ± 0.12	2.86	2.63	80
1983	4-12	6.76 ± 0.14	4-13	7.08 ± 0.16	0-6	3.38 ± 0.12	2.44	2.39	109
1984	4-8	6.15 ± 0.16	6-13	8.85 ± 0.20	1-4	2.39 ± 0.10	2.29	2.40	92
1985	3-11	5.67 ± 0.13	5-13	9.85 ± 0.12	0-5	2.09 ± 0.08	2.22	2.49	144
1986	4-13	7.83 ± 0.18	6-15	10.25 ± 0.20	1-4	2.46 ± 0.08	2.57	2.48	92
1987	2-13	6.50 ± 0.15	6-15	11.91 ± 0.14	0-4	1.91 ± 0.07	2.78	2.59	129
1988	2-13	8.82 ± 0.24	6-15	10.25 ± 0.16	0-4	1.88 ± 0.10	2.65	2.50	93
1989	3-13	8.33 ± 0.21	5-16	9.39 ± 0.22	0-4	2.39 ± 0.12	2.71	2.53	83
1990	3-11	6.36 ± 0.19	7-16	12.00 ± 0.18	0-4	1.36 ± 0.11	2.14	2.42	85
1991	4-11	8.39 ± 0.18	6-14	9.81 ± 0.16	0-3	1.31 ± 0.09	2.59	2.36	88

Note. Scales collected by Clutter-Whitesel method (1956).

Table 64. The significance of coefficients of rank correlation in the analysis of the number of sclerites in the scales of adult sockeye in the fresh water zone and the mean abundance of *Cyclops scutifer* in the summer-fall period in Kyril L. (Bugaev et al., 1989)

Age	Growth year	May-June	June-July	July-August	August-September	September-October	October-November
2.2	1	$r_s = 0.385, n=19$ - -	$r_s = 0.253, n=19$ - -	$r_s = 0.540, n=19$ P < 0.05, a = 0.00015, b = 5.32	$r_s = 0.763, n=18;$ P < 0.01, a = 0.00019, b = 5.32	$r_s = 0.483,$ n=18, P < 0.05, a = 0.00016, b = 4.96	$r_s = 0.440*, n=19$ - -
2.2	2	$r_s = 0.253, n=20$ - -	$r_s = 0.432, n=19$ - -	$r_s = 0.583, n=20;$ P < 0.01, a = 0.00022, b = 8.06	$r_s = 0.734, n=18,$ P < 0.01, a = 0.00025, b = 7.34	$r_s = 0.723, n=18,$ P < 0.01, a = 0.00026, b = 7.20	$r_s = 0.505, n=19;$ P < 0.05, a = 0.00020, b = 7.98
2.3	1	$r_s = 0.138, n=19$ - -	$r_s = 0.364, n=18$ - -	$r_s = 0.540, n=19,$ P < 0.05, a = 0.00013, b = 5.12	$r_s = 0.616, n=17,$ P < 0.01, a = 0.00016, b = 4.65	$r_s = 0.703, n=17,$ P < 0.01, a = 0.00019, b = 4.44	$r_s = 0.606, n=18,$ P < 0.01, a = 0.00020, b = 4.50
2.3	2	$r_s = 0.28, n=19$ - -	$r_s = 0.446, n=19$ - -	$r_s = 0.672, n=19,$ P < 0.01, a = 0.00025, b = 7.99	$r_s = 0.930, n=18,$ P < 0.01, a = 0.00029, b = 7.17	$r_s = 0.816, n=18,$ P < 0.01, a = 0.00028, b = 7.25	$r_s = 0.607, n=19,$ P < 0.01, a = 0.00026, b = 7.61

Note. "a" and "b" – regressive equation coefficient $Y=ax + b$, where "x" – *Cyclops scutifer* abundance, with per m³, "Y" – number of sclerites; n – number of compared pairs.

As we can see from fig. 86, the coefficients of rank correlation in September (the period corresponding to hydrological summer in the lake) vary consistently with depth. However, as we have already pointed out, the correlations derived from the available material ($n=17-19$) were statistically unreliable, except for one.

The derivation of reliable correlations between the number of sclerites and the abundance of *Cyclops* (table 64) and mainly unreliable correlations with the water temperatures in the lake indicates that it is the development of the forage base that has a decisive effect on the growth of the juvenile sockeye of Kuril L. during the freshwater period. This conclusion is fully consistent with the present-day concepts of fish growth, whereby the availability of food in a natural environment is considered to be the limiting factor that determines their growth (Nikolsky, 1974; Brett, 1983). Taking this into consideration, we distributed the entire material according to the years of long-term stability of overall low abundance of juvenile sockeye in the lake (1970-1978) and the years of high abundance of young sockeye (the rest of the years studied) when examining the effect of water temperature on the spacing of the sclerites. The correctness of this type of distribution is confirmed by two-dimensional analysis, i.e. the 1970-1978 population of points on the graph was distributed quite separately from all the rest of the years being studied. A correlation analysis (fig. 87) has shown that the coefficients of rank correlation for the same age groups and for the same years of growth differ during the years of high and low abundance of the young. Unfortunately, we have not recorded many years of low abundance of juveniles in the lake (only 6 years), and therefore, despite the fairly strong correlations in some cases, we consider them to be statistically unreliable at the present time (fig. 87).

During the years of high abundance of juveniles, where we had 11-13 years of observations for comparison, we observed a reliable correlation with the water temperatures at 10-20 m in age groups 2.2 and 2.3 in the first year of growth, and with water temperatures at 20-30 m in age group 2.2, and at 0-20 m in age group 2.3 in the second year of growth ($P<0.05$ in nearly all the cases, in some $P<0.01$).

Based on the results of A. S. Nikolayev's hydroacoustic surveys (1988a, 1990) which revealed two sublayers of juvenile sockeye in the 0-50 m layer, one can assume that the derived reliable correlations with the water temperatures at certain depths are the result of the nonuniform vertical distribution of juvenile sockeye during the lake period of life.

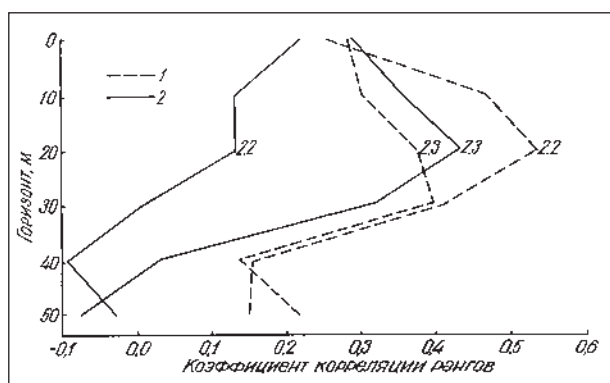


Fig. 86. Coefficients of rank correlation between the average number of sclerites in the central part of the scales of sockeye spawners (age 2.2 and 2.3) and the water temperature by layers in September in Kuril L. (Bugayev et al., 1989). Y-axis – layer, m; X-axis – coefficients of rank correlation.

1 – first year, 2 – second year.

Analysis of the coefficients of multiple correlation between the number of sclerites and the distances between them in relation to the abundance of *Cyclops* in August–October and the water temperature in September (Bugayev et al., 1989), similar to the coefficients of rank correlation (table 64, figs. 86 and 87), indicate that, in a natural environment, the availability of food has a greater effect than temperature on the number of sclerites and the distances between them. Proceeding from this, Vaganov's hypothesis (1978) regarding the stronger influence of feeding conditions on the number of sclerites formed on the scales, and of temperature factors on the distances between the sclerites can be considered accurate within certain limits for juvenile sockeye in a natural environment. Temperature conditions do have some influence on the distances between the sclerites, but the number of the latter is governed primarily by the feeding conditions which may depend on and vary with the number of individuals foraging in the lake.

The literature (Krogus, 1974; Brett, 1971; Goodlad et al., 1974; Brett, 1983) indicates that the thermal structure of the waters in any body of water foraged by the young of the sockeye can intensify or inhibit the growth of the latter during the summer. At the same time, thermal stratification is considered to be detrimental to sockeye growth in some cases (Goodlad et al., 1974), and conducive to their growth in others (Krogus, 1974; Brett, 1971).

We analyzed the correlation between the average number of sclerites in the zones of scale growth and the abundance of *Cyclops* in the lake with the years of foraging distributed into two groups depending on the temperature difference (gradient) between the near-surface waters (20 m) and the deeper layers in the lake (40 and 50 m). If the difference between the temperature in the 20 and 40 m (long-term average 1.80°C) and 20 and 50 m (long-term average 2.44°C) was higher than the long-term average difference, it was considered, on the basis of this characteristic, that the near-surface and deep layers had a higher temperature gradient (a higher degree of water stratification), and if it was lower, then the temperature gradient was considered to be low (low degree of water stratification).

When the abundance of *Cyclops* in September–October is low, the young of the sockeye grow better with low temperature gradients (figs. 88 and 89). However, when the abundance of *Cyclops* exceeds a certain limit (during different years of growth and in different age groups), juvenile sockeye grow better with high temperature gradients, these correlations are reliable in the majority

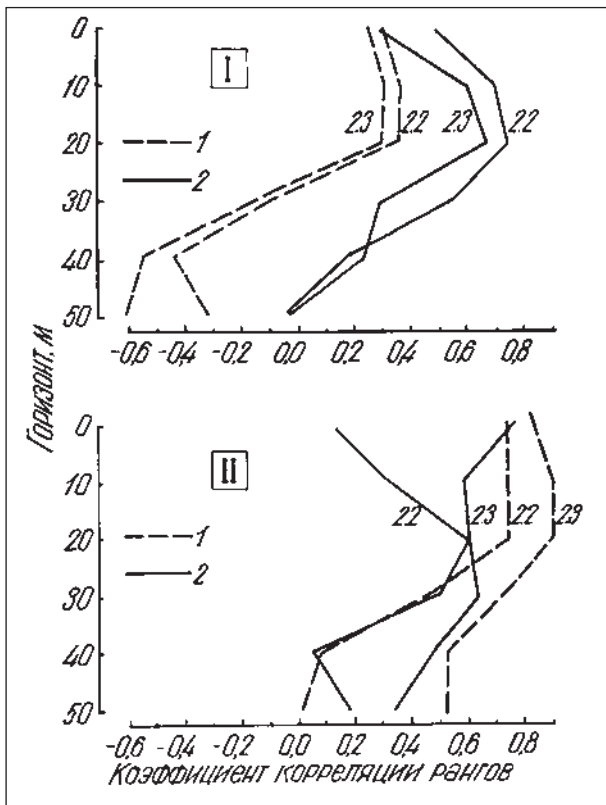


Fig. 87. Coefficients of rank correlation between the average spacing of sclerites in the central part of the scales of sockeye spawners (age 2.2 and 2.3) and the water temperature by layers in September in Kuril L. (Bugaev et al., 1989). Y-axis – layer, m; X-axis – coefficients of rank correlation.

I – first year, II – second year;

1 – low abundance of juveniles, 2 – high abundance of juveniles.

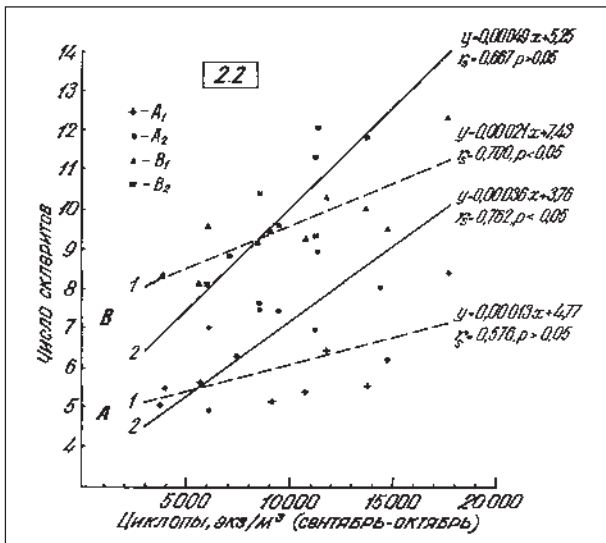


Fig. 88. Number of sclerites in the central part of the scales in sockeye spawners of age 2.2, depending on the average abundance of *Cyclops scutifer* in September–October in Kuril L. (Bugaev et al., 1989). Y-axis – number of sclerites during the first (A) and the second (B) year of growth; X-axis – average abundance of *Cyclops scutifer* in September–October, specimens/m³.

1 – small temperature gradient between depths of 20–40 and 20–50 m in September;

2 – large temperature gradient between depths of 20–40 and 20–50 m in September.

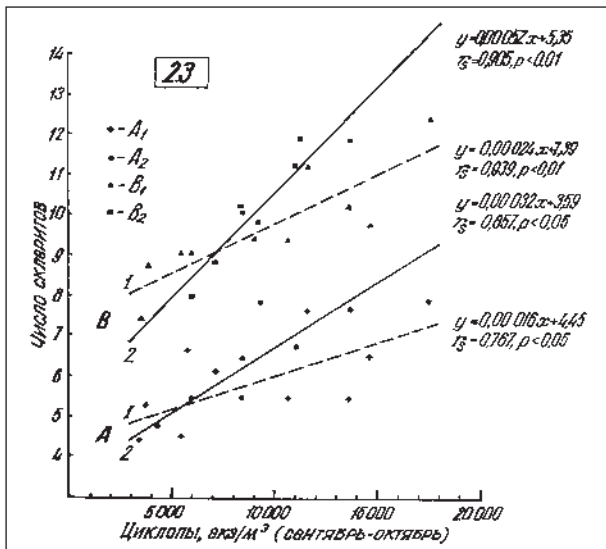


Fig. 89. Number of sclerites in the central part of the scales in sockeye spawners of age 2.3, depending on the average abundance of *Cyclops scutifer* in September–October in Kuril L. (Bugaev et al., 1989). Y-axis – number of sclerites in first (A) and second (B) year of growth;

X-axis – average abundance of *Cyclops scutifer* in September–October, specimens/m³.

1 – small temperature gradient between depths of 20–40 and 20–50 m in September;

2 – large temperature gradient between depths of 20–40 and 20–50 m in September.

of cases. Our conclusion that the thermal structure of the waters in Kuril L. can affect the growth of juvenile sockeye differently, depending on the development of the forage base, explains to some extent the successful outcome of the fertilization of this lake in 1981 and 1982, when the improvement of the forage base after fertilization in the summer and autumn coincided with favourable thermal conditions in the lake during 1981-1984. Similar conclusions were also obtained for August and September.

Let us now examine the scale structure in smolts (table 65). Our analysis of the correlations between the number of sclerites in the zone of scale growth in age 2+ smolts, the largest group of downstream migrants (Dubynin, Bugaev, 1988), and the average abundance of *Cyclops* in May-June, June-July, July-August, etc. has shown (table 66) that the correlations with the abundance of *Cyclops* for September-November in the first year of growth are the strongest; no outstanding correlations are observed in the second year of growth, though the highest values are noted in June-July (no such correlation was noted for the scales of mature fish, Bugaev et al., 1989) and in October-November. As a whole, the results presented in table 66 indicate that the correlation between the number of sclerites on the scales of smolts and the abundance of *Cyclops* is considerably weaker than in adult sockeye (Bugaev et al., 1989). We attribute this primarily to the fact that specimens of sockeye of the different age (2.2 and 2.3) were analyzed separately in the second case, whereas in the case of the smolts we were dealing with a group of fish which would spend 1-4 years (mainly 2-3 years) at sea. Despite the fact that individuals of the same year-classes which have remained at sea for a different number of years often have the same number of sclerites in the zones of scale growth, noticeable differences are observed in some cases (Bugaev et al., 1989; tables 63 and 64). Unfortunately, at this level of research, we have no way of reliably differentiating sockeye smolts according to their potential life span at sea. Another factor which may have caused the comparatively weak correlations between the number of sclerites on the scales of juvenile sockeye and the abundance of *Cyclops* in the lake (table 66) in comparison with the results derived for the scale structure of adult fish (Bugaev et al., 1989) could be the fact that our research was carried out mainly during the years of relatively good foraging conditions. This lowered the variance range of the latter and of the growth of juvenile sockeye in Kuril L. (Bugaev et al., 1989).

Figs. 90 and 91 illustrate some of the correlations presented in table 66 for the periods when the most significant relationships were noted for the first and second years of growth. Analyzing the correlation between the number of sclerites in the first year and the abundance of *Cyclops* in the lake, we first of all note that the points characterizing individual years of observation are distributed in two fairly separate groups (first year, lines 1 and 2). Spearman's coefficients of rank correlation between the number of sclerites and the abundance of *Cyclops* in these year groups (in the first year of life) are quite high in the majority of cases, though in some they are statistically unreliable due to the fact that observations were carried on for only a few years. Based on the presence of these separate groups during the first year (figs. 90 and 91), we examined these two variants separately for the second year as well. As a rule, the coefficients of rank correlation in this case were also quite high, but they too were unreliable because of the limited series of observations.

Table 65. Number of sclerites in the growth zones of smolt scales of migrants from Kuril L. (age 2+, two ZAS) (V. A. Dubynin, personal communication; Bugaev et al., 1995)

Migrating year	First year		Second year		Migrating year		Distance between sclerites		Number of fish
	Range	Average	Range	Average	Range	Average	First year	Second year	
							Average	Average	
1975	4-13	6.70 ± 0.20	5-17	10.50 ± 0.20	0-5	1.51 ± 0.17	2.91 ± 0.08	2.98 ± 0.06	196
1976	4-11	6.90 ± 0.20	5-15	11.50 ± 0.30	0-5	1.87 ± 0.20	1.79 ± 0.07	2.75 ± 0.05	51
1977	4-12	7.90 ± 0.10	6-16	11.10 ± 0.10	0-6	1.90 ± 0.07	2.30 ± 0.03	2.57 ± 0.02	373
1978	2-9	4.60 ± 0.10	7-18	12.30 ± 0.10	0-6	1.71 ± 0.07	1.95 ± 0.05	2.48 ± 0.03	187
1979	3-13	7.40 ± 0.10	5-16	9.60 ± 0.10	0-6	0.57 ± 0.04	2.20 ± 0.02	2.61 ± 0.01	614
1980	3-12	6.20 ± 0.10	4-15	8.40 ± 0.10	0-6	2.83 ± 0.08	2.39 ± 0.04	2.32 ± 0.03	296
1981	3-13	5.60 ± 0.10	5-19	10.40 ± 0.10	0-5	1.94 ± 0.06	2.00 ± 0.03	2.15 ± 0.02	329
1982	2-9	4.69 ± 0.07	6-17	10.75 ± 0.08	0-5	1.88 ± 0.05	1.76 ± 0.03	2.23 ± 0.02	383
1983	3-14	6.44 ± 0.11	4-16	9.61 ± 0.12	0-5	2.05 ± 0.07	2.40 ± 0.05	2.36 ± 0.03	252
1984	2-11	4.78 ± 0.08	6-18	11.76 ± 0.11	0-4	1.79 ± 0.04	1.69 ± 0.03	2.28 ± 0.02	499
1985	2-15	6.47 ± 0.14	4-17	10.04 ± 0.13	0-4	1.27 ± 0.05	2.21 ± 0.06	2.44 ± 0.03	283
1986	3-13	7.20 ± 0.10	5-14	8.62 ± 0.09	0-4	1.85 ± 0.06	2.35 ± 0.03	2.30 ± 0.02	330
1987	2-11	5.29 ± 0.10	5-17	11.45 ± 0.12	0-3	0.81 ± 0.04	1.82 ± 0.04	2.33 ± 0.03	273
1988	3-13	6.83 ± 0.09	4-16	9.28 ± 0.10	0-3	0.98 ± 0.05	2.31 ± 0.04	2.33 ± 0.02	299
1989	3-13	5.84 ± 0.08	5-20	11.57 ± 0.10	0-5	1.74 ± 0.05	1.84 ± 0.03	2.17 ± 0.02	430
1990	3-13	7.22 ± 0.11	6-15	11.66 ± 0.11	0-5	0.65 ± 0.05	2.38 ± 0.04	2.24 ± 0.02	249

Note. Scales collected by Clutter-Whitesel method (1956).

Table 66. The significance of coefficients of rank correlation in the analysis of the number of sclerites in sockeye smolt scales and the mean abundance of *Cyclops scutifer* in the summer-fall period in Kuril L.

Growth year	May-June	June-July	July-August	August-September	September-October	October-November
First	0.152	0.156	0.103	0.349	0.481	0.653*
Second	0.459	0.635*	0.407	0.407	0.473	0.503

Note. Due to severe discrepancies in values for 1979, 1985 in some seasonal growth periods, these years were excluded from calculations, the critical value for P=0.05 (in 14 years of observation) was $r_s=0.540$. "*" – indicates instances where $P<0.05$.

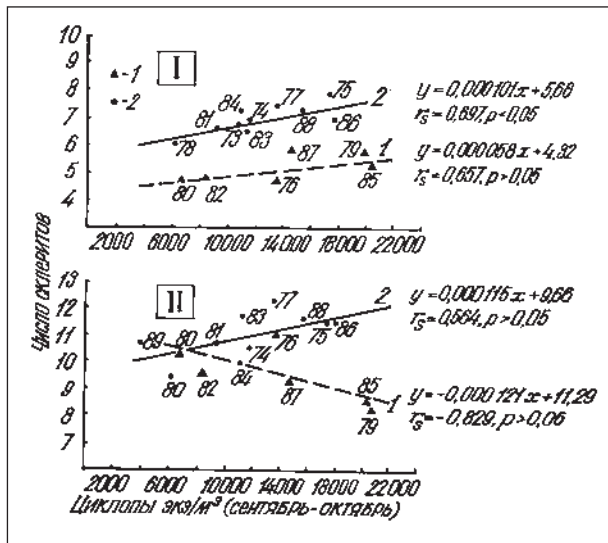


Fig. 90. Variation in the number of sclerites in the zones of scale growth in Kuril L. sockeye smolts of age 2+, depending on the average abundance of *Cyclops scutifer* and *Daphnia longiremis* in September–October during the foraging period.

Y-axis – number of sclerites in the first and the second year of growth;
 X-axis – average abundance of *Cyclops scutifer* in September–October, specimens/m³.

I – first year of growth, II – second year of growth.
 1 – low average abundance of *Daphnia longiremis* in September–October;
 2 – high average abundance of *Daphnia longiremis* in September–October.

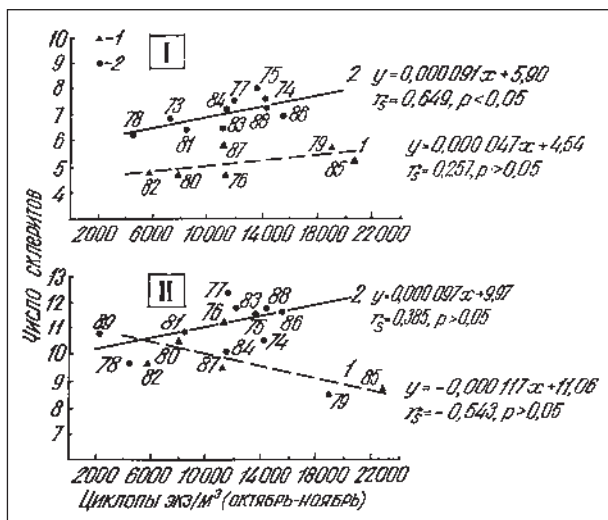


Fig. 91. Variation in the number of sclerites in the zones of scale growth in Kuril L. sockeye smolts of age 2+, depending on the average abundance of *Cyclops scutifer* and *Daphnia longiremis* in October–November during the foraging period.

Y-axis – number of sclerites in the first and the second year of growth;
 X-axis – average abundance of *Cyclops scutifer* in October–November, specimens/m³.

I – first year of growth, II – second year of growth.
 1 – low average abundance of *Daphnia longiremis* in October–November;
 2 – high average abundance of *Daphnia longiremis* in October–November.

All our attempts to explain and correlate the two level of growth noted in the first year of life (lines 1 and 2) with the differences in the lake’s temperature conditions and temperature gradients of the water at different depths, which had been previously used by researchers in scale analysis of Kuril L. sockeye spawners (Bugaev et al., 1989), were unsuccessful. In both cases, both “warm” and “cold” years (years with a high degree of temperature stratification at different depths and years with a low degree of temperature stratification) were found next to each other in the isolated groups of points (Bugaev et al., 1989). Our attempts to explain the existence of the two above-mentioned levels of growth (figs. 90 and 91, lines 1 and 2), the high and low abundance of juvenile sockeye in the lake, during the first year were also unsuccessful.

A comparison of the mean abundance of *Daphnia* in September–October and October–November shows that regression line 1 corresponds to an average 303 (157-443) *Daphnia* per m³ in September–October (fig. 90), and an average 425 (90-1150) specimens/m³ in October–November (fig. 91); regression line 2 corresponds to an average 897 (430-1510) and 992 (435-1348) specimens/m³ respectively. In other words, the existence of different levels of relationships (figs 90 and 91) can be attributed to the fact that the growth of juvenile sockeye in Kuril L., besides being affected by the abundance of *Cyclops*, is also influenced by the abundance of *Daphnia* in the lake.

The high degree of isolation of the groups of points in the first year of life (lines 1 and 2) can be explained by the fact that *Daphnia* are a favourite and sometimes preferred species of food for underyearling sockeye; the indexes of selection vary from 2 to 7 (up to 16), and the individual indexes of fullness in Kuril L. sockeye reach 200 ‰, which amounts to 30-60 % of the stomach contents (Nosova, 1988).

We should note that, despite the differences in the mean characteristics of *Daphnia* abundance in October–November (lines 1 and 2, fig. 91), the range of variance in *Daphnia* abundance during this period transgresses the limit (1150 specimens/m³ was noted in 1987). If we exclude the year 1987, the mean abundance of *Daphnia* (line 1, fig. 91) will amount to 243 (90-330) specimens/m³. In our opinion, this transgression may be due to the fact that the juvenile sockeye of Kuril L. stop growing at the beginning–in the middle of November, the range of variance being from 22 October to 3 December (Bugaev, Dubynin, 1991), and the high abundance of *Daphnia* in November no longer has the same decisive effect on growth as it did in September–October. Based on the data for September–October, 1987 is a typical year of low *Daphnia* abundance. As a whole, it should be said that 1987 is characterized as a year of extremely delayed development of *Daphnia*, the highest

abundance of which was noted in November–December, which is sooner an exception than a rule for the Kuril L. watershed (Nosova, 1988; Milovskaya, 1988).

We also note that the points on the graph for 1976 were located closer to line 1 in the first year (line 1, figs. 90 and 91), and closer to line 2 in the second year. The opposite is observed for the points on the 1984 graph, the noted redistribution of points on the graphs (figs. 90 and 91) may be due to the fact that the juvenile sockeye of older and younger age groups usually consume food organisms of different size (even in the same species), and to the fact that the food of major importance to the growth of young sockeye in Kuril L. is still *Cyclops*, not *Daphnia* which apparently is only a “finishing” food at the end of the growing season.

Figs. 90 and 91 show that total growth in the second year when most freshwater growth to made in Kuril L. is less during the years of high *Cyclops* abundance and low *Daphnia* abundance than in other years. In 1979 and 1985 (both cold years), the lowest annual increments during the second year in two-year-olds (three-year-olds were not analyzed due to their low numbers) were observed when the abundance of *Cyclops* was at its highest and the abundance of *Daphnia* was low. This can be attributed to the fact that the amount of copepodite plankton consumed during this years was significantly smaller than in the other years as a result of the slower development of *Cyclops* up to the 3rd-6th copepodite stages which are the predominant food of young sockeye. The slower development of *Cyclops* during these years is definitely due to the low water temperatures in the lake, and probably also to their high abundance.

The slower development of *Cyclops* in 1979 and 1985 affected the growth of juvenile sockeye in the second year, but not their growth in the first year when they were still very small. Since there is a positive correlation between the size of the juveniles and the food organisms consumed by them (O’Neil, Hyatt, 1987; Kyle et al., 1988; section 8.5.3-8.5.4), the shortage of older-instar *Cyclops*, which the young of the sockeye prefer to younger instars, was responsible for the decrease in their growth rate during the second year when they were already fairly large.

We have already mentioned the unusual growth in 1979 (Bugaev et al., 1989), but this was the only case noted over the 20-year period examined. At that time, it was regarded as an atypical year, and was excluded from the study. However, with the introduction of systematic fertilization and the possibility of over-fertilization in some cases. situations of this type can arise more frequently than in conditions of irregular natural reproduction.

In earlier studies (Bugaev et al., 1989), due to the short series of observations on *Daphnia* abundance in Kuril L. for the different periods of the growing season, we did not analyze the effect of *Daphnia* abundance on the growth of the sockeye. This type of analysis has now become possible, for the series of observations on *Daphnia* abundance has increased since 1973, and the use of scales from juveniles instead of adult fish makes it possible to apply the available data more fully.

Our analysis of the correlations between the number of sclerites in the zones of scale growth in two-year-old sockeye and the mean abundance of *Daphnia* in May–June, June–July, July–August, etc. has shown (table 67) that the strongest correlations exist in the first year of growth for the August–November abundance of *Daphnia* (maximum values were in September–October), and in the second year of growth for the June–November period (maximum values in September–October). Fig. 92 illustrates the cases where the strongest correlations are noted both in the first, and in the second year simultaneously (table 67).

Table 67. The significance of coefficients of rank correlation in the analysis of the number of sclerites in sockeye smolt scales and the mean abundance of *Daphnia longiremis* in the summer-fall period in Kuril L.

Growth year	May-June	June-July	July-August	August-September	September-October	October-November
First	-0.054 (n=15)	0.168 (n=15)	0.257 (n=15)	0.665* (n=14)	0.747** (n=13)	0.704** (n=15)
Second	0.230 (n=16)	0.489 (n=16)	0.556* (n=16)	0.440 (n=14)	0.676* (n=13)	0.518* (n=15)

Note. The number of observation years is indicated in brackets; “+” – indicates instances where $P < 0.05$ (exception – the second growth year in October–November when $P = 0.05$), “**” – where $P < 0.01$.

There was practically no correlation between the abundance of *Cyclops* and *Daphnia* in Kuril L. in the same years and for the same periods. The coefficients of rank correlation for the above-mentioned periods during 1973-1989 varied from -0.191 to 0.248 ($P > 0.05$).

While studying the scale structure in juvenile sockeye foraging in Kuril L. (Bugaev, Dubynin, 1991), we noted supplementary zones of adjacent sclerites (ZAS) on the scales of underyearlings and yearlings at the end of October through November of certain years; these ZAS had formed during this period, and they were sometimes followed by a new increment of sclerites. We believe that the formation of supplementary ZAS in these cases is related to the drastic increase in *Daphnia* abundance, which in this lake occurs mostly in September–October–November (Nosova, 1988; Milovskaya, 1988). Experimental observations indicate (Bilton, Robins, 1971) that an improvement in feeding conditions results in the formation of supplementary ZAS on the scales of sockeye, and that the deterioration of these conditions does not.

V. F. Bugaev (1976) noted the presence of supplementary ZAS in the marginal zone of the freshwater part of the scales in sockeye spawners of Kuril L.; the explanation for this was that the samples included fish from the small Etamynek L. located in the Kuril L. watershed. In Bugaev’s opinion (1976), the supplementary ZAS (fig. 46.2) formed on the scale as a result of the

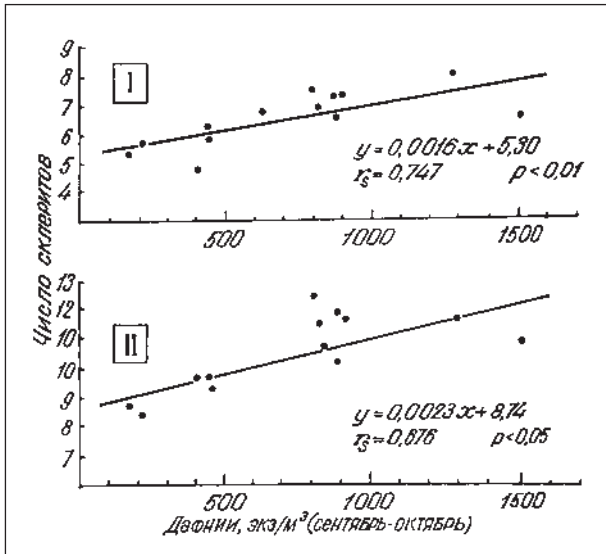


Fig. 92. Variation in the number of sclerites in the zones of scale growth in Kuril L. juvenile sockeye of age 2+, depending on the average abundance of *Daphnia longiremis* in September–October during the foraging period.

Y-axis – number of sclerites in the first and the second year of growth;

X-axis – average abundance of *Daphnia longiremis* in September–October, specimens/m³.

I – first year of growth, II – second year of growth.

seaward migration of sockeye smolts from Etamynk L. via Kuril L., which altered the ecology of the young fish. It now appears that, in some cases, the supplementary ZAS could have formed as a result of an increase in the abundance of *Daphnia* at the end of the growing season. Proof of this may be the fact that, apart from the Etamynk R. where supplementary ZAS were encountered in 36 % of the cases (74 % in Etamynk L.), supplementary ZAS were also encountered in 4-14 % of the fish from other areas of the lake. Considering the insignificant number of fish from Etamynk L. in comparison with the abundance of individuals from Kuril L., as well as the strong homing instinct of the sockeye towards its native spawning grounds (Hartman, Raleigh, 1964; Il'in et al., 1983; Varnavsky, Varnavskaya, 1985), we can now say with certainty that the ZAS noted in some cases on the scales of sockeye spawners (Bugaev, 1976) were due partly to an increase in the abundance of *Daphnia* at the end of the growing season. We should emphasize that, according to our observations, the supplementary ZAS on the scales of juvenile sockeye are usually formed during the years of good growth in the lake, and are practically never encountered during the years of poor (below-average) growth.

As a whole, the *Daphnia* in Kuril L. should be regarded as the “finishing” food for the young at the end of the growing season, and the higher the abundance of *Daphnia*, the greater the possibility and probability of its use (by the young of the sockeye). The end of the growing season of fish in a natural environment is related primarily to the shortening of the photo-period below a certain limit, and not to the feeding and temperature conditions (Mina, Klevezal, 1976).

Fig. 93 illustrates the interannual variability of the freshwater zone of a scale from Kuril L. sockeye spawners of age 2.3. It should be said that immature sockeye usually stay in the lake for a third year (fig. 93.4) during the years of poor growth in the lake (fig. 93.3). The interannual variability of the scales of sockeye smolts migrating from Kuril L. was depicted earlier (fig. 74.2-4).



Fig. 93. Interannual variability in the structure of the central part of the scales in sockeye spawners of Kuril L. (outfall of the Ozernaya R.). Arrows mark ZAS – annuli.

1–12 August 1974, AC=630 mm, male, age 2.3; 2 – 5 August 1979, AC=595 mm, female, age 2.3; 3–26 August 1983, AC=590 mm, male, age 2.3; 4 – 6 August 1984, AC=610 mm, male, age 3.3.

8.8. Interannual variability of *Diphyllbothrium* sp. infestation in sockeye of the Kamchatka R.

Planktivorous fish can serve as supplementary (secondary) intermediate hosts of tapeworms of the genus *Diphyllbothrium*, they become infected when they feed on Copepoda infested with plerocercoids (Dogel, 1947).

Our data on the types of waters foraged by the young of the sockeye in the Kamchatka R. watershed and data on the feeding habits of young sockeye in the watershed of this river (Belousova, 1974; Bugaev, Nikolayeva, 1979; section 8.5.2) indicate that the possibility of sockeye becoming infected with plerocercoids in the Kamchatka R. watershed should be examined preferably in connection with the presence of various species of Copepoda, rather than the definitive hosts (fish-eating birds and mammals) in these waters.

There are only two bodies of water in the Kamchatka R. watershed, namely lakes Dvukhyurtochnoye and Azabach, where the young of the sockeye become infected with plerocercoids of *Diphyllbothrium* sp. in mass numbers (Bugaev, 1982; Bugaev, Nikolayeva, 1989).

Research has shown that the fish of the Kamchatka R. watershed become infected mainly because they spend their fresh-water period foraging in Azabach L. (Bugaev, 1982).

Table 68 is a clear illustration of this, the nearly complete absence of infected fish around the upper reaches of the Kamchatka R.–Kirganik R. (fig. 2) (several hundreds of specimens of adult sockeye were examined) is due to the fact that practically all of the early sockeye of the upper reaches migrate downstream to the sea as underyearlings (group “S”), while the late sockeye forage and overwinter in the vicinity of the spawning grounds and migrate seaward the following year (group “V”).

In the area of the Kimitina and Shchapina rivers, most of the fish belong to the “S” and “V” groups, but some belong to group “E” which migrates to Azabach L. at the underyearling stage. Due to the fact that these young fish become infected in Azabach L. (Bugaev, 1982), infested fish are more common in the samples (table 68).

From Bystraya–Kozyrevka–M. Khapitsa river area, most of the young migrate to the foraging grounds in Azabach L. where we observe the highest degree of infestation of the river stocks in the Kamchatka R. watershed (table 68), not taking into account the fish from Dvukhyurtochnoye L. (stock “D”).

Table 68. Infestation of Kamchatka R. adult sockeye by *Diphyllbothrium* sp. plerocercoids

Region, data	Female					Male				
	Number of fish	Incidence, %	Intensity, number of specimens			Number of fish	Incidence, %	Intensity, number of specimens		
			Range	Average	Number of infested fish			Range	Average	Number of infested fish
Early sockeye										
Upper of Kamshatka R. to Kirganik R., 1975–1978	320	0.0	–	–	–	375	0.8	1-2	1.33	3
Rivers: from Kimitina R. to Shapina R., 1976-1977	138	9.4	1-8	3.15	13	147	10.9	1-8	2.44	16
Rivers: from Bystraya-Kozyrevka to Malaya Khapitsa, 1976-1979	396	44.7	1-6	1.89	177	387	53.7	1-8	2.10	208
Dvukhyurtochnoye L., 1975-1978	78	69.2	1-9	1.96	54	72	83.3	1-8	3.18	60
Azabach L., 1972-1976	144	45.8	1-7	2.06	66	298	75.2	1-14	2.92	224
Raduga R., 1976, 1978-1979	118	7.6	1-4*	2.67	9	110	18.2	1-6	2.35	20
Nozovtsevo L. (Raduga R. watershed), 1976-1977	52	7.7	1-7	2.75	4	41	46.3	1-9**	3.26	19
Late sockeye										
Azabach L., 1972-1974	65	47.7	1-5	1.87	31	98	83.7	1-10	2.84	82
Nozovtsevo L. (Raduga R. watershed), 1977-1979	46	17.4	1-5	1.87	8	116	12.1	1-2	1.29	14

* Not included 1 sockeye infested with 20 plerocercoids. ** Not included 1 sockeye infested with 16 plerocercoids.

In the Raduga R., the mouth of which lies opposite the Azabachye side channel (fig. 2), the percentage of infested fish is significantly lower, due to the fact that not all of the young fish from this river migrate to the foraging grounds in Azabach L. Some forage in the small lakes of the Raduga R. watershed, and others migrate to the foraging grounds in the brackish Nerpichye L. where they do not become infected with *Diphyllbothrium* sp. (Bugaev, 1982).

In Azabach L., individuals of the Azabach L. stock (stock "A") and group "E" forage together prior to their downstream migration. The fish of stock "A" spend two years in the lake, and those of group "E" one year (Bugaev, 1981a; Bugaev, Bazarkin, 1987).

Approximately 90 % of the total number of adult fish of infested stocks spawn in the tributaries of the lower Kamchatka R., in the breeding area of the group "E" and Azabach L. sockeye. Our investigations (Bugaev, 1982) have shown that the extensity of infection in adult sockeye usually increases with the number of ZAS on their scales, while the intensity of infection does not show the same correlation. The males show a higher degree of infestation in comparison with the females.

The results of our investigations (Bugaev, 1982) show that the sea catches of S. M. Konovalov (1971) included not only individuals of the Azabach L. stock, which averages 10-15 % of all the sockeye of this river, but also individuals of group "E", the young of which forage in Azabach L., and have a scale structure that is somewhat similar in addition to being different (Bugaev, 1981a; Bugaev, Bazarkin, 1987; Bugaev, 1989). As we have already mentioned, the total numbers of these two groups constitute a significant part (up to 50-70 %) of the entire sockeye stock of the Kamchatka R. The additional information (Bugaev, 1982) is extremely important to the study of the sea period in the life cycle of the sockeye from this river, and to the calculation of its removal by the sea fishery.

The data on the extensity and intensity of infection in adult sockeye of the Kamchatka R. watershed, together with their scale characteristics, are already being used for identification of spawners from local groups and individual stocks of the sockeye from this area in the catches of the domestic fishery (Bugaev, 1986a; Bugaev, 1987).

Let us now examine the interannual variability of *Diphyllbothrium* sp. plerocercoid infection in the sockeye of the Kamchatka R. watershed.

The material for our study consisted of data on the incidence of infestation with plerocercoids of *Diphyllbothrium* sp. in sockeye smolts that had migrated from Azabach L. in 1979-1980 and 1984-1991, as well as in adult sockeye of the Azabach L. stock for the period 1981-1991. As additional material, we examined data on the feeding behaviour of juvenile sockeye from Azabach L. in 1979-1981 and 1984-1985.

As we can see from table 69, the incidence of infestation in sockeye smolts migrating from Azabach L. varied significantly during the observation period from 1979 to 1991. For instance, the extensity of infection in male smolts of stock "A" reached its highest level in 1979-1980. It then began to decrease, and in 1985-1986 dropped to its lowest level, 13.9-16.7 % (as compared with 86.7-90.3 % at the beginning of the observation period). Finally, since 1987, we have noted a gradual increase in the extensity of infection, which in 1989-1991 was very close to the level noted at the beginning of the observation period. A comparison of the intensity of infection of stock "A" male smolts also reveals differences from 1979 to 1991, though they are not as obvious as in the case of the extensity of infection.

By and large, the incidence of infestation in female smolts of stock "A" over the period of our observations changed in the same way as in the males, except that the lowest extensity of infection was noted in 1986-1988.

Another very interesting fact is that the male and female smolts of stock "A" differ in several other ways from mature fish as regards infestation (table 69) (Bugaev, 1982). For instance, the extensity of infection was nearly always higher in the male adult sockeye of stock "A" (Bugaev, 1982; table 70), whereas it was often higher in the female smolts of the same stock (table 69), while the intensity of infection was lower, as in the adult fish (Bugaev, 1982; table 70).

The incidence of infestation with plerocercoids was slightly lower in group "E" smolts than in stock "A" individuals (table 69). This was noted earlier in the adult sockeye of the Kamchatka R. watershed (Bugaev, 1982). The same characteristics as in stock "A" were noted in group "E" individuals during the period from 1979 to 1991, the extensity of infection in group "E" females, as in the females of stock "A", is often higher than in the males (table 69). The lower incidence of infestation in group "E" sockeye is due to the fact that the latter spend about a year in Azabach L., while stock "A" individuals spend two years in this lake (Bugaev, 1981a, 1982; Bugaev, Bazarkin, 1987).

The incidence of infestation in sexually mature stock "A" fish of age 2.3 from the same generation of smolts described in table 69 is analyzed in table 70. For instance, the smolts of the 1979 downstream migration (table 69) returned in 1982 at age 2.3, and those of the 1988 downstream migration returned in 1991. The smolts that migrated downstream in 1989-1991 (table 69) have not returned as yet (except for the individuals that migrated downstream in 1989 and returned in 1991 at age 2.2).

The relationship between the intensity and extensity of *Diphyllbothrium* sp. infection in sockeye smolts of stock "A" and group "E" (which migrated downstream during the same years) for the period 1979-1991 is shown in table 71 with the help of Spearman's coefficient of rank correlation.

As we can see from table 70, the incidence of infestation in fish of age 2.2 and 2.3 exhibit the same interannual fluctuations do the corresponding year-classes of stock "A" smolts (table 69). In another group of male fish of age 2.2 (downstream migration in 1979, return in 1981), we observed the same characteristics as in male that had spent three years at sea (table 70).

Table 72 shows the correlation between the incidence and intensity of infection in adult male and female sockeye of stock

Table 69. Infestation of sockeye smolts migrating from Azabach L. by *Diphyllbothrium sp. plerocercoids*

Migrating year	Stock "A" (age 2+)								Group "E" (age 1+)							
	Male				Female				Male				Female			
	Number of fish	Incidence, %	Intensity, number of specimens		Number of fish	Incidence, %	Intensity, number of specimens		Number of fish	Incidence, %	Intensity, number of specimens		Number of fish	Incidence, %	Intensity, number of specimens	
			Range	Average			Range	Average			Range	Average			Range	Average
1979	72	90.3	1-22	3.71	70	87.1	1-10	3.31	111	52.3	1-9	3.45	83	56.6	1-7	3.13
1980	30	86.7	1-13	4.00	23	91.3	1-12	3.29	68	76.5	1-14	3.56	58	81.0	1-12	3.74
1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1982	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1984	50	52.0	1-8	2.35	36	72.2	1-5	1.65	39	23.1	1-4	2.33	30	20.0	1-4	2.00
1985	36	13.9	1-4	1.80	49	51.0	1-2	1.32	67	11.9	1-2	1.13	54	9.3	1-2	1.20
1986	6	16.7	1-1	1.00	4	0.0	-	-	28	7.1	1-1	1.00	24	0.0	-	-
1987	25	36.0	1-2	1.33	23	26.1	1-1	1.00	79	12.7	1-2	1.10	61	6.6	1-2	1.25
1988	76	27.6	1-3	1.29	48	25.0	1-3	1.33	59	18.6	1-2	1.09	37	27.0	1-2	1.10
1989	98	69.4	1-0	2.65	68	75.0	1-9	2.47	42	30.9	1-5	2.46	28	35.7	1-4	1.60
1990	42	78.6	1-9	3.12	42	97.6	1-8	3.10	41	14.6	1-6	2.67	34	5.9	1-2	1.50
1991	72	69.4	1-12	2.88	55	65.5	1-8	2.83	114	55.3	1-7	1.87	73	54.8	1-6	2.00

Table 70. Infestation of early sockeye brood stock from Azabach L. by *Diphyllbothrium sp. plerocercoids* in 1981-1991 (by principal age groups)

Spawning year	Male – age 2.2				Male – age 2.3				Female – age 2.3			
	Number of fish	Incidence, %	Intensity, number of specimens		Number of fish	Incidence, %	Intensity, number of specimens		Number of fish	Incidence, %	Intensity, number of specimens	
			Range	Average			Range	Average			Range	Average
1981	27	92.6	1-11	3.63	-	-	-	-	-	-	-	-
1982	29	72.4	1-7	2.24	26	84.6	1-9	3.23	26	57.7	1-10	2.67
1983	7	85.7	1-5	2.33	50	84.0	1-6	2.10	40	57.5	1-6	1.87
1984	12	91.7	1-6	2.36	41	70.7	1-6	2.24	66	51.5	1-4	1.85
1985	7	85.7	2-4	2.67	35	85.7	1-6	2.43	49	63.3	1-7	2.19
1986	12	75.0	1-3	1.67	37	56.8	1-6	2.24	40	65.0	1-7	2.08
1987	12	25.0	1-3	1.67	44	47.7	1-4	1.76	72	19.4	1-3	1.36
1988	15	0.0	-	-	51	17.7	1-5	1.78	62	14.5	1-2	1.33
1989	37	32.4	1-4	1.87	41	14.6	1-2	1.50	115	6.1	1-3	1.43
1990	77	45.5	1-3	1.66	40	27.5	1-7	1.91	37	8.1	1-1	1.00
1991	76	60.5	1-7	2.02	94	48.9	1-5	1.85	62	29.0	1-3	1.33

"A" for the period 1982-1991, which was determined by the coefficient of rank correlation. The characteristics of infestation with plerocercoids in spawners of age 2.2 and 2.3 are presented for the same years of downstream migration.

Table 73 shows the correlation between the incidence and intensity of infection in smolts and adult sockeye of stock "A" (of the same year-classes), which was determined with the help of the coefficient of rank correlation. Analysis of this table shows that the incidence of *Diphyllbothrium sp.* infestation in smolts and returning adult sockeye of stock "A" is very similar.

Considering that the sockeye in Kamchatkan waters become infected with plerocercoids of *Diphyllbothrium sp.* mainly when the young begin to feed on *Cyclops* (Kurenkov, 1977; Bugaev, 1982; Bugaev, Nikolayeva, 1989), we examined the summer feeding strategy of young sockeye in Azabach L. during 1979-1980 and 1984-1985. During these periods, the differences in the incidence of infestation in juvenile sockeye of stock "A" were already apparent (table 69), and the sockeye smolts differed significantly in size as well (Dubynin, Bugaev, 1988; Bugaev, 1989). For instance, the mean length of stock "A" sockeye smolts varied from 95.3 to 102.6 mm in 1979-1980, and from 78.4 to 88.9 mm in 1984-1985. In our opinion (Bugaev, 1983a; Dubynin, Bugaev, 1988; Bugaev, 1989; section 8.7.2), the decrease in the size of stock "A" smolts was due to the deterioration of foraging conditions for juvenile sockeye in the lake.

Table 71. Significance of rank correlation in the analysis of infestation of stock “A” and group “E” sockeye smolts by *Diphyllbothrium* sp. plerocercoids during the migrations years 1979-1980 and 1984-1991

Sex, stock, group	Males of stock “A”	Females of stock “A”	Males of group “E”
Incidence, %			
Males of stock “A”, age 2+	–	–	–
Females of stock “A”, age 2+	$r_s = 0.854, P < 0.01$	–	–
Males of group “E”, age 1+	$r_s = 0.720, P < 0.05$	$r_s = 0.450, P > 0.05$	–
Females of group “E”, age 1+	$r_s = 0.554, P > 0.05$	$r_s = 0.233, P > 0.05$	$r_s = 0.900, P < 0.01$
Intensity, number of specimens			
Males of stock “A”, age 2+	–	–	–
Females of stock “A”, age 2+	$r_s = 0.933, P < 0.01$	–	–
Males of group “E”, age 1+	$r_s = 0.950, P < 0.01$	$r_s = 0.883, P < 0.01$	–
Females of group “E”, age 1+	$r_s = 0.854, P < 0.01$	$r_s = 0.787, P < 0.05$	$r_s = 0.829, P < 0.01$

Note. All situations covered by 9 observation years (not included data for 1986).

Table 72. Significance of rank correlation coefficients in the analysis of infestation males and females adult sockeye of stock “A” in 1982–1991 (by age 2.3)

Sex, age	Males of 2.3 age	
	Incidence, %	Intensity, number of specimens
Females of 2.3 age	$r_s = 0.867 (P < 0.01, n = 10);$ $a = 0.79, b = -5.39$	$r_s = 0.744 (P < 0.05, n = 9);$ $a = 0.93, b = -0.24$
Males of 2.3 age	$r_s = 0.887 (P < 0.01, n = 10);$ $a = 0.76, b = 8.04$	$r_s = 0.916 (P < 0.01, n = 9);$ $a = 0.70, b = 0.61$

Note. “a” and “b” – infestations ratio $Y = ax + b$, where “x” – males aged 2.3 (in comparison with females) and males aged 2.2 (in comparison with males); “n” – number of observations years.

Table 73. Significance of rank correlation in the analysis of infestation *Diphyllbothrium* sp. plerocercoids of stock “A” smolts and adult sockeye (of the same generations)

Sex, age	Incidence, %	Intensity, number of specimens
Smolt males, 2+ age		
Adult males, 2.3 age	$r_s = 0.905 (P < 0.01; n = 8)*$ $a = 0.83, b = 6.47*;$ $r_s = 0.857 (P < 0.05, n = 7)$	$r_s = 0.762 (P < 0.05, n = 8)*;$ $a = 0.33, b = 1.28*;$ $r_s = 0.643 (P > 0.05, n = 7)$
Adult males, 2.2	$r_s = 0.881 (P < 0.01, n = 8);$ $a = 0.88, b = 7.01$	$r_s = 0.847 (P < 0.05, n = 7);$ $a = 0.46, b = 0.99$
Smolt females, 2+ age		
Adult females, 2.3 age	$r_s = 0.833 (P < 0.05, n = 8)*;$ $a = 0.50, b = 2.15*;$ $r_s = 0.750 (P > 0.05, n = 7)$	$r_s = 0.991 (P < 0.01, n = 7)*;$ $a = 0.50, b = 0.57*;$ $r_s = 0.986 (P < 0.05, n = 6)$

Note. “A” and “b” coefficient equation $Y = ax + b$, “x” – incidence and intensity of smolt infestation; “Y” – incidence and intensity of adult infestation. “n” – number of observations years. * Indicated situations where theoretical levels and extent of infestation were projected for male and female specimens aged 2.2 in 1992, based on 1992 figures for 2.2 year old males.

As we know (Krogus, Krokhin, 1956; Foerster, 1968; Belousova, 1974; Bugaev, Nikolayeva, 1989; sections 8.5.2 and 8.5.3), the young of the sockeye during the freshwater period prefer to feed on lake zooplankton, and in the case where the latter is in short supply are forced to turn to another food.

Considering that the sockeye smolts migrating from Azabach L. in 1979-1980 were much smaller than the individuals migrating in 1984-1985 (Dubynin, Bugaev, 1988; Bugaev, 1989), we expect that the forage zooplankton in the lake, mainly *Cyclops* and *Daphnia* (*D. galeata*), was far more abundant during the first of these periods. The juvenile sockeye of stock “A” are characterized by inter-annual variability in growth, depending on the numbers of the sockeye and, therefore, the availability of food (Bugaev, 1983a; section 8.7.2).

We studied the feeding behaviour of the juvenile sockeye in the lake by combining the data on the feeding of yearlings and two-year-olds during the summer. Not in the least denying that the feeding behaviour of different age groups and size categories of juvenile sockeye has its own specific characteristics (Belousova, 1974; sections 8.5.2 and 8.5.3), we nevertheless used combined data. for it was to our purpose to do so, and they also characterized the feeding strategy of the juvenile sockeye in Azabach L. during different years, which eventually helped us to determine the incidence of *Diphyllbothrium*

sp. infestation in sockeye smolts. The grouping of sockeye according to age groups, which in some cases does not yield any data for some periods of the foraging season, does not provide the same graphic picture for the summer–autumn period of different years.

A study of the food spectrum of the young during the summer period at the outlet of the Azabach side channel (depth 2-4 m), at station No. 2 (in the centre of the lake on the traverse of the Ponomarka and Lotnaya rivers, depth about 20 m) and at station No. 3 (an area of the lake near the Ponomarka R., depth 3-5 m) showed that, during this period, the young of the sockeye fed mainly on three food components, *Cyclops scutifer*, chironomid pupae and the imagoes of flying insects (not chironomids) (up to 90-100 % of the food bolus by weight).

In nearly all the cases in 1979-1980, the diet of juvenile sockeye consisted mainly of *Cyclops*, to a smaller extent chironomid pupae, and a small quantity of insect imagoes. On the other hand, their diet in 1984-1985 during different periods of the summer foraging season consisted mainly of chironomid pupae and insect imagoes; a high percentage of *Cyclops* was noted in only a few stomachs of the young (table 74). In other words, judging by the food spectrum, one can assume that the abundance of *Cyclops* in the lake in 1979-1980 was greater than in 1984-1985.

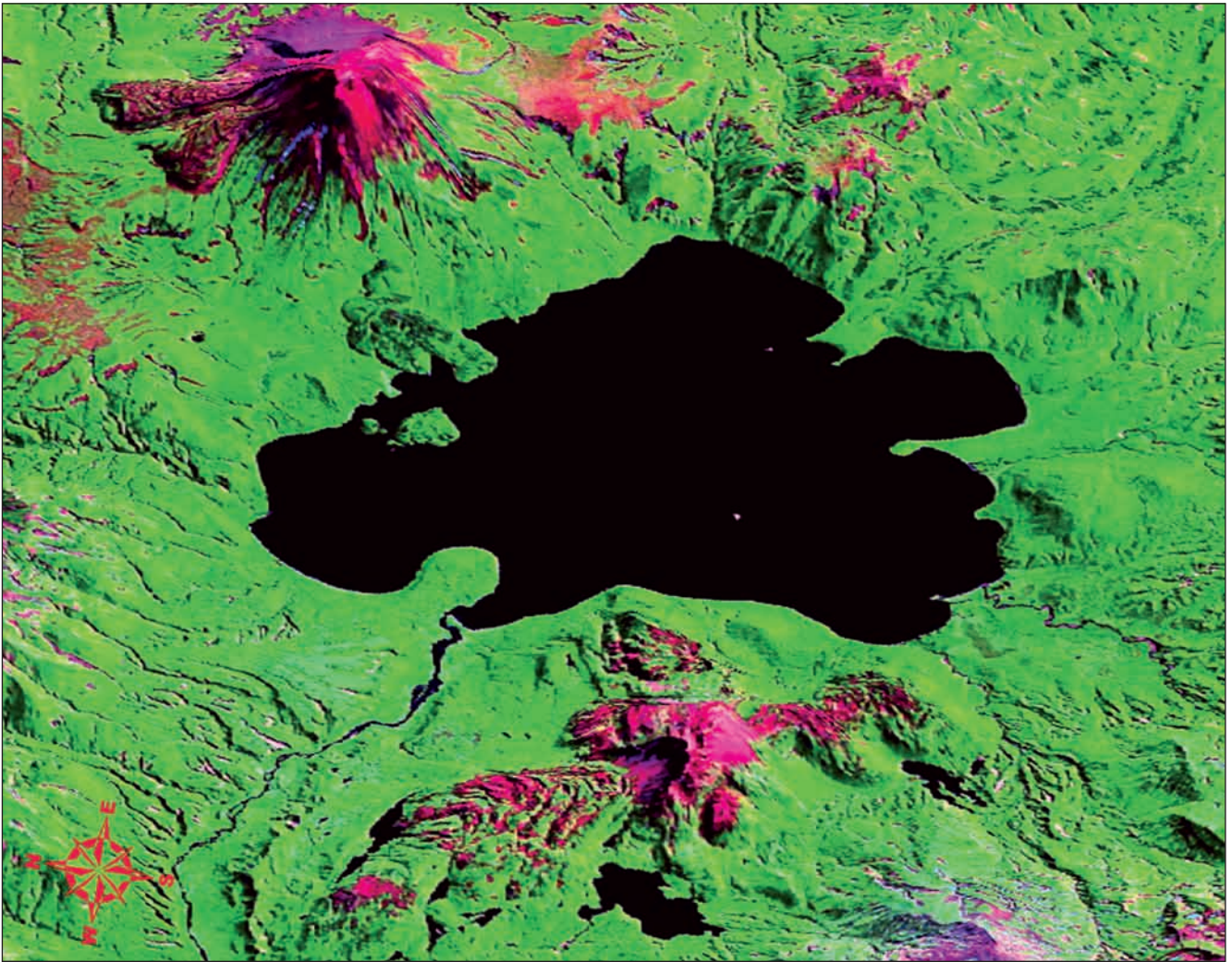
Table 74. Ratio of basic food components in the stomachs of young sockeye foraging in Azabach. L. (as a portion of food weight), %

Data	Outlet of Azabach L.					
	<i>Cyclops scutifer</i>		Chironomidae pupae		Insecta imago	
	1979-1980	1984-1985	1979-1980	1984-1985	1979-1980	1984-1985
17-19.06	70.5	1.1	28.1	94.7	0.1	0.0
27-28.06	70.5	49.1	28.1	54.9	0.1	3.8
03-05.07	80.5	0.0	18.2	98.1	0.7	1.9
11-15.07	39.3	10.8	31.7	30.7	25.5	57.0
20-23.07	3.7	0.0	95.9	0.0	0.4	99.1
02-05.08	81.4	0.0	17.6	14.4	1.0	79.6
12-15.08	80.6	No data	1.6	No data	9.6	No data
Station No. 2						
17-19.06	No data	60.6	No data	39.4	No data	0.0
27-28.06	No data	5.9	No data	56.6	No data	34.7
03-05.07	74.2	17.1	20.4	81.9	5.4	1.0
11-15.07	67.7	17.5	29.9	77.5	2.1	5.1
20-23.07	14.9	13.5	81.5	49.3	0.0	37.2
02-05.08	99.8	55.0	0.2	23.0	0.0	22.0
12-15.08	91.4	35.7	0.0	26.2	8.6	18.8
Station No. 3						
17-19.06	82.6*	68.0	0.0*	32.0	17.4*	0.0
27-28.06	No data	44.0	No data	55.6	No data	0.0
03-05.07	58.4	0.0	37.0	98.4	2.3	1.6
11-15.07	72.7	24.0	23.2	44.7	3.2	15.5
20-23.07	52.6	0.0	30.2	5.1	9.5	79.3
02-05.08	No data	0.0	No data	14.8	No data	14.1
12-15.08	56.0	9.5	25.8	40.1	18.2	34.3

Note. 1979-1980 – migrating period of large bodies sockeye smolts; 1984-1985 – migrating period of small bodies sockeye smolt. * Included supplementary data for 1981.

According to research data (Bugaev et al., 1993; Appendix, table 16), the average abundance of *Cyclops* (at station No. 5) in October 1979-1980 amounted to 95.145 specimens/m³, and it was only 18.951 specimens/m³ in 1984-1985. We cannot compare the abundance of *Cyclops* in the Azabach L. watershed for other periods of the foraging season, as we have only the October figures on the numbers of *Cyclops* in 1979-1980, and no data at all for 1970-1978.

As we can see from table 75, the average indexes of consumption in stock “A” and group “E” sockeye smolts with two



1. The Kuril Lake (Bugaev, Kirichenko, 2008)



2. The Kuril Lake (July 2000, photo by A. V. Maslov)



3. The outlet of Kuril Lake (September 2008, photo by A. V. Maslov)



4. The bears are catching sockeye in source of the Ozernaya River (8 October 2008, photo by A. V. Maslov)



5. The Azabach Lake (Bugaev, Kirichenko, 2008)



6. The Azabach Lake (7 September 2007, photo by A. A. Zenkov)



7. The Azabach Lake (June 2008, photo by V. F. Bugaev)



8. The Azabach Lake (July 2009, photo by A. V. Maslov)



9. *The Palana Lake (Bugaev, Kirichenko, 2008)*



10. *The Palana Lake (22 October 2006, photo by S. V. Schubkin)*



11. The Dvukhyurtochnoye Lake (Bugaev, Kirichenko, 2008)



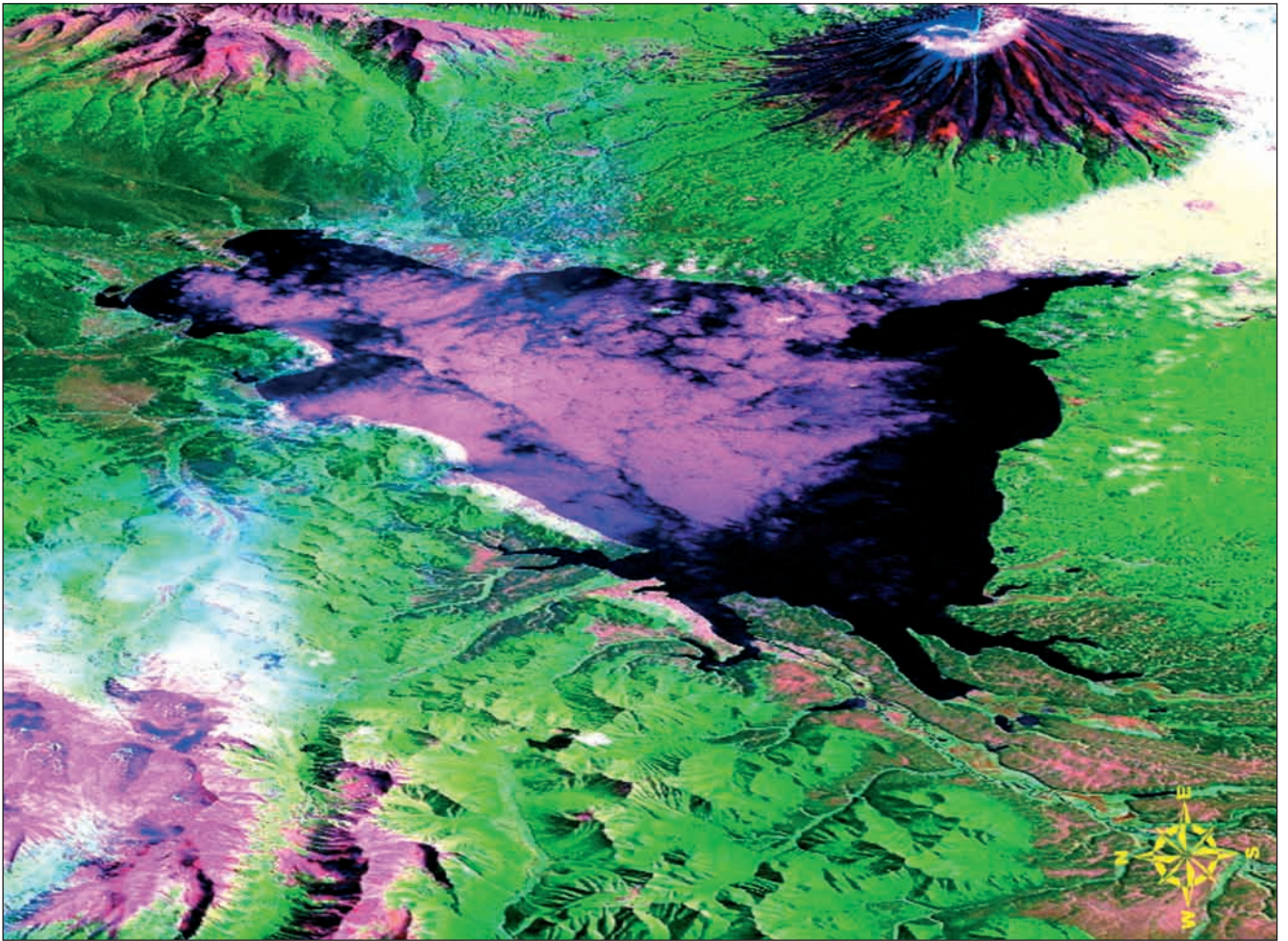
12. The Dvukhyurtochnoye Lake (22 May 2000, photo by A. V. Maslov)



13. The Nachikinskoye Lake (Bugaev, Kirichenko, 2008)



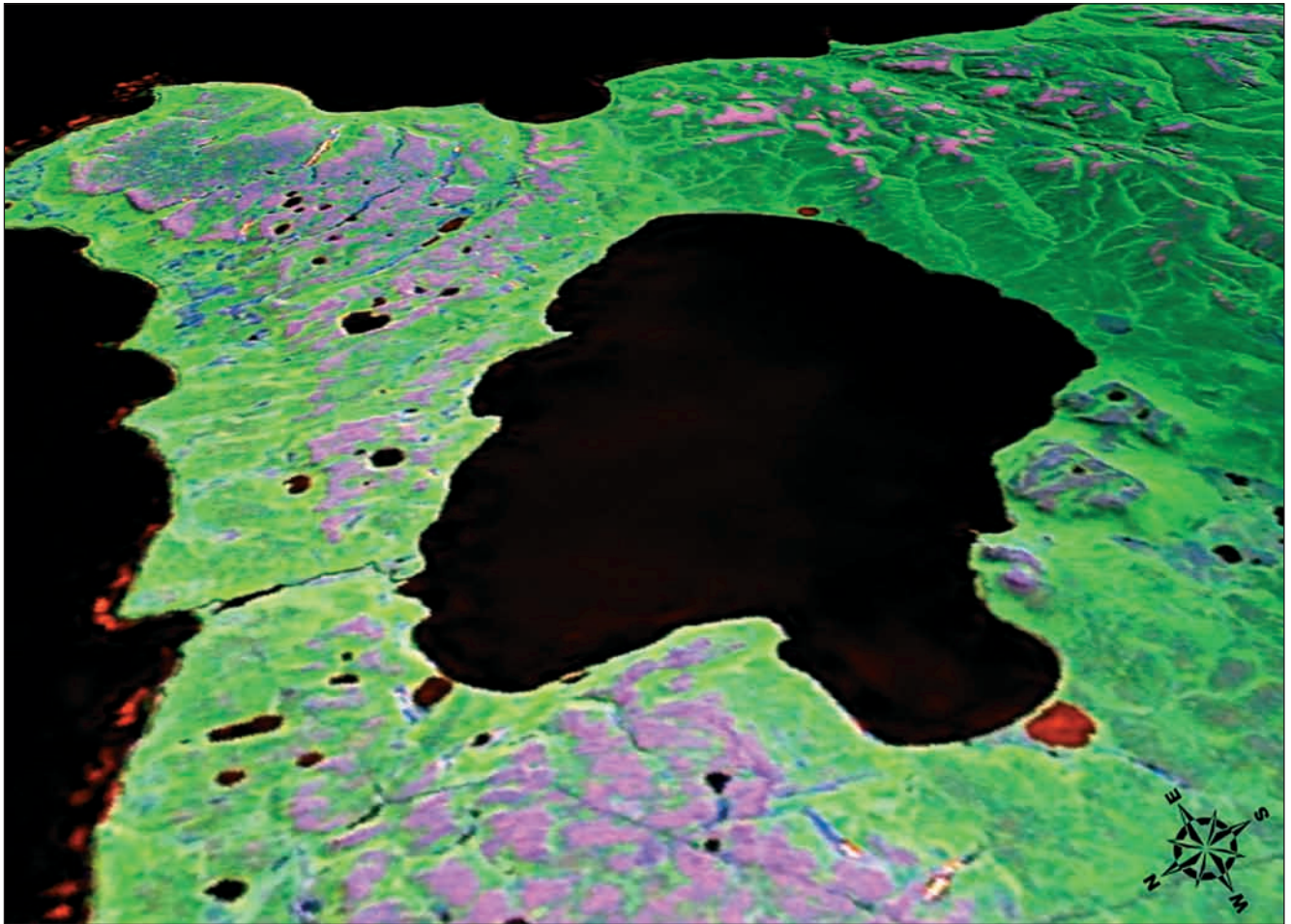
14. The Nachikinskoye Lake (August 2003, photo by P. G. Panfilov)



15. The Kronotskoye Lake (Bugayev, Kirichenko, 2008)



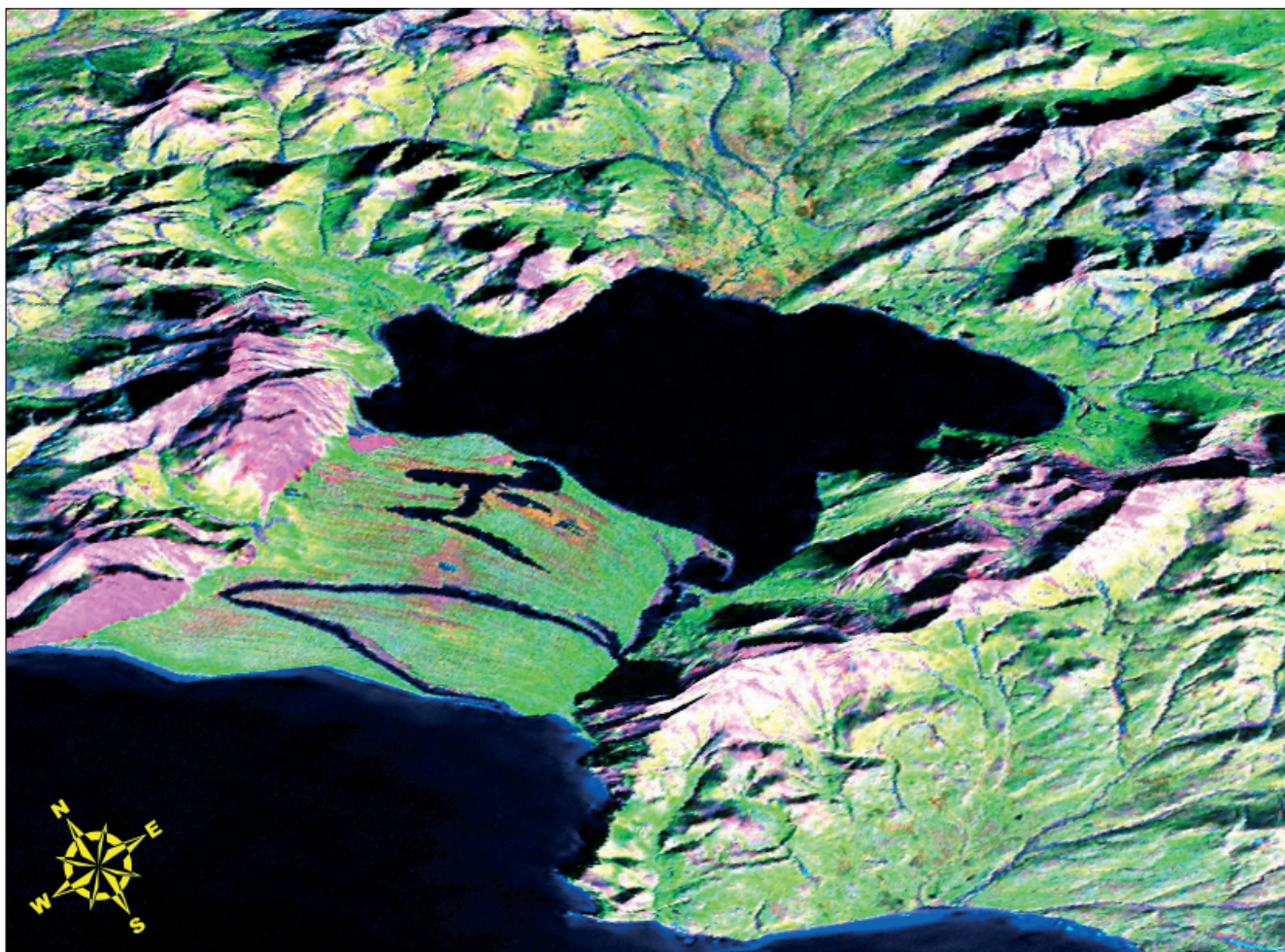
16. The Kronotskoye Lake (10 August 2003, photo by V. F. Bugayev)



17. The Sarannoye Lake (Bugayev, Kirichenko, 2008)



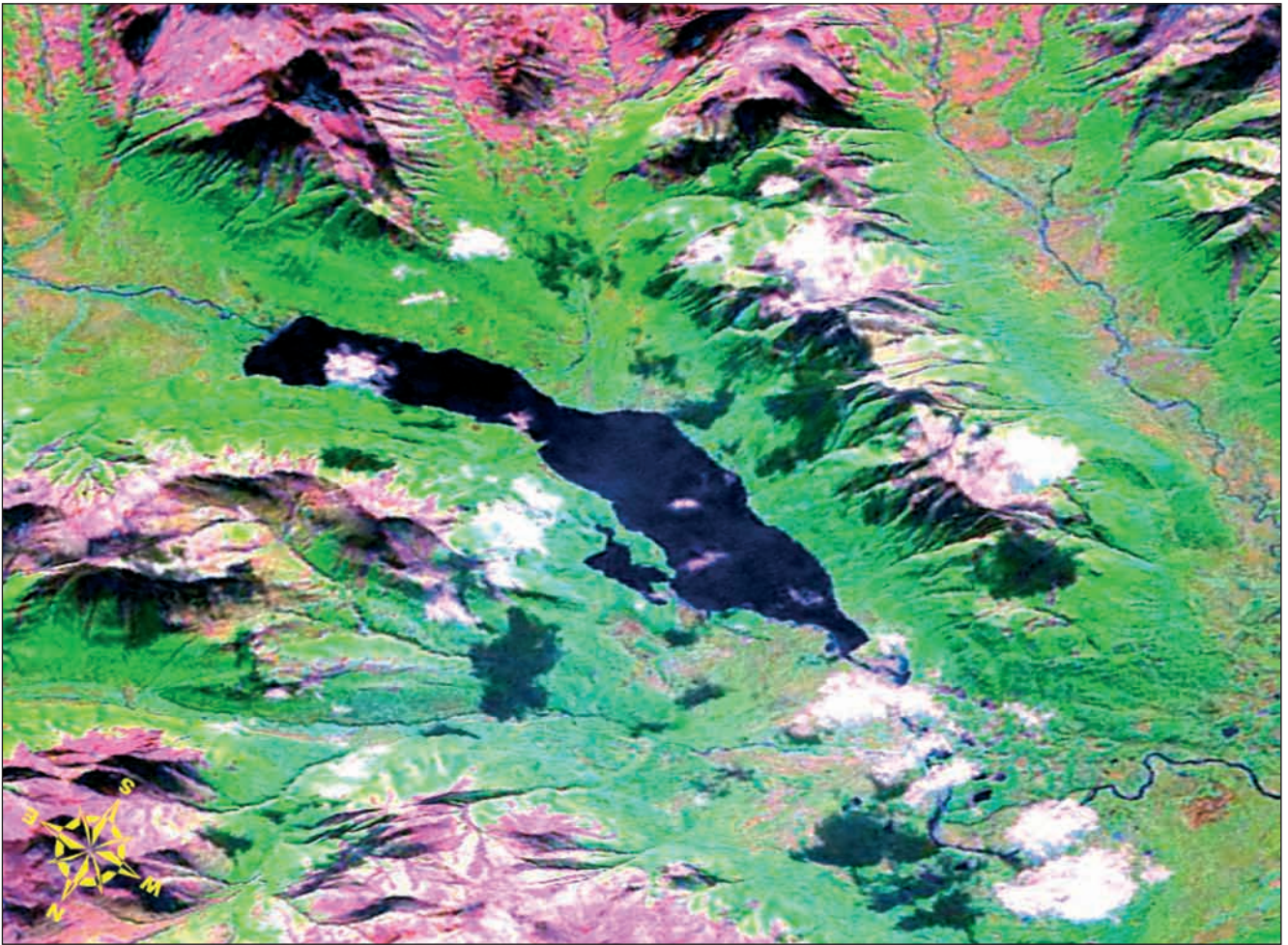
18. The Sarannoye Lake (5 September 2004, photo by V. V. Lisovsky)



19. The Lagoon Anana Lake (Bugaev, Kirichenko, 2008)



20. The Lagoon Anana Lake (5 August 2009, photo by A. V. Maslov)



21. *The Ilir-Gythyn Lake (Bugaev, Kirichenko, 2008)*



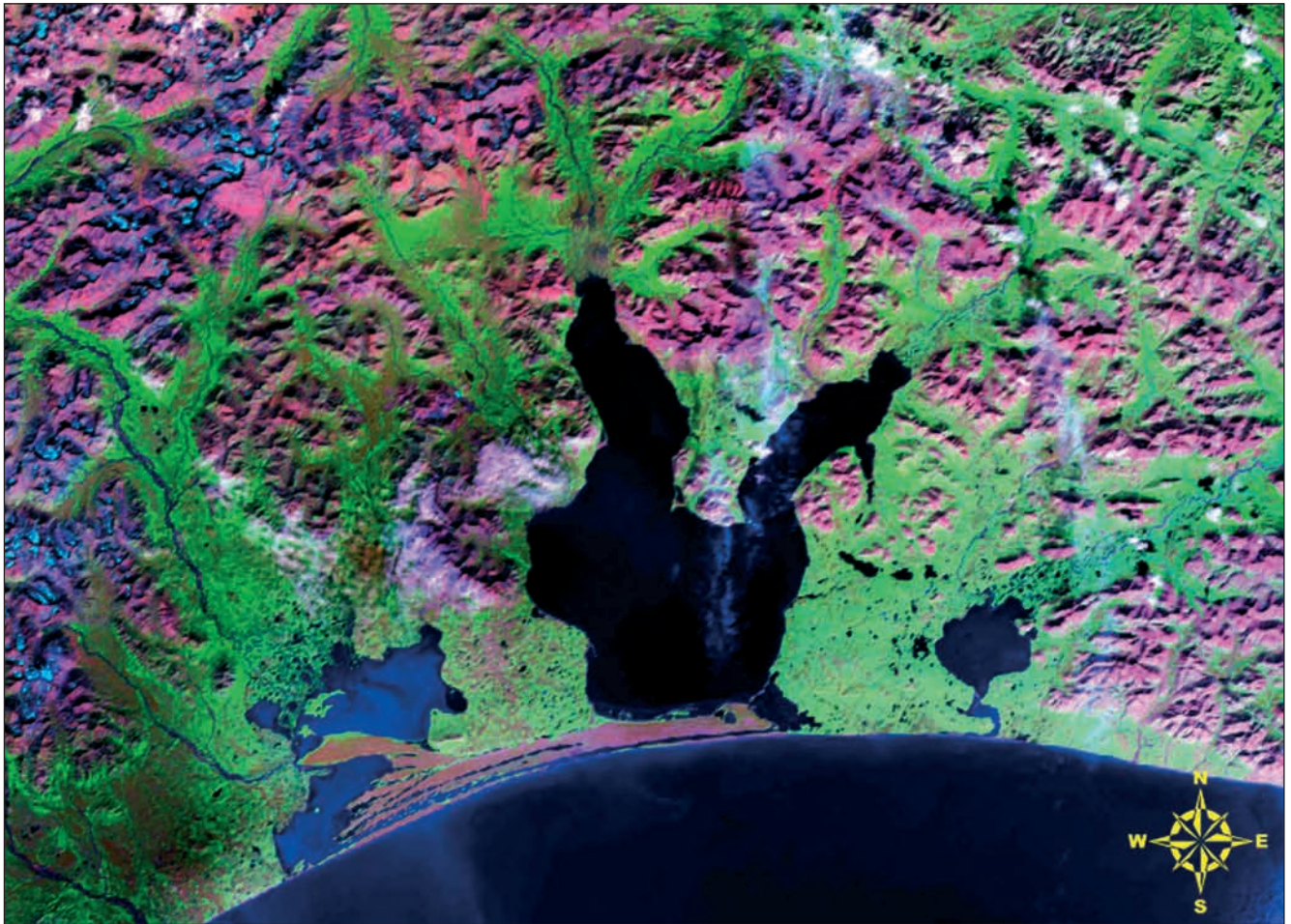
22. *The Ilir-Gythyn Lake (5 August 2009, photo by A. V. Maslov)*



23. *The Potat-Gythyn Lake (Bugaev, Kirichenko, 2008)*



24. *The Potat-Gythyn Lake (5 August 2009, photo by A. V. Maslov)*



25. The Meynypylgyn Lake-River System, in center is Pekulneiskoye Lake (Bugaev, Kirichenko, 2008)



26. The Pekulneiskoye Lake (26 October 2006, photo by E. V. Golub)



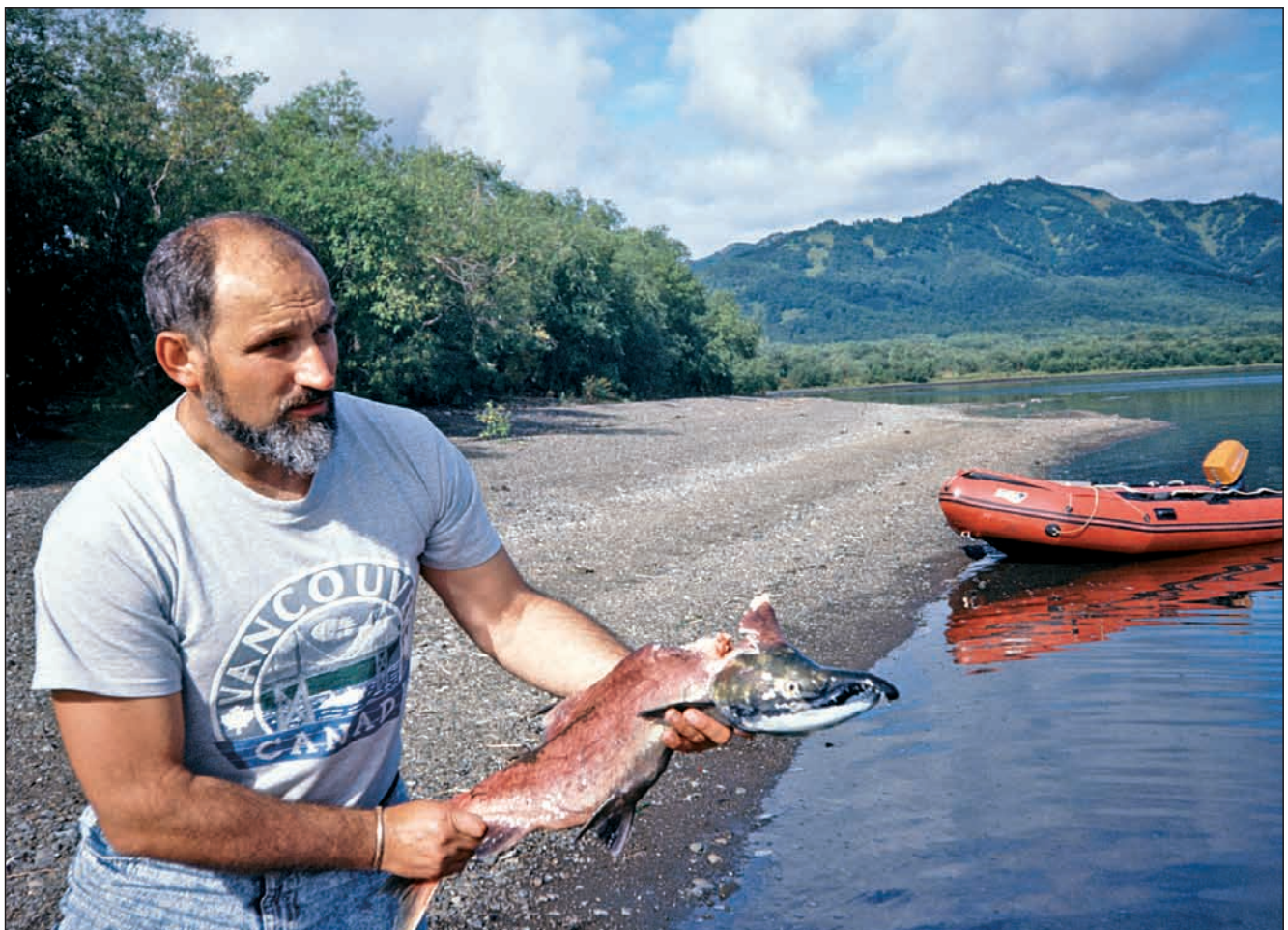
27. *The Mainitz Lake* (Bugaev, Kirichenko, 2008)



28. *The Mainitz Lake* (25 August 2007, photo by Ju. N. Khokhlov)



29. Before defending candidate degree dissertation in the Moscow State University (3 November 1983)



30. The Azabach Lake (5 September 1993)



31. Nanaimo City, April 1995 (left to right – Victor Bugaev, David Welch, Masako Welch and William Ricker)



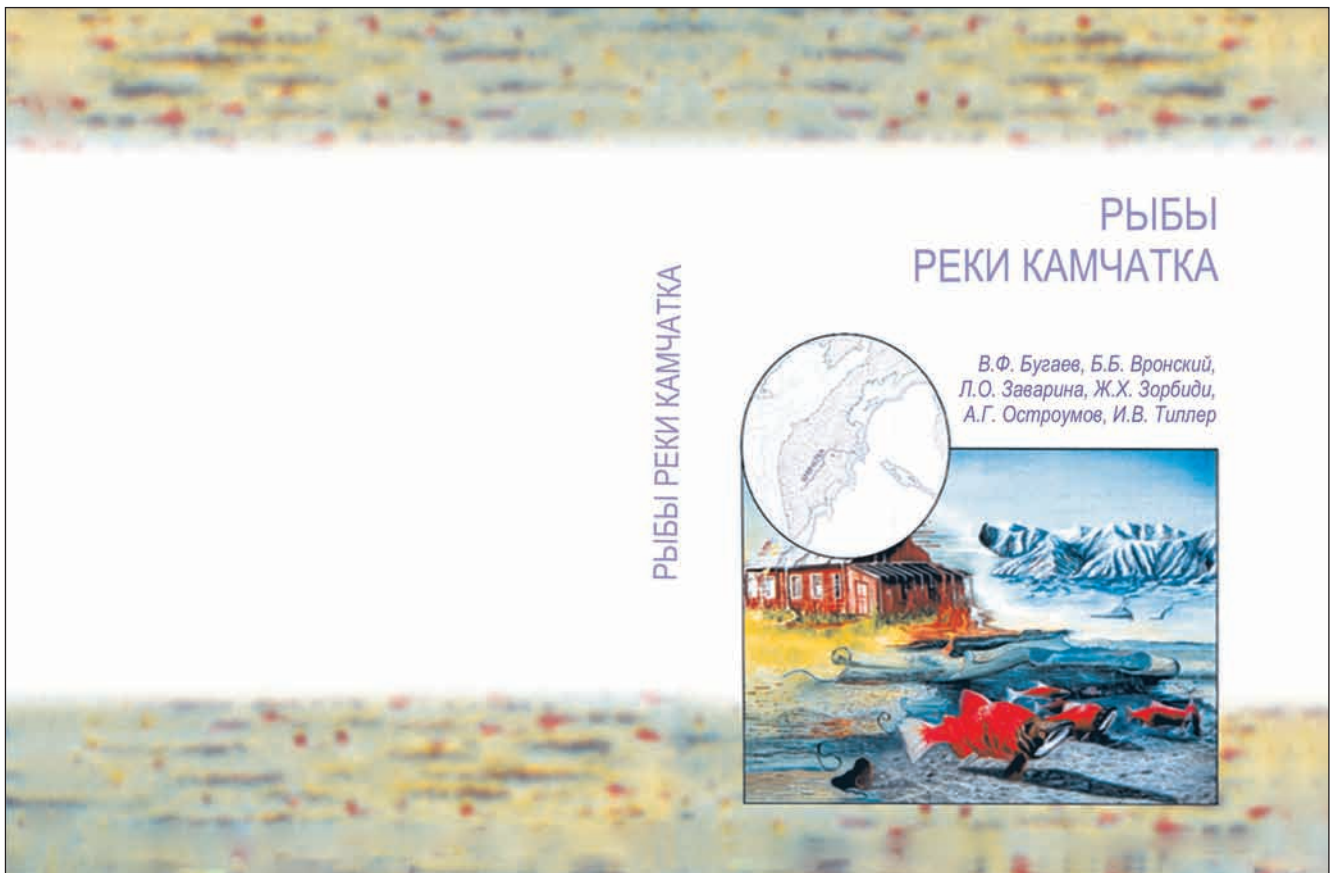
32. Vancouver, March 2002 (left to right – Richard Beamish, Victor Bugaev and Wakako Morris)



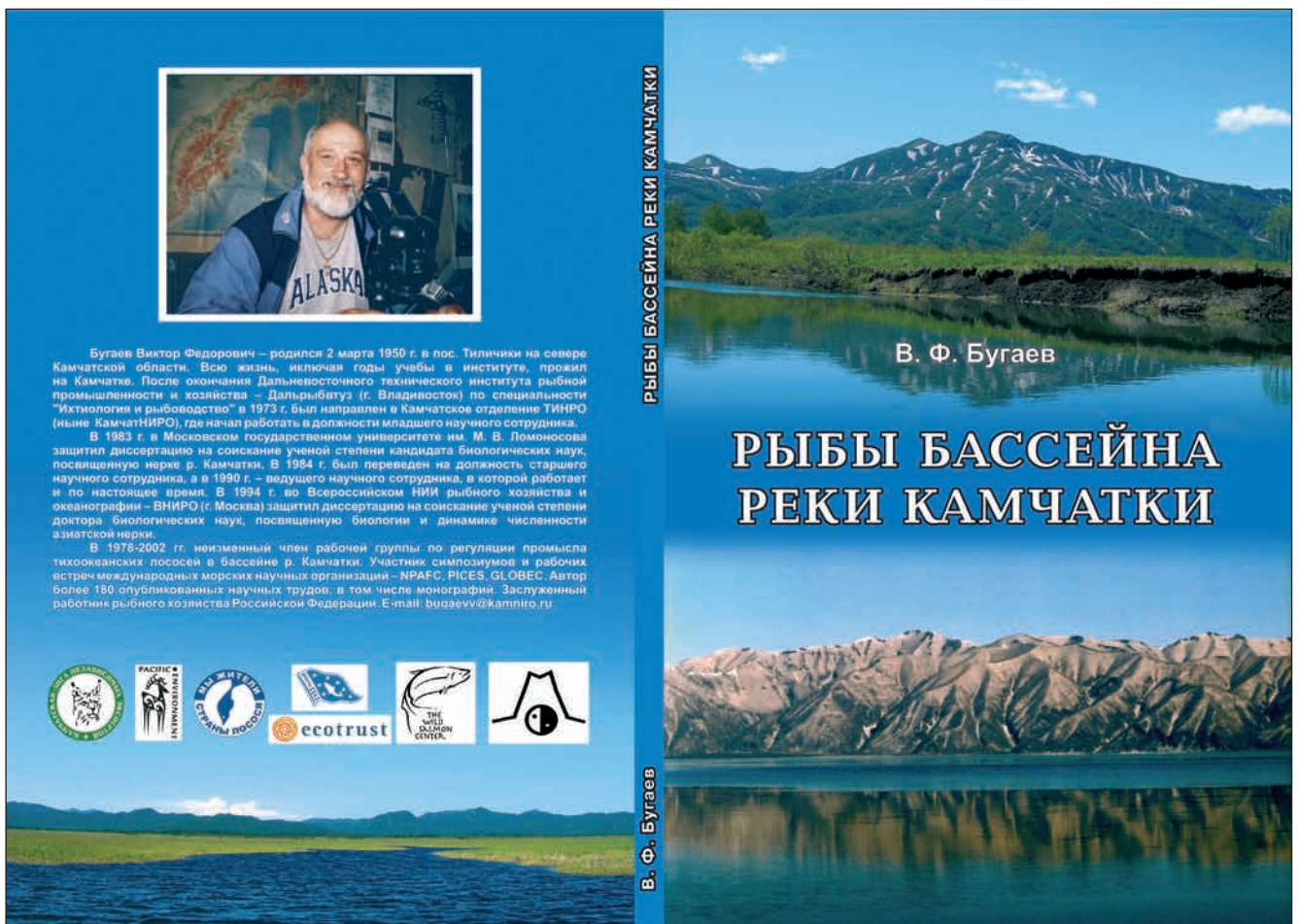
33. Vladivostok, October 2002 (left to right –Katherine Myers, Douglas Eggers, Victor Bugaev and Robert Walker)



34. Seattle, May 2004 (left to right – Victor Bugaev, Donald Rogers and Robert Burgner)



35. The cover of the book by V. F. Bugaev, B. B. Vronskiy, L. O. Zavarina, Zh. Kh. Zorbidi, I. V. Tiller, A. G. Ostroumov “The Fishes of Kamchatka River” (2007)



36. The cover of the book by V. F. Bugaev “The Fish of the Kamchatka River Watershed (Abundance. Utilization. Issues)” (2007)



37. The cover of the book by V. F. Bugaev and V. Ye. Kirichenko “Rearing and Spawning Lakes for Asian Sockeye Salmon Stocks (including several additional water bodies in range)” (2008)



38. The cover of the book by V. F. Bugaev and A. V. Maslov and V. A. Dubynin “Sockeye Salmon of the Ozernaya River (Life History. Abundance. Utilization)” (2009)



39. The cover of the book by V. F. Bugaev "Sockeye Salmon of the Kamchatka River (Life History. Abundance. Utilization)" (2010)



40. The cover of the book by A. V. Maslov and V. F. Bugaev "The Flight Over the Sockeye Salmon Redd" (2010)

Table 75. Average consumption index for young sockeye in Azabach L., ‰

Data	Outlate of Azabach L., smolts sockeye with 1-2 ZAS on the scales		Main body of lake, specimens sockeye with 1-2 ZAS on the scales	
	1979-1980	1984-1985	1979-1980	1984-1985
16-30.06	$\frac{61.1 (n=2)}{31.7-90.5}$	$\frac{77.5 (n=4)}{59.7-113.7}$	$\frac{63.5 (n=4)*}{56.8-77.4}$	$\frac{31.2 (n=6)}{6.8-81.5}$
1-15.07	$\frac{28.8 (n=4)}{22.2-37.9}$	$\frac{90.8 (n=3)}{32.7-123.3}$	$\frac{78.9 (n=10)}{27.9-233.9}$	$\frac{53.0 (n=8)}{7.7-104.1}$
16-31.07	$\frac{56.7 (n=1)}{56.7-56.7}$	$\frac{121.6 (n=3)}{59.5-196.6}$	$\frac{96.9 (n=4)}{70.7-145.8}$	$\frac{134.9 (n=7)}{85.7-195.4}$
1-15.08	$\frac{52.1 (n=2)}{21.5-82.8}$	No data No data	$\frac{64.4 (n=5)}{19.7-120.7}$	$\frac{99.5 (n=5)}{44.8-174.5}$

Note. Upper value – average, lower value – range; “n” – number of stations. ** Included supplementary data for 1981.

zones of adjacent sclerites (ZAS) on the scales (ages 2+ and 1+), taken at the outlet of the Azabachye side channel in 1984-1985, were even higher than in 1979-1980 when the sockeye migrating downstream were larger. In juvenile sockeye with one and two zones of adjacent sclerites on the scales (ages 1+ and 2+), caught in the lake in the second half of June and in the first half of July during 1979-1989, the indexes of consumption were slightly higher than in 1984-1985, but in the second half of July–first half of August they were slightly lower than in 1984-1985 (table 75). Therefore, a comparative analysis has not revealed any key differences in the indexes of consumption of individual sockeye between the summer of 1979-1980 and the summer of 1984-1985, though the smolts and the foraging juveniles of the sockeye differed significantly in size during these years (Dubynin, Bugaev, 1988; Bugaev, 1989; Bugaev, Dubynin, 1991).

The results of our analysis of the effect of *Cyclops* abundance in Azabach L. on the incidence of infestation in sockeye smolts migrating from the lake in 1984-1991 (stock “A”) and in 1980 and 1984-1991 (group “E”) are presented in table 76. As we can see from this table, the coefficients of rank correlation between the abundance of *Cyclops* and the incidence of infestation are higher in stock “A” than in group “E”. This is due primarily to the fact that the young of group “E” spend less time (one year) in the lake in comparison with the young of stock “A” which spend mostly 2 years in the lake. Furthermore, the fish of stock “A” are more planktivorous than those of group “E”, an indication of which is the larger number of gill rakers in the adult fish of stock “A” (fig. 41).

Table 76. Significance of rank correlation coefficients in the analysis of the mean abundance of *Cyclops scutifer* in October (for two years before migration) and the infestation of sockeye smolts from Azabach L. by *Diphyllbothrium* sp. in 1980-1991

Stock, group	Male	Female
Incidence, %		
Stock “A”, age 2+	$r_s = 0.874 (P < 0.05, n = 8);$ $a = 0.00037, b = 17.43$	$r_s = 0.905 (P < 0.01, n = 8);$ $a = 0.00044, b = 18.17$
Group “E”, age 1+	$r_s = 0.617 (P > 0.05, n = 9);$ $a = 0.000067, b = 22.79$	$r_s = 0.467 (P > 0.05, n = 9);$ $a = 0.00011, b = 18.69$
Intensity, number of specimens		
Stock “A”, age 2+	$r_s = 0.905 (P < 0.01, n = 8);$ $a = 0.000011, b = 1.19$	$r_s = 0.964 (P < 0.01, n = 7);$ $a = 0.000012, b = 0.92$
Group “E”, age 1+	$r_s = 0.617 (P > 0.05, n = 9);$ $a = 0.0000063, b = 1.44$	$r_s = 0.595 (P > 0.05, n = 8);$ $a = 0.0000061, b = 1.62$

Note. Stock “A” – smolts, 1984-1991 stock, group “E” – 1980-1991 migration. “a” and “b” coefficient equation $Y = ax + b$, where “x” – abundance of *Cyclops scutifer* in October, units per m³; “Y” – *Diphyllbothrium* sp. infestation; “n” – number of observations years.

Section 9. Methodological aspects of determining the duration of the freshwater period in the life cycle of the sockeye

The scientific literature devoted to age determination in fish from scales, otoliths, vertebrae, etc. (Mina, Klevezal, 1970) is quite extensive (Chugunova, 1959; Bryuzgin, 1969; Mina, 1973, 1976; Vaganov, 1978, etc.). The use of these structures to determine age is based on the assumption that some element of the structure (a layer or ring) is formed in one year of growth,

and is related to the seasonal growth of the fish (Nikolsky, 1974; Mina, Klevezal, 1976). In fish from temperate latitudes, this rhythm is usually characterized by annual cyclicality, which leads to the formation of annual rings (layers) on the scales, bone and otoliths; in fish from tropical latitudes, up to several rings (layers) may form regularly on the scales, etc. in one year. There are data indicating that the seasonal rhythm of growth and the formation of annual layers and rings can also have an endogenic nature (Mina, Klevezal, 1976, 1980).

When age is determined on the basis of the scales, errors can result from the initial termination of the scale at an age older than one year, and from the formation of supplementary annuli as a result of irregular changes in the growth of the fish during the growing season; the latter is especially characteristic of tropical fish (Chugunova, 1959; Nikolsky, 1974; Mina, 1976; Mina, Klevezal, 1976; Vaganov, 1978).

For sockeye in the northern part of the Pacific Ocean, the seasonal rhythm manifests itself in the form of annual rings on the scales annual zones of adjacent sclerites (annual ZAS). They appear as a result of the resumption of growth following its cessation at a specific time of the year (Birman, 1968; Marshall, 1978; Bugaev, 1981; Bugaev, Dubynin, 1991). The ZAS formed during the growing season are considered to be supplementary ones (Bugaev, 1984, 1984a, 1986).

Most recently, we have obtained data on the influence of internal (genetic) factors on the seasonal growth of the sockeye (Bugaev, 1984b, 1991).

Age determination in the Asian sockeye showed that the number of ZAS on the scales did not always reflect the duration of the freshwater (brackish-water) period of the life cycle, since it is possible for supplementary ZAS to form on the scales in some of the fish of certain stocks during this period. In some cases, the supplementary ZAS are formed during the sea period as well, which usually lasts 2-3 (very rarely 1-4) years, and several times we have encountered fish with five sea annuli.

This section of the book sums up our ideas regarding the method of age determination in this species, based on our own long-term research and the literature.

9.1. Recommendations on age determination in the sockeye

Analysis of the periods of annulus formation and the periods of scale formation in juvenile sockeye from the same bodies of water (Koo, 1962; Marshall, 1978; Bugaev, 1981a; Bugaev, Bazarkin, 1987) has shown that the resumption of seasonal growth (the formation of annuli) in all the waters studied occurs prior to the initiation of scales in underyearlings, or, in rare cases, the resumption of growth and the initiation of scales take place simultaneously in underyearlings. This fact is indirectly corroborated by the research on sockeye scale structure, which indicates that the average number of sclerites that form on the scales of sockeye in the second year of growth in waters where the age of the fish was determined absolutely correctly is always greater than the number formed in the first year (Selifonov, 1970; Mosher, 1969, 1972; Bugaev, Kurenkov, 1985; tables 54, 62, 63). The data of the above-mentioned authors indicate that fewer sclerites usually form during the third year of growth of the sockeye as compared with the second year. These data are consistent with the already established growth characteristics of this species, i.e. with an increase in age, the growing season becomes shorter (Nikolsky, 1974).

Therefore, if the number of sclerites in the first zone of scale growth is greater than in the second, we can expect that there will be supplementary ZAS here, and in this situation we must use other methods of analysis to determine whether the annulus is a true, or a false one. One of such methods is the determination of ZAS definition, for annual ZAS are usually more distinct than supplementary ones (Mina, 1976; Bugaev, 1978). Exactly the same approach should be taken in cases where the number of sclerites in the third zone of scale growth is greater than in the second one.

Experience has shown that, during certain years of growth in extremely poor feeding and temperature conditions, we still encounter, though very rarely, individuals without supplementary scale structures, in which the number of sclerites in the first zone of scale growth is greater than in the second zone. This often occurs in very deep lakes; the probability of this type of scale occurring is greater in waters where the period of resumption of seasonal growth, and therefore the period of initiation of annuli, is very lengthy, as, for example, in Kuril L. (Bugaev, Dubynin, 1991).

Generally speaking, if certain zones of scale growth in the sockeye have a significantly greater or smaller number of sclerites than the rest, this indicates that there may be supplementary ZAS among the annuli. If there are few sclerites in the first zone of growth, the above rule does not apply fully to the situations related to the position of the first annual ZAS (annulus) on the scales, since significant fluctuations in body length are characteristic of all underyearling sockeye from any body of water on the same dates. This diversity is due partly to the long periods of spawning of the adults and to the different conditions of egg incubation. For example, the sockeye of the Ozernaya R. spawns from the end of July up to February. As a result, the emergence of alevins from the nests continues over an extended period of time, from March to October (Yegorova, 1970, 1970a). The first convergence of sclerites can be regarded as a supplementary ZAS only in the case where the first of two ZAS is not as clear as the second one, or in the case where three or more ZAS are present, if the acceptance of the first ZAS as a supplementary one does not result in the appearance of annual zones with an abnormally high or low number of sclerites, which would be inconsistent with the rule that "the number of sclerites in each subsequent annual zone is usually smaller than in the preceding one (with the exception of the first zone)". The presence of indistinct ZAS before, between, or after distinct ones can also be an indication of the supplementary nature of the indistinct structures.

The most important growth characteristic of juvenile sockeye in lakes (data not yet available for river stocks) is the inter-annual variability of their growth in relation to the feeding and temperature conditions in the lake (Krogus, 1961; Burgner et al., 1969; Goodlad et al., 1974; Bugaev, 1983a; Bugaev et al., 1989, etc.), which has already been discussed by us in section 8.7. Figs. 85 and 93 illustrate the variability of growth in the freshwater part of the scales in the sockeye of lakes Kuril and Azabach.

The observed variability gives rise to the question of what is the minimum number of sclerites that could be regarded as an annual increment instead of a false annual zone in the second and third zones of growth (there could be any number of sclerites in the first annual zone).

Earlier (Bugaev, 1978), on the basis of scale pattern analysis in spawners, prior to the final decision regarding the method to be used for identifying supplementary annuli on the scales of Kamchatkan sockeye, we considered five sclerites to be the minimum increment for the second year of growth if it was consistent with the above-stated condition rule that each subsequent annual zone (except the first one) must have fewer sclerites than the preceding one and if the ZAS were clearly defined. In this particular book, we also accept five sclerites (for river stocks) and four sclerites (for lake stocks), as being the minimum increment in the second year of growth, and four sclerites as the minimum increment in the third year.

When determining the length of the freshwater period of the life cycle, it is also important to determine the number of sclerites in the marginal zone of the scales during the year of the seaward migration. For instance, some of the juveniles of lake stocks can migrate downstream to the sea even before resuming their seasonal growth (Selifonov, 1970; Bugaev, Bazarkin, 1987; Bugaev, Dubynin, 1991), i.e. without an annulus, whereas the young of river stocks never migrate downstream without an annulus, for the timing of the seaward migration of yearling–three-year-old sockeye of river and lake stocks coincides on the whole, but the young fish in rivers resume their seasonal growth sooner than those in lakes (Bugaev, 1981; sections 8.3.2 and 8.3.4). Therefore, the marginal zone of a scale with one ZAS, and 5-6 sclerites may be an annual increment without an annulus in individuals of lake stocks, but only a new increment (“plus”) after the seasonal cessation of growth in autumn–winter in individuals of river stocks. However, if the increment in the marginal zone of the scales in lake sockeye, even an increment of 6-7 sclerites, is visually distinguished by a greater distance between sclerites than in the preceding zone, this should be regarded not as an increment without an annulus, but as an increment of a new year (“plus”). Our research (Bugaev, 1984b; section 8.3.3) has shown that a greater than usual distance between sclerites during the year of downstream migration is a sign of true compensation growth which is probably controlled by hereditary factors. An increment of 6-7 sclerites in the marginal zone of the scales with signs of compensation growth is quite common in the sockeye of river stocks.

Utilizing the results of our own research over the years, as well as the literature mentioned above, we now present the most frequently encountered ratings of the freshwater period in the life cycle of the Asian sockeye (fig. 94):

- 1 – underyearling, migrated downstream with several freshwater sclerites;
- 2 – underyearling, migrated downstream to the sea without scales (characterized by a greater than usual distance between sclerites – Bugaev, 1984);
- 3 – same as No. 2, with supplementary ZAS of unknown origin (Bugaev, 1984);
- 4 – yearling, migrated from brackish waters (greater than usual distance between sclerites – Bugaev, 1984a); first ZAS supplementary, second one annulus;
- 5 – yearling;
- 6 – yearling with signs of compensation growth during the year of the seaward migration (Bugaev, 1984b);
- 7 – yearling; first ZAS supplementary, second one annulus; supplementary ZAS probably formed as a result of foraging migrations in the river prior to the seasonal cessation of growth (Bugaev, 1981a, 1986);
- 8 – the same as No. 7, but with signs of compensation growth during the year of the seaward migration (Bugaev, 1981a, 1984b, 1986);
- 9 – yearling; first and second ZAS supplementary, third one annulus; supplementary ZAS probably formed as a result of foraging migrations in the river prior to the seasonal cessation of growth (Bugaev, 1981a, 1986);
- 10 – the same as No. 9, but with signs of compensation growth during the year of the seaward migration (Bugaev, 1981a, 1984b, 1986);
- 11 – yearling; first ZAS annulus, second one supplementary; supplementary ZAS formed while migrating downstream during the year of the seaward migration;
- 12 – yearling; definition of first and second ZAS equal; special investigations in river watersheds necessary to determine exactly which ZAS is the supplementary one; by analogy with No. 11, first ZAS annulus, second ZAS supplementary;
- 13 – yearling, overwintering in the spawning areas; second ZAS annulus, sclerites very close together; several randomly distributed ZAS may be observed (Bugaev, 1984b, 1986);
- 14 – the same as No. 13, but with signs of compensation growth during the year of the seaward migration (Bugaev, 1984b, 1986);
- 15 – yearling; first and third ZAS supplementary, second one annulus;
- 16 – two-year-old;
- 17 – two-year-old; first ZAS supplementary, second and third ones annuli;
- 18 – two-year-old, the same as No. 17, but with signs of compensation growth during the year of the seaward migration;
- 19 – yearling;

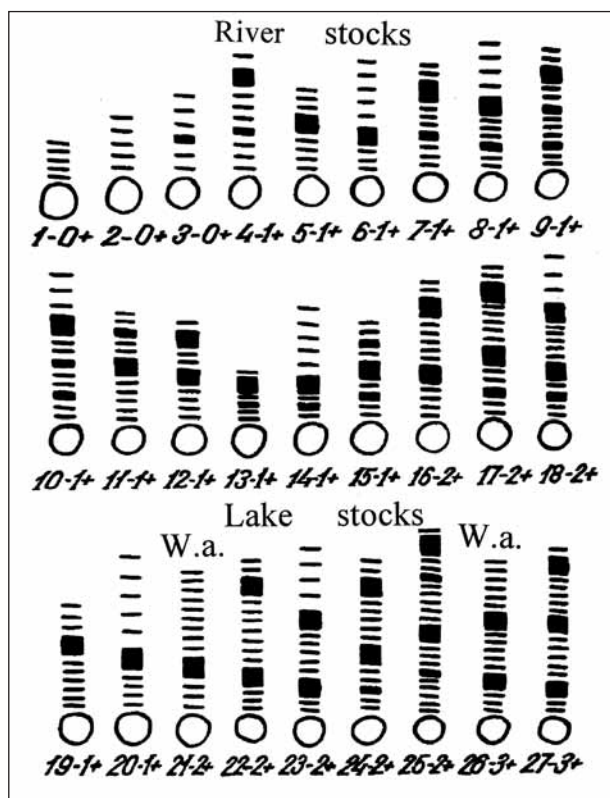


Fig. 94. Types of central parts of scales in spawners of the Asian sockeye (explained in text). Thin lines – separate sclerites, lines of average thickness – indistinct zones of adjacent sclerites, thickest lines – distinct zones of adjacent sclerites; “W.a.” – without annulus.

20 – the same as No. 19, but with signs of compensation growth during the year of the seaward migration;

21 – two-year-old, but without second initiated annulus;

22 – two-year-old;

23 – two-year-old, but with signs of compensation growth during the year of the seaward migration;

24 – two-year-old; first ZAS supplementary, second and third ZAS annuli; 1st variant – supplementary ZAS formed after downstream migration of underyearlings with scales to lake from river located in lake watershed; 2nd variant – spawning ground located in river flowing out of lake; juveniles forage in the river for a while, then migrate upstream to the lake; supplementary ZAS formed after migration of underyearlings to lake;

25 – two-year-old; second and fourth ZAS annuli, first and third ones supplementary; formation of this type of supplementary ZAS observed in some lakes during years of good juvenile growth (may be due to seasonal changes in feeding behaviour of juveniles);

26 – three-year-old, without third annulus;

27 – three-year-old.

The knowledge of the biology of the fish during the freshwater period of their life cycle can contribute significantly to more accurate age determination. Therefore, the most accurate determination of the length of the freshwater (brackish-water) period in samples from sea catches is possible only if we know the body of water or the type of lake in which the fish grew, or at least its origin (Asian or American sockeye).

In the sea period of the life cycle, supplementary ZAS can form on the scales of some sockeye during certain years. Research has shown that during this period, the initiation of the annulus and the resumption of seasonal growth in the sockeye and other salmonids occur later with each year (Birman, 1968, 1972). As a result, the average number of sclerites decreases in each subsequent annual zone (Birman, 1968, 1972; Bilton, 1970). By analogy with the freshwater period of the life cycle, supplementary ZAS of the sea period are not difficult to identify, as they are often less clearly defined than the annual ZAS (annuli).

Let us now examine what causes these supplementary ZAS to form on the scales of the sockeye.

We believe that the seasonal changes in the ecology of the fish are the main cause of this in a natural environment (Nikolsky, 1974). Among the young sockeye that reproduce in rivers and in the watersheds of small lakes (less than 13-18 m deep) with a variable forage base throughout the year (Kurenkov, 1978), the underyearlings typically migrate to lakes with better feeding conditions, where they spend a certain length of time before migrating downstream (Burgner et al., 1969; Marshall, 1978; Bugaev, 1981a, 1986). After their migration to the foraging grounds, some of the underyearlings develop supplementary ZAS on their scales (Bugaev, 1981a, 1986). We also know of a case where supplementary ZAS formed in sockeye smolts (Bugaev, 1976).

Under experimental conditions, changes in the volume and frequency of feeding of juvenile sockeye also resulted in the formation of supplementary ZAS on their scales, but hunger did not (Bilton, Robins, 1971, 1971a, 1971b). Another very interesting and important fact is that changes in the frequency of feeding up to the point of satiation (daily, once in 4 days

and once in 7 days) led to the formation of supplementary ZAS on the scales of juvenile sockeye only when feeding conditions improved, and not when they deteriorated (Bilton. Robins. 1971). These data suggest that the foraging migrations of the sockeye, when the young choose waters with good feeding conditions, result in the formation of supplementary ZAS more often than in smolts, for they rarely remain to forage in these waters during the year of downstream migration. The question concerning the formation of supplementary ZAS on the scales of juvenile sockeye is still extremely vague, for researchers have so far studied mainly abundant sockeye stocks which are not characterized by the formation of supplementary ZAS on the scales of the young. Experience has shown that supplementary ZAS are more commonly encountered in sockeye populations which are not very large and reproduce in rivers and small lakes.

As we have mentioned, supplementary ZAS form in the sockeye during the sea period as well. In individuals that have spent three years at sea, supplementary ZAS form between the first and second, or between the second and third annuli. Furthermore, in fish from the same areas, the supplementary ZAS may be found between the first and second annuli during certain years, and between the second and third annuli during others. The factors causing the appearance of supplementary ZAS at sea are still unknown for the sockeye, and further investigations are necessary to determine them.

In conclusion, a few words to describe the central part of the scale in some stocks of the Asian sockeye, in which we encountered supplementary ZAS.

For instance, many individuals with supplementary ZAS on their scales were encountered by us in the Paratunka River watershed, i.e. in lakes Dalneye and Blizhneye (fig. 95).



Fig. 95. Central part of scales in sockeye spawners of the Paratunka R. watershed.

1 – Dalneye L., 3 August 1943, AC=530 mm, female, age 1.2, arrows mark ZAS (first arrow –supplementary ZAS, second arrow – annulus);
 2 – Dalneye L., 3 August 1943, AC=490 mm, female, age 2.2, arrows mark ZAS (first and third ones the supplementary ZAS, second and fourth ones the annuli);
 3 – Blizhneye L., 28 July 1949, AC=520 mm, male, age 2.2, arrows mark ZAS (first arrow –supplementary ZAS, second and third arrows – annuli);
 4 – Dalneye L., 2 August 1962, AC=550 mm, male, age 2.2, arrows mark ZAS – annuli.

In the generalizations available on the biology of the Dalneye L. sockeye, we could not find any data on the supplementary ZAS of this sockeye (Krogius et al., 1969, 1987), probably because the supplementary ZAS that form on the scales of these fish during the freshwater period (due to their extremely poor definition) do not interfere significantly with age determination (fig. 95.1-2), and during certain years they do not form in large numbers (fig. 95.4). However, F. V. Krogius et al. (1987) have noted the formation of supplementary ZAS on the scales of juvenile sockeye from Blizhneye L. in August (fig. 95.3).

The formation of supplementary ZAS on the scales of Dalneye L. underyearlings sockeye in August–September is corroborated by the scale samples of Ye. G. Pogodayev (verbal communication). We should note that Pogodayev (1991) believes that the juvenile sockeye of Dalneye L. have a high growth rate in winter as well. While developing a mathematical model of the pelagic fish of Dalneye L., F. V. Krogius et al. (1969) proceeded from the fact that the juvenile sockeye of this lake do not grow during the winter–spring period (December–May). Our examination of the first scale samples from juvenile sockeye of Dalneye L. (kindly provided by Ye. G. Pogodayev) enabled us to reach a unanimous conclusion that the juvenile sockeye of this lake do not grow during the winter.

We frequently encounter supplementary ZAS in the central part of the scale in the adult sockeye of Lake Sarannoye (fig. 96), and in practically all the individuals of Sopochnoye L. (fig. 97). As yet, we do not have any observation data on the growth of juvenile sockeye from lakes Sarannoye and Sopochnoye, or the seasonal changes that occur in the structure of their scales, but the poor definition of a series of ZAS definitely indicates that they are supplementary ones.

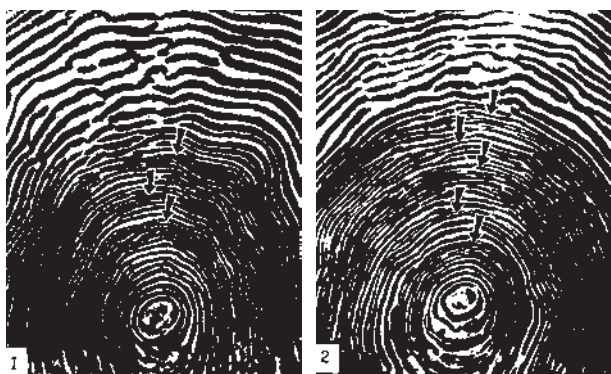


Fig. 96. Structure of the central part of the scales in sockeye spawners of the Sarannoye L. watershed (Bering Is.).

1 – 1 June 1990, AC=550 mm, female, age 2.3, arrows mark ZAS (first and third arrows – annuli, second arrow – supplementary ZAS);
2 – 2 June 1990, AC=500 mm, male, age 3.2, arrows mark ZAS (first, third and fifth ones – annuli, second and fourth ones – supplementary ZAS).



Fig. 97. Structure of the central part of the scales in sockeye spawners of the Sopochnoye L. watershed (Iturup Is.).

28 August 1990, AC = 520 mm, female, age 1.3, arrows mark ZAS (first arrow – supplementary ZAS, second arrow – annulus)

9.2. Influence of hereditary factors on scale structure in the sockeye

The available published data on the compensation growth in juvenile sockeye of the Kamchatka R. watershed (Bugaev, 1984b; section 8.3.3) and the resumption of seasonal growth in the juvenile sockeye of Kuril L. (Bugaev, Dubynin, 1991; Bugaev, 1991; section 8.3.4.) indicate that hereditary factors do influence the growth of individuals in specific freshwater situations. We now have new data on the possible influence of hereditary factors on the growth of juvenile sockeye.

Our analysis of the scale structure in juvenile sockeye and kokanee from three Kamchatkan lakes, which had been reared at the Paratunka Experimental Geothermal Station (PEGS) of the Kamchatka branch of TINRO, revealed the presence of supplementary ZAS on their scales; the appearance of these ZAS can be attributed to the influence of endogenous factors. Let us examine the results of this analysis.

Our material consisted of scales taken from juveniles of the anadromous and freshwater form (kokanee) of the sockeye of lakes Kuril, Dalneye and Kronotskoye (reared under experimental conditions), as well as the data available to us on the scale structure of naturally reproducing sockeye from the same lakes.

The eggs were fertilized on the spawning grounds in the Kuril L. watershed on 25 August 1988, in the Dalneye L. watershed on 25 September 1988, and in the Kronotskoye L. watershed on 1 October 1988. The eggs were shipped in isothermic containers to PEGS where the experiment was being conducted.

The mass emergence of the alevins took place on 25-26 December 1988 in the Kuril L. sockeye, on 24 January 1989 in the Dalneye L. sockeye, and on 4 February 1989 in the Kronotskoye L. sockeye (kokanee).

The eggs were incubated in spring water. The temperature of the water was adjusted to the season, but it was kept higher than in a natural environment (not lower than 4°C in winter). The young were raised under similar conditions in different watersheds (Kuril L. sockeye in watershed No. 2, Dalneye L. sockeye in watershed No. 2, Kronotskoye L. sockeye in watershed No. 4).

The water temperature during the rearing period was quite stable, and the changes noted in the growth rate of the individuals during the rearing period were inconsistent with the changes in temperature (fig. 98).

Food was given to the young sockeye from the time they began to swim, and it was rationed in accordance with the biotechnological standards. Upon attaining a weight of more than 1 g, the fish were given dry granulated feed three times a day (to satiety).

The density of stocking with immature fish was the same in all the watersheds, and corresponded to the optimal level. Once every month, 25-30 individuals were taken from each watershed to check the changes in size and weight.

For analysis we used scales from juvenile sockeye samples taken on 21 November 1989 and 21 December 1989; at this point in time, the fish had been reared for about 10-11 and 11-12 months respectively.

In 1991, we attempted to repeat the experiment of rearing immature sockeye from several populations under the same conditions in order to monitor the growth of the scales from the time of their initiation up to the end of the rearing period, but unfortunately, due to a water supply mishap, we lost all the juveniles with scales.

As we can see from table 77, linear growth was noted in the juvenile sockeye from lakes Kuril and Dalneye from 21 No-

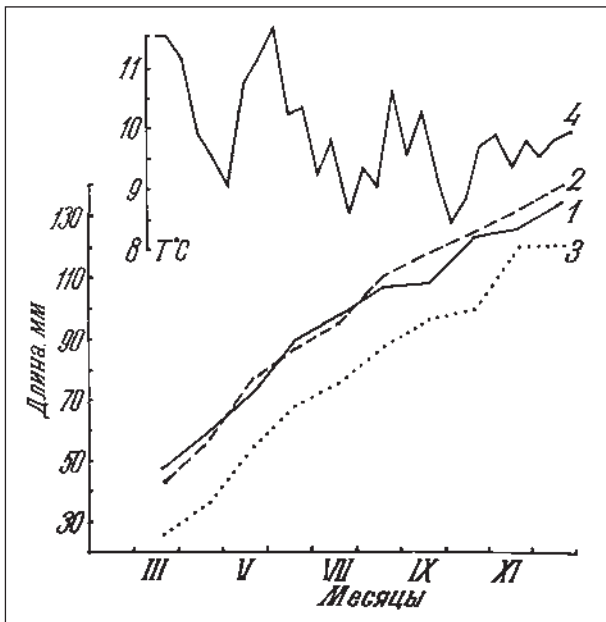


Fig. 98. Growth curves of juvenile sockeye in experimental conditions at the Paratunka Experimental Geothermal Station. Y-axis: lower curve – body length, mm; upper curve – water temperature during growing period, °C; X-axis – months.

1 – body length of sockeye from Kuril L.; 2 – body length of sockeye from Dalneye L.; 3 – body length of kokanee (landlocked sockeye) from Kronotskoye L.; 4 – water temperature.

vember to 21 December 1989, the period when immature sockeye do not grow in a natural environment (Koo, 1962; Krogius et al., 1969; Bugaev, Dubynin, 1991). Practically no linear growth was noted in the juvenile kokanee from Kronotskoye L. If we compare the number of ZAS on the scales of the fish (table 77), we note that individuals with three ZAS predominated in the sockeye of Kuril L., and individuals with two ZAS predominated in the kokanee from Kronotskoye L. both on 21 November 1989, and on 21 December 1989. Individuals with two ZAS predominated in the sockeye of Dalneye L. on 21 November 1989, and individuals with three ZAS predominated (54.2 %) on 21 December 1989, but fish with two ZAS were also abundant (45.8 %). This can be explained by the fact that the ZAS in the sockeye of Kuril L. and the kokanee of Kronotskoye L. were more clearly defined than in the sockeye of Dalneye L. (fig. 99). Individuals without ZAS on their scales were not found in the samples.

The more uniform growth of the Dalneye L. juvenile sockeye in comparison with the Kuril L. sockeye saknib and the Kronotskoye L. kokanee is also corroborated by the graph of linear growth of the young from the three abovementioned populations (fig. 98). As we can see from this diagram, the Kuril L. sockeye, and Kronotskoye L. kokanee clearly manifested periods of slow growth, which probably resulted in the appearance of more clearly defined ZAS on the scales.

In the sockeye of Dalneye L. (in the case where two and three ZAS were observed), the first and the first-second ZAS were, as a rule, very weakly defined, but the most recent ZAS, located closer to the edge of the scale, was quite distinct (fig. 99.4). Due to the poor definition of the first ZAS on the scales of the Dalneye L. sockeye and the fact that they were counted on different sampling dates (table 77), it is possible that they could have been miscounted. The clearer definition of the ZAS in the Kuril L. sockeye and Kronotskoye L. kokanee in comparison with the Dalneye L. sockeye is responsible for the greater similarity of the sockeye samples taken on different dates from the first two lakes (table 74). Among the fish reared in experimental conditions (fig. 99), we found individuals with a scale pattern reminiscent of the typical scale pattern (during the freshwater period) in individuals from the same lake (figs. 93.4, 95.1-2 and 134.1-2).

For instance, the most characteristic of Kuril L. sockeye during the years of a highly abundant population are individuals that migrate downstream after spending three years in fresh water (fig. 93.4), which constitute a significant percentage in all the years (Selifonov, 1982); the percentage of these fish increases as the abundance of juveniles increases and their foraging conditions deteriorate (Dubynin, Bugaev, 1988). Individuals with three ZAS are the most characteristic of juveniles reared in experimental conditions (table 77, fig. 99.1-2).

When analyzing the scales of kokanee (Bugaev, Kurenkov, 1985), we noted that the annuli in Kronotskoye L. kokanee were quite distinct, particularly in the first two years (fig. 134.1-2). Clearly defined supplementary ZAS were also observed in some cases in kokanee reared in experimental conditions (fig. 99.3).

Nevertheless, individuals with poorly defined ZAS are also encountered among the juvenile sockeye of Kuril L. (fig. 100) and the kokanee of Kronotskoye L. (diagram not included).

As for the central part of the scale in the sockeye of Dalneye L., the most characteristic are individuals with three distinct ZAS (annuli) which sometimes have poorly defined supplementary ZAS between them (fig. 95.2). Yearlings with one supplementary (poorly defined) and one clearly defined ZAS (annulus) are less common (fig. 91.1). A specific arrangement of poorly defined (closer to the centre) and clearly defined ZAS (following the clearly defined ones) is characteristic of the scales of Dalneye L. juvenile sockeye reared in experimental conditions (fig. 99.4). This is reminiscent of the pattern in the central part of the scales of adult sockeye from Dalneye L. (fig. 95.1-2).

If we compare the growth of sockeye and kokanee in a natural environment, we have to say that the growth of the Dalneye L. sockeye and the Kronotskoye L. kokanee is on the whole better in the first 2-3 years (the size of the young correlates quite well with the total number of sclerites in all the annual zones of the scale) as compared with the sockeye of Kuril L. (Bu-

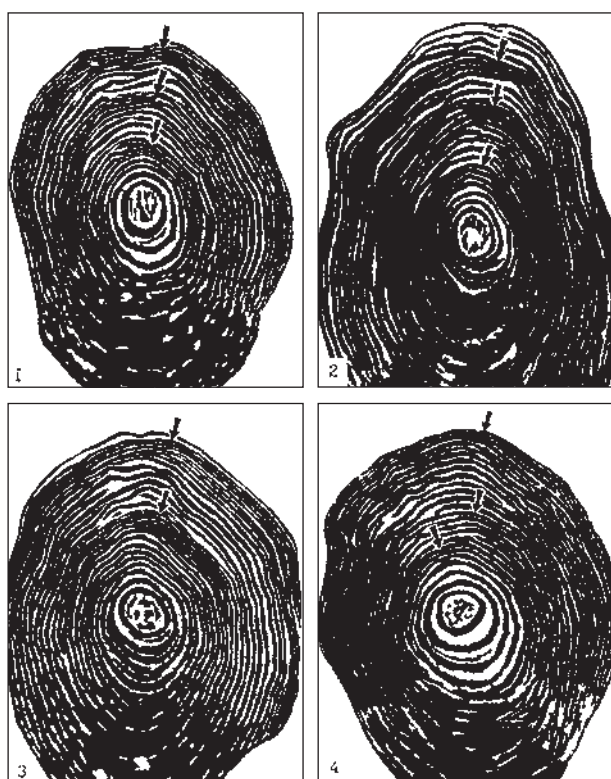


Fig. 99. Scale structure in juvenile sockeye raised at the Paratunka Experimental Geothermal Station.

1 – sockeye of Kuril L., 21 November 1989, AC=118 mm, male (hatched out on 27 December 1988);

2 – sockeye of Kuril L., 21 December 1989, AC=150 mm, male (hatched out on 27 December 1988);

3 – kokanee from Kronotskoye L., 21 December 1989, AC=140 mm, female (hatched out on 4 February 1989);

4 – sockeye from Dalneye L., 21 December 1989, AC=135 mm, female (hatched out on 24 January 1989).

All ZAS marked with arrows are supplementary ones.

Table 77. Body length and scale structure of young sockeye and kokanee raised at the Paratunka Experimental Hatchery

Watershed	Data	Body length, cm		ZAS number, %				Number of fish
		Range	Average	1	2	3	4	
Kuril L.	21.11.89	8.71-18.00	12.53 ± 0.46	8.0	28.0	52.0	12.0	25
Kuril L.	21.12.89	11.00-16.00	13.23 ± 0.31	4.0	40.0	52.0	4.0	25
Dalneye L.	21.11.89	11.51-16.10	13.03 ± 0.26	16.7	58.3	25.0	–	24
Dalneye L.	21.12.89	11.00-17.00	13.87 ± 0.37	–	45.8	54.2	–	24
Kronotskoye L.	21.11.89	8.60-14.22	10.79 ± 0.36	–	68.2	31.8	–	22
Kronotskoye L.	21.12.89	8.50-13.50	10.87 ± 0.32	12.0	68.0	16.0	4.0	25

Note. For Dalneye L. sockeye, when two or three ZAS are present on scales, then the respective first and first-second ZAS, as a rule were very indistinct when compared to fish scales of specimens with the same ZAS number, originating in Kuril L. and Kronotskoye L.

gaev, Kurenkov. 1985; Bugaev, 1989). However, three fairly distinct ZAS are more commonly observed under experimental conditions in the sockeye of Kuril L., which often spend three years in fresh water under natural conditions.

All of the ZAS observed on the scales of fish reared in the watersheds of the Paratunka Experimental Station (table 77) were supplementary structures, as their formation was not related to the seasonal cessation of growth.

In earlier experimental rearing of sockeye (Bilton, Robins, 1971), it was shown (eggs taken from one population) that supplementary ZAS form on the scales when feeding conditions improve, and do not form when feeding conditions deteriorate. Bilton and Robins (1971) do not mention supplementary ZAS forming without apparent causes. Due to the fact that different sockeye populations react differently to rearing under similar conditions (table 77), the data of these researchers are not inconsistent with our own results.

In our case, a pattern differing in the number and definition of ZAS emerged on the scales of juvenile sockeye in 10-12 months of growth under similar temperature and feeding conditions (table 77, figs. 99 and 100); in some cases, it resembled the pattern of the freshwater part of the scales of fish from the same lakes where the eggs were taken. In a natural environment, scales with 2-3 ZAS are formed over a period of 2-3 years in these lakes. An analysis of the number of sclerites in the existing zones of scale growth in fish from the experiment and from a natural environment has shown that supplementary ZAS are formed on the scales of the experimental fish in much the same way as they are in the same, but usually slightly larger, positions of the radius (number of sclerites) of the scales where annuli form in sockeye under the natural conditions specific for each lake.

In the experimental groups of sockeye and kokanee from the lakes where good growth is observed in natural conditions (from lakes Dalneye and Kronotskoye), two ZAS are formed in approximately the same period of time; in populations from lakes with a slower growth rate (e.g. Kuril L.), three ZAS are formed over a similar (slightly longer) period of time. Table 77

shows that the size of the young fish does not have much bearing on the number of ZAS on their scales, which depends primarily on the population being studied.

In the light of the data presented here, one can assume that the formation of supplementary ZAS in the sockeye in a natural environment can in some cases occur also under the influence of internal (hereditary) factors, i.e. when the young, because of certain conditions (e.g. favourable feeding and temperature conditions), reach a size that is on average characteristic of the immature sockeye of a particular lake (or of the species as a whole) sooner than usual, by the end of the first or second year of growth.



Fig. 100. Scale structure in juvenile sockeye from Kuril L. with indistinct ZAS, raised at the Paratunka Experimental Geothermal Station. 10 January 1990, AC=212 mm, female (hatched out on 27 December 1988). All ZAS marked with arrows are supplementary ones.

Yu. S. Basov (1989) has shown that the number of sclerites in the first zone of scale growth in accelerated juvenile coho salmon reared in experimental conditions is usually greater than in juveniles from natural populations, i.e. the positions of ZAS formation on the scales of individuals from natural populations are not the same as in accelerated groups.

In our earlier analysis of Basov's data (1989), we attributed the formation of supplementary ZAS on the scales of the coho salmon largely to nonstandard rearing conditions. Our study of the scales of three populations of juvenile sockeye, which reiterates Yu. S. Basov's results (1989) to some extent, indicates that the situation here may be far more complex.

The ZAS that form as a result of internal (hereditary) factors are probably not as clearly defined as the annuli that form under the influence of both internal and external factors which usually produce a simultaneous effect.

In summarizing, it can be said that the essence of the facts stated above apparently lies in the fact that some of the changes in the growth rate and the natural environment, which are synchronized with the calendar dates (seasons), occur when the young fish in the experiment have attained similar or slightly larger sizes characteristic of the given population. In connection with this, the scale pattern in accelerated juvenile sockeye reared in experimental conditions does not reflect the true age of the individuals.

As a whole, in the Asian sockeye of the majority of lakes (judging by the scales of mature fish), 5-7 sclerites form on the scales with two ZAS (the most typical of the sockeye) in the first year of growth, and 5-8 sclerites in the second year of growth (Bugaev, 1989).

Our investigations (Bugaev, 1984, 1984a) have shown that supplementary poorly defined ZAS form on the scales of juvenile sockeye in some cases. For instance, in group "S" Kamchatka R. sockeye which migrate downstream as underyearlings without scales, a poorly defined supplementary ZAS forms on the 6th sclerite on the average, and one also forms on the sixth sclerite (Bugaev, 1989) in the sockeye of stock and group "N" which forage in brackish Nerpichye L. to which juvenile sockeye migrate as underyearlings (without scales or with 1-2 sclerites – Bugaev, 1984a).

In the underyearlings of group "E" sockeye that migrate to Azabach L. from the tributaries of the lower Kamchatka R., supplementary ZAS (not as clearly defined as annuli) form on the 6th sclerite on the average, judging by the scale structure of mature fish (Bugaev, 1989). We attribute their formation to the changes in the ecology of the young sockeye after their migration to Azabach L. (Bugaev, 1981a).

The definition of the first ZAS on the scales of group "E" individuals is slightly higher than that of groups "S" and "N" (Bugaev, 1978, 1984, 1984a). This can now be explained, in our opinion, by the fact that the underyearling sockeye of group "E", by the time they attain the size at which a supplementary ZAS forms, undergo ecological changes by migrating to feed and grow in Azabach L., which increases the definition of the supplementary ZAS.

I have mentioned earlier (Bugaev, 1978) that two types of ZAS, indistinct and more clearly defined, exist among the river-type supplementary ZAS (containing 0-2 sclerites) which are not as clearly defined as the lake-type ZAS (3-8 sclerites) (see "Material and Method" section). A typical example of an indistinct ZAS (modal value in distributions 0 sclerites) is the ZAS in the central part of the scale of group "S" individuals (fig. 35.1) and the first ZAS in stock and group "N" individuals (Fig. 42.3). In the fish of group "E", the first supplementary ZAS usually belongs to the second type (modal value 2 sclerites) (fig. 42.1).

Proceeding from the results of this study, one can assume that perhaps the formation of an indistinct ZAS is a manifestation of internal (genetic) growth regulation, and the formation of a more distinct ZAS of the river type is the result of ecological changes or the simultaneous effect of internal and external factors.

In one of our previous papers (Bugaev, 1983), we noted the absence of an annulus on the scales of yearling sockeye caught in the Soldatskaya R. in the Nerpichye L. watershed (fig. 101). At first we attributed the absence of an annulus in larger juveniles considered to be yearlings (fig. 101.2) to the abrupt cessation of their growth on the strength of the morphological characters of the Soldatskaya river bed where the temperature conditions in autumn can deteriorate rapidly, causing a more abrupt cessation of growth than in fish from other bodies of water. On the strength of the lengthy formation of one sclerite on the scales of juvenile sockeye in this body of water (17.5-18.7 days), the abrupt cessation of seasonal growth may not have affected their scale structure.

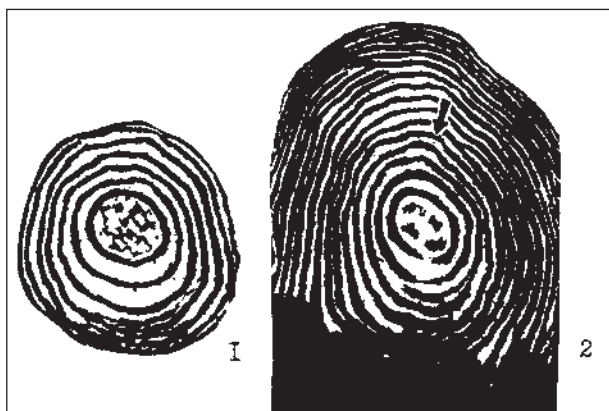


Fig. 101. Scale structure in juvenile sockeye from the Soldatskaya R. (Nerpichye L. watershed).

1 – 17 October 1977, AC=67 mm, age 0+;

2 – 17 October 1977, AC=107 mm, age 0+?. 1+?, arrow marks ZAS (supplementary?, annulus?).

Taking into account the above-mentioned hypothesis regarding the influence of hereditary factors on scale structure, we can introduce another version, i.e. the juvenile sockeye (fig. 101.2) considered to be yearlings at first (Bugaev, 1983) were actually underyearlings with a supplementary zone of scale growth, which had formed because these juvenile sockeye (about 3-5 %) outgrew the rest due to certain factors.

Future investigations will show which of these two theories is more accurate, but for the time being we are inclined to believe that the juvenile sockeye scale depicted in fig. 101.2 sooner belongs to an underyearling, than to a yearling.

An interesting situation which, in our opinion, is relevant to the question at hand, was observed by us in Alaska in the material kindly provided by C. Kalb of the Big Lake Fish Hatchery.

We examined the scale structure of sockeye smolts from two lakes located not far from each other, Big L. and Nancy L. (fig. 102). The young sockeye from Big L. are of artificial origin (Clupach, Jyle, 1990), while those from Nancy L. are of natural origin.

The Big Lake Hatchery incubates the eggs of sockeye, and then releases the fry into Big L. where they grow and migrate downstream to the sea the following year.

The Big L. smolts in our samples were mainly yearlings with two ZAS on their scales; the first ZAS was classified by us as basically indistinct and. Therefore, not an annulus, but only a supplementary formation (fig. 102.1). We encountered only several two-year-old smolts among the more than one hundred fish examined by us (fig. 102.2).

The smolts from Nancy L. were basically two-year-olds with mainly three ZAS on their scales; the first ZAS was classified by us as a supplementary one, i.e. it was formed when the fish were still underyearlings (fig. 102.3-4).

By I. I. Kurenkov's classification (1978), these lakes are "shallow" ones according to their average depths of 9 m for Big L. (area 1213.3 ha) (Clupach, Kyle, 1990) and 7.7 m for Nancy L. (area 308.1 ha); their maximum depths are 27.0 and 19.8 m respectively.

As we can see from fig. 102, the annual and supplementary ZAS on the scales of the smolts from Nancy L. are far more distinct than in those from Big L. The Nancy L. smolts are much smaller than the Big L. smolts, despite the fact that they are older than the latter.

We believe that the formation of supplementary ZAS on the scales of under-yearling sockeye from Nancy L. is related to the morphological characters of this lake. Nancy L. has a number of fairly deep coves which are separated from its main part by shallower areas, i.e. it has a number of local zones with their own hydrological and probably hydrobiological characteristics. We assume that the young of the year spend a certain period of time feeding and growing in these coves in masses, after which they migrate to the main and deeper part of the lake where they continue to forage. In our opinion, it is mainly this change in foraging conditions that causes the formation of supplementary ZAS on the scales of the young salmon from this lake.

On the other hand, the formation of supplementary ZAS on the scales of yearling sockeye from Big L. could also be related to the growth acceleration of underyearlings due to artificial incubation of the eggs (fig. 102.1), though other factors related to the ecology of the freshwater period may be responsible for this. On the scales of two-year-olds from this lake (fig. 102.2), we also note indistinct supplementary ZAS between the annual ones, but they are not clear enough to be identified with any degree of reliability.



Fig. 102. Scale structure in sockeye smolt from Big L. and Nancy L. (Alaska).

1 – Big L., 9 June 1985, AC=125 mm, age 1+, arrows mark ZAS (first arrow – supplementary ZAS, second arrow – annulus);

2 – Big L., 4 June 1985, AC=162 mm, age 2+, arrows mark ZAS (first and second – annuli);

3 – Nancy L., 23 May 1985, AC=97 mm, age 2+, arrows mark ZAS (first arrow – supplementary ZAS, second and third arrows – annuli);

4 – Nancy L., 23 May 1985, AC=96 mm, age 2+, arrows mark ZAS (first arrow – supplementary ZAS, second and third arrows – annuli).

It is not excluded that the supplementary (indistinct) ZAS observed in the central part of the scales in adult sockeye of Dalneye L. (fig. 95.1-2), Sarannoye L. (fig. 96) and Sopochnoye L. (fig. 97) may in some cases, apart from the possible seasonal change in feeding habits, have something to do with the influence of hereditary factors on the growth of immature sockeye in these lakes due to the high (judging by the scale structure) growth rate of young fish in these waters.

In conclusion, we should emphasize that experiments performed on fish in a controlled environment are not only time-consuming, but also do not cover the whole range of changes that are characteristic of fish populations in a natural environment. Therefore, the hypotheses discussed by us in this section of the book unquestionably require further verification in both types of environments.

Section 10. Biological structure of local stocks of the Asian sockeye

10.1. Age composition

Table 78 lists the age groups characteristic of the Asian sockeye, as we can see from the table, individuals of age 1.3 predominate in the sockeye of the Sea of Okhotsk coast and western coast of Kamchatka, with the exception of the sockeye of the Ozernaya R. where fish of age 2.3 predominate in the highly abundant year-classes (1940-1944), and fish of age 2.2 in year-classes of low abundance (1970-1975) (Selifonov, 1982). Instead of presenting our own results on the age structure of the Ozernaya R. sockeye, we utilized M. M. Selifonov's data (1982), in view of the fact that the age determination carried out by us together with Selifonov in the same material yielded practically the same results.

In the sockeye of the eastern coast of Kamchatka, the differences in the age structure of individuals from different bodies of water are greater than in the sockeye of the western coast, but fish of age 1.3 usually predominate in the river stocks. The sockeye of the Ananavayam R. (Ananapylgen R. watershed) have a highly characteristic age composition; many of the fish encountered there have 4-6 freshwater years of growth, which is unusual for the sockeye (fig. 103). An interesting fact is that the Ananavayam R. adult sockeye which stay in fresh waters for 4-6 years usually spend two years at sea, and those with a freshwater period of 1-3 years spend three years at sea; i.e. a longer freshwater period means a shorter sea period (table 78).

Also of interest are the data on the age structure of the sockeye of the Ananavayam R. where fish of age 1.4 (with four sea years) were encountered more frequently than usual in 1962, and were rarely encountered in 1985-1986. During certain years, we noted a higher than usual frequency of age 1.4 sockeye in the Bolshaya and Khailyulya rivers as well. In 1991, a large number of age 1.4 fish was also encountered in the Kikhchik R.

In the sockeye of Dalneye L. (table 78), fish of age 1.2, 1.3 and 2.2 predominated during the highly abundant years of the population (1935-1947), and individuals of age 1.2, 2.2 and 3.2 during the years of low abundance (1948-1964), i.e. as the numbers diminished and the feeding conditions in the lake improved, the age of the spawners increased due to an increase in the length of the freshwater period, which has already been noted by the researchers of this stock (Krogus et al., 1969). However, we believe that the situation in the case of Dalneye L. is much more complex, and it is not excluded that the processes

by which the age structure of this sockeye stock is formed here are of an inverse nature, i.e., as the feeding conditions in the lake improve, the age of the spawners drops because of a shorter sea period. The fact is that some of the sockeye of this stock always produce the freshwater (residual) form which attains maturity mostly in the second, less commonly the third, and very rarely the fourth year without migrating downstream to the sea (Krogius et al., 1969, 1987; Varnavskaya, Varnavsky, 1988).

The data presented in table 78 do not take into account the age of the residual (Russ. "dwarf") form of the sockeye from Dalneye L. These residual sockeye (from anadromous spawners mostly, not kokanee) fake an active part in the spawning of the anadromous sockeye. The abundance of the residual sockeye cannot be taken into account with full accuracy, but estimates show that from 1938 to 1969 the abundance of residual sockeye fluctuated from 5.8 to 18.9 % of the smolts in the year-classes (Krogius et al., 1987). Male fish predominate significantly (usually constituting 95 %) among the residual sockeye. A noteworthy fact is that the conditions necessary for the formation of a large number of residual sockeye are linked to a depressive state in the population of the anadromous sockeye and the improvement of feeding conditions for the young as a result of the low abundance of foraging individuals. During other years, residual sockeye are formed only in small numbers (Krogius et al., 1987). We still have not established whether this dwarfism is a hereditary characteristic, or not (Krogius et al., 1969, 1987; Gorshkova, Gorshkov, 1977).

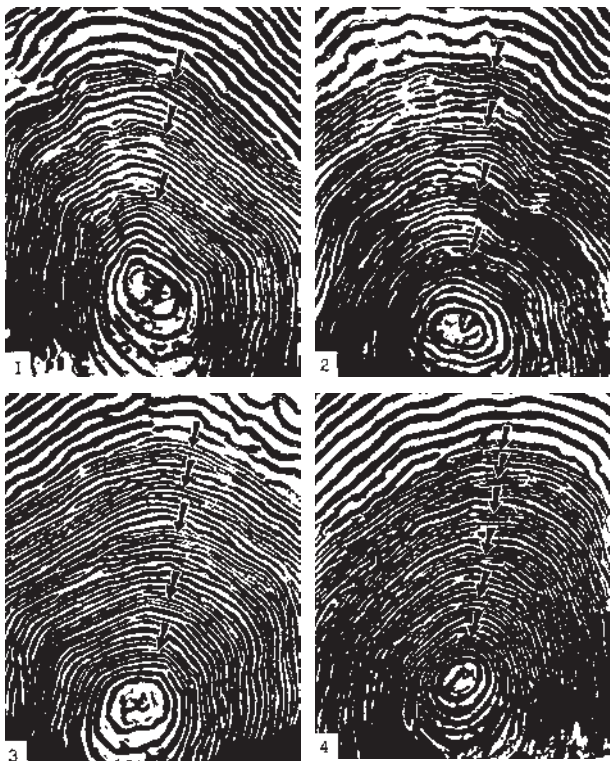


Fig. 103. Structure of the central part of the scales in sockeye spawners of the Ananavayan R. (Ananapylgen R. watershed) (26 June 1980). All ZAS marked with arrows are annuli.

1 – AC=710 mm, male, age 3.3, duration of freshwater period 3+;
 2 – AC=730 mm, male, age 4.3, duration of freshwater period 4+;
 3 – AC=650 mm, male, age 5.2, duration of freshwater period 5+;
 4 – AC=600 mm, female, age 6.2, duration of freshwater period of life 6+.

In recent years, intrapopulation differentiation of the residual (dwarf) form of the sockeye was detected in the sockeye of Dalneye L. (Varnavskaya, Varnavsky, 1988) with the help of polymorphic marker genes for coding lactate dehydrogenase (Ldh-B₁), phosphoglucumutase (Pgm) and peroxidase (Px). In genotype distributions, a reliable excess of heterozygotes was noted for the Pgm and Px loci in male residual sockeye. The Frequency of heterozygotic genotypes is significantly higher in residual sockeye with a higher than usual rate of growth. With no pressure from the fishery, the residual sockeye contributes significantly to the formation of a reproductively successful population. The residual sockeye and the anadromous form are not isolated reproductively, and their interaction obviously ensures the functioning of the population's adaptive mechanisms which allow it to survive in conditions of high pressure from the fishery (Varnavskaya, Varnavsky, 1988).

The change in the age composition of the fish from Listvenichnoye L. has attracted our attention (table 78). Compared with 1980, the incidence of fish with three freshwater years in this lake declined in 1984. This can be attributed to the fact that Listvenichnoye L. was fertilized in 1980. This improved the feeding conditions for juvenile sockeye in the lake, and resulted in a shorter freshwater period (Kurenkov, Kurenkov, 1988). We ourselves determined the age of the sockeye for this book.

According to the data of S. I. Kurenkov (1974), the adult kokanee (freshwater, or landlocked, sockeye) of Kronotskoye L. have five age groups on the average. 2+ (1.8 %), 3+ (19.6 %), 4+ (37.1 %), 5+ (33.8 %), and 6+ (7.7 %).

A small part of the young kokanee migrates downstream from Kronotskoye L. Because of the rapids, the downstream migrants are unable to return to the lake. An indication of this is the structure of the scales in the adult sockeye spawning below the rapids of the Kronotskaya R. (Bugaev, Kurenkov, 1985). The sockeye spawners examined by us (for 1991), which had migrated downstream from Kronotskoye L. as juveniles, were of age 2.3, while the sockeye spawners that did not come from Kronotskoye L. (at least in this year-class) were of age 1.3 (fig. 134). It is interesting to note that, of the 20 fish examined from below the Kronotskaya R. rapids, three individuals (15 %) were from Kronotskoye L.

During the 1960s, individuals of age 2.2 and 2.3 predominated in Sarannoye L. (Bering Is.) (table 78). In 1985-1990, the age of the adult sockeye in Sarannoye L. increased in comparison with the preceding years, and fish of the 3.3 age group began to predominate in the population. This may well have resulted from the increase in the abundance of the sockeye stock in this lake after limits were set on the rate of exploitation by the Japanese high seas fishery in 1977-1978 (these limits are still in effect). The latter has resulted in an overall increase in the abundance of spawners in the Asian stocks of the sockeye.

During the 1960s, individuals of age 2.2 and 2.3 also predominated in Krasivoye L. (Iturup Is.) (table 78), but in 1990 spawners of age 3.2, 2.3 and 3.3 began to predominate. As in the previous case, this was probably due to the increase in the abundance of sockeye in Krasivoye L.

According to I. A. Chereshnev (1981), individuals of age 1.3 and 2.3 predominate in Achchen L., and fish of age 1.3 and 1.2 in Seutakan L. on the eastern coast of the Chukchi Peninsula (table 78). According to our own data, individuals of age 2.3 constituted 69.2 %, age 2.4 – 7.7 % and age 3.3 – 23.1 % in the meager material (only 39 specimens) collected on 15-25 July 1975 in Achchen L. and kindly forwarded to us by A. S. Agapov and I. A. Chereshnev. This differs considerably from Chereshnev’s data (1981), and therefore additional material is required to check the data.

At the present time, we do not have any scale specimens from the sockeye of the Maynopylgen R. Nevertheless, back in 1978, we managed to analyze the age of about 100 adult sockeye from this river, and found that most of them were of age 1.3.

As a whole, a negative relationship between the duration of the freshwater and sea periods of life is noted for the Asian sockeye (fig. 104). The data on Dalneye L. (Paratunka R. watershed), taken from F. V. Krogius et al. (1969), do not quite fit this general relationship (fig. 104), and were not taken into account in the calculation of Spearman’s coefficient of rank correlation. In our opinion, the significant deviations of the data on the Dalneye L. sockeye from the general relationship (fig. 104) are most likely due to the existence of a highly abundant population of residual sockeye in this lake, which develops from the eggs of the anadromous sock-eye salmon (Krogius et al., 1969, 1987; Varnavskaya, Varnavsky, 1988), and also to the underestimation of the age of these fish in the overall age structure of the Dalneye L. sockeye (table 78).

This hypothesis is confirmed by the fact that the same material was used by us to compare our age determinations in the sockeye with those of F. V. Krogius (archival material), which basically matched.

In addition to data on Dalneye L., the literature indicates that residual sockeye (lendlacked, not kokanee) can be found in other Asian waters as well (Nikulin, 1970; Gorshkova, Gorshkov, 1977; Chereshnev, 1981).

In our opinion, the numbers of the kokanee in Azabach L., even during the years of exceptionally low abundance of this stock, were apparently insignificant, for researchers managed to catch only ten of them (Gorshkov, Gorshkova, 1977).

As for Achchen L., the presence of residual sockeye (not kokanee) in this lake is only mentioned (Chereshnev, 1981), which is probably an indication of, their low abundance.

Finally, a fairly large number of residual sockeye (not kokanee) was encountered in Uyeginskoye L. (Nikulin, 1970). However, we must keep in mind that this area of sockeye reproduction does not represent all the spawning grounds of this

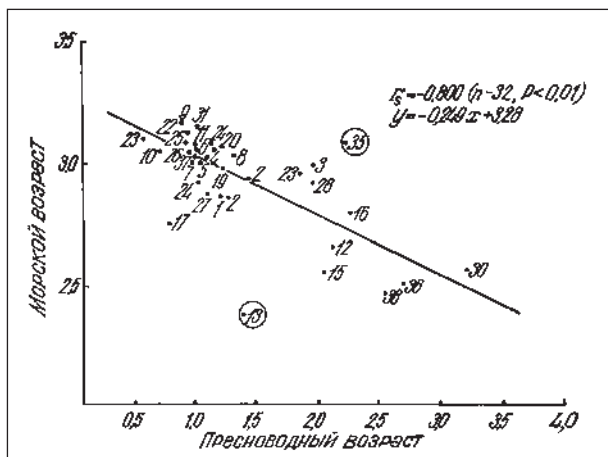


Fig. 104. Correlation between the average duration of the sea and freshwater periods of the life cycle in the Asian sockeye. Y-axis – duration of sea period, years; X-axis – duration of freshwater period, years. Areas marked as in fig. 1. The circled dots were not included in the calculation of the coefficients of rank correlation (explained in the text).

species in the Okhota R. watershed, and the percentage of residual sockeye encountered in the sockeye stock of this river is unquestionably lower than in Uyeginskoye L. This is probably why we do not observe any significant deviations from the general relationship in the sockeye of the Okhota R. (Fig. 104).

We intentionally have not used (fig. 104) the available published data on lakes Seutakan and Achchen (Chereshnev, 1981), in view of the fact that we did not conduct any age determinations with the above-mentioned author. As in the case of the Achchen L. sockeye, it was not by chance that we took this precaution. However, in fig. 104, we did include the data on the sockeye of Sopochnoye L. (Iturup Is.), which was kindly sent to us by Chris Wood (Nanaimo Biological Station, Canada); this material was collected by this author and N. V. Varnavskaya and A. I. Zhulkov in 1990, and included both scale specimens and age determination results. Our age determination results matched those of the above-mentioned authors.

Table 26 (Appendix) contains the average ages of the males and females of the Asian sockeye; when interpreted graphically

Table 78. Age group composition of *Asia sockeye*, %

Watershed	Data and years	Age groups																Number of fish					
		0.2	1.1	0.3	1.2	2.1	0.4	1.3	2.2	3.1	0.5	1.4	2.3	3.2	1.5	2.4	3.3		4.2	2.5	3.4	4.3	
Okhotsk Sea continental shelf																							
West coast of Kamchatka Peninsula																							
Palana R.	15.06-27.07.83	-	-	-	-	-	-	0.7	4.3	-	-	-	92.6	-	-	1.4	1.0	-	-	-	-	-	299
Tigil R.	21.06-30.07.81	-	-	7.9	-	-	78.9	-	-	-	-	5.3	7.9	-	-	-	-	-	-	-	-	-	38
Khairyuzova R.	09-24.07.84	-	-	3.7	-	-	92.9	-	-	-	-	0.7	2.7	-	-	-	-	-	-	-	-	-	298
Icha R.	05.07-18.08.86	-	-	-	-	-	94.1	-	-	-	-	-	3.9	-	-	2.0	-	-	-	-	-	-	51
Krutogorova R.	05-22.07.71	-	-	6.5	-	-	85.0	1.0	-	-	-	1.0	6.5	-	-	-	-	-	-	-	-	-	93
Vorovskaya R.	17.06-11.08.65	-	-	4.0	1.0	-	77.8	2.0	-	-	-	8.1	7.1	-	-	-	-	-	-	-	-	-	99
Kikhchik R.	27.07.31	-	-	10.1	2.3	-	51.7	-	-	-	1.1	22.5	5.6	-	1.1	-	-	-	-	-	-	-	89
Utka R.	11-30.07.65	-	-	26.8	1.2	-	65.9	-	-	-	-	4.9	-	-	-	-	-	-	-	-	-	-	82
Bolshaya R.	1935-1947	-	0.9	4.8	10.4	-	70.1	2.1	-	-	-	7.1	1.8	-	-	-	-	-	-	-	-	-	No data ²
Bolshaya R.	01-30.06.57-71	-	-	3.1	1.0	0.4	57.3	3.3	0.2	-	-	17.8	9.9	1.2	0.2	1.2	0.6	-	0.2	-	-	-	484
Ozernaya R.	1940-1944	-	-	-	-	-	-	-	25.8	-	-	-	74.2	-	-	-	-	-	-	-	-	-	No data ³
Ozernaya R.	1970-1975	-	-	-	3.2	-	-	-	48.8	-	-	-	32.9	10.8	-	0.3	4.0	-	-	-	-	-	No data ³

Watershed		Data and years	Age groups																	Number of fish				
			0.2	1.1	0.3	1.2	2.1	0.4	1.3	2.2	3.1	0.5	1.4	2.3	3.2	1.5	2.4	3.3	4.2		2.5	3.4	4.3	
Dalneye L. (Paratunka R.)		1935-1947	-	-	-	37.0	-	-	25.0	32.0	-	-	-	-	5.0	-	-	<1.0	-	-	-	-	-	No data ⁴
Dalneye L. (Paratunka R.)		1948-1963	-	-	-	33.0	-	-	10.0	32.0	-	-	-	-	7.0	-	-	1.0	-	-	-	-	-	No data ⁴
Blizhneye L. (Paratunka R.)		No year	-	-	-	34.5	-	-	17.8	38.0	-	-	-	-	-	-	-	-	-	-	-	-	-	No data ⁵
Medvezhie L. (Avacha R.)		1961	-	-	-	6.7	-	-	20.0	16.7	-	-	-	-	56.6	-	-	-	-	-	-	-	-	30 ⁶
Avacha R.		09-22.07.88	-	-	-	0.7	-	-	9.5	37.1	-	-	-	-	32.4	19.6	-	0.7	-	-	-	-	-	148
Listvenichnoye L. Listvenichnoye L.		24.06-1.07.80 03-05.08.84	-	-	-	-	8.5 4.1	-	-	21.3 6.1	2.1	-	-	-	19.2 83.7	8.5	-	34.0	-	-	4.3	2.1	-	47 49
Tikhaya R.		18-23.07.81	2.5	-	22.5	22.5	-	-	45.0	2.5	-	-	-	2.5	2.5	-	-	-	-	-	-	-	-	40
Kamchatka R. (marine trap)		01-30.06.78-83 01-30.07.78-83	0.2 0.1	-	6.9 10.7	5.8 5.4	0.3 0.3	0.3 3.2	54.9 56.9	5.7 3.9	-	-	2.9 1.8	19.6 17.0	-	-	0.1 0.3	0.1 0.3	-	-	-	-	-	1697 ⁷ 1166 ⁷
Stolbovaya R.		04.06-10.08.84	-	-	4.4	2.6	-	2.6	66.1	0.9	-	-	4.3	13.9	-	-	2.6	2.6	-	-	-	-	-	115
Malamvayam R.		21.06-22.07.83	-	-	4.7	2.3	-	-	43.0	4.7	-	-	1.1	44.2	-	-	-	-	-	-	-	-	-	86
Khailyulua R.		22.06-11.07.77-86	0.3	-	7.6	3.3	-	1.6	56.3	0.6	-	-	25.4	2.8	-	0.1	1.4	0.6	-	-	-	-	-	701
Ivashka R.		05.08-23.08.66	-	1.1	36.2	2.2	-	6.6	45.0	-	-	-	6.6	1.2	-	-	1.1	-	-	-	-	-	-	91
Karaga R.		16.06-28.07.88	0.9	-	2.3	18.3	-	0.5	63.4	0.5	-	-	5.0	9.1	-	-	-	-	-	-	-	-	-	219
Tymlat R.		27.06-06.08.73	-	-	9.4	-	-	2.3	76.5	1.2	-	-	7.1	3.5	-	-	-	-	-	-	-	-	-	85
Kichiga R.		20.06-28.06.81	-	-	9.8	-	-	2.0	81.4	-	-	-	2.9	2.9	-	-	1.0	-	-	-	-	-	-	102

Olyutorsk Region																	
Ayuayayam R.	30.06.62	-	1.7	-	5.3	31.6	-	-	42.1	10.5	-	-	-	8.8	-	-	57
Ayuayayam R.	03.06-01.07.85-86	0.8	0.8	11.9	0.2	81.3	0.5	-	2.3	2.0	-	-	-	0.2	-	-	395
Ihir-Gytkhyn (Kultushnaya R.)	09.08.83	-	-	2.0	-	4.0	10.0	-	-	72.0	-	-	-	8.0	2.0	-	50
Aruka R.	12.06-06.07.85	-	2.9	4.9	-	77.5	-	-	8.8	5.9	-	-	-	-	-	-	102
Ananaylgen R.	26.06-24.08.80	-	-	-	4.2	0.7	7.0	-	-	22.3	4.2	-	-	-	32.9	4.9	143
Anadyr-Navarin Region																	
Ukalayat R.	06.07-06.08.89	-	6.4	-	-	70.8	-	-	14.6	7.6	-	-	-	0.6	-	-	171
Tumanskaya R.	24-27.07.28	-	1.1	0.6	0.6	12.6	6.9	-	0.6	70.8	1.7	-	-	3.4	1.7	-	175
Eastern ChukotkaВосточная Чукотка																	
Seutakan L. (Seutakan R.)	1976	-	-	45.6	-	52.6	1.8	-	-	-	-	-	-	-	-	-	57 ⁸
Achchen L. (Achchen R.)	1975 15-25.07.75	-	-	1.6	-	41.0	24.6	-	-	32.8 69.2	-	-	-	-	-	-	61 ⁸ 39
Bering Island																	
Sarannoye L. (Sarannaya R.)	1960-1965 01.06-17.07.85-90	-	-	3.5	6.5	0.9	34.4	2.6	-	23.0	14.8	-	-	1.7	12.2	0.4	230 ⁹
		-	-	-	1.5	-	2.9	7.3	-	16.1	11.7	-	-	3.6	51.8	0.7	137
Iturup Island																	
Sopochnoye L. (Sopochnay R.)	26-29.08.90	-	-	19.7	-	58.9	-	-	-	21.4	-	-	-	-	-	-	56 ¹⁰
Krasivoye L. (Urumpet R.)	1964-1967 1990	-	-	4.0	-	3.8	48.3	0.3	-	20.5	11.9	0.3	-	10.2	-	0.7	345 ¹¹
		-	-	-	-	-	12.0	-	-	32.0	42.0	-	-	-	14.0	-	100

Note. Table excludes sockeye groups in the Ananaylgen R.: 5.2 – 13.3 %, 4.4 – 0.7 %, 5.3 – 0.7 % and 6.2 – 7.0 %. In the column "Number of fish" numbers indicate source materials: 1 – Nikulin, 1975; 2 – Semko, 1964; 3 – Seliphonov, 1982; 4 – Krogius et al., 1969; 6 – Krokhin, Kurenkov, 1967; Bugaev, 1987; 8 – Chereshev, 1981; Kurenkov, 1970; 10 – C. Wood (personal communication); 11 – Ivankov, 1984.

Under the heading "Age groups" the first number – duration of fresh water period, second number – duration of marine period.

cally, the data in this table confirm the conclusions drawn on the basis of the combined data for the male and female sockeye (fig. 104).

Table 27 (Appendix) characterizes the average age of the mature fish of the early and late seasonal races of the sockeye from the Bolshaya R., Dalneye L. and the Kamchatka R. (separately for the males and females). Except for one case (in the males of the late sockeye of the Bolshaya R.), we observe a tendency towards some increase in the length of the sea period with a shortening of the freshwater period in all the rest.

Table 28 (Appendix) gives the average age of mature individuals (males and females) of the local stocks and groups of the sockeye of the Kamchatka R. watershed (fig. 2) caught with trap nets at sea. As a whole, the data in this table show the same tendency towards an increase in the length of the sea period and a shortening of the freshwater period for all the stocks and groups of the sockeye.

Table 29 (Appendix) characterizes the age composition and abundance of certain age groups of the mature part of the sockeye stock of the Ozernaya R. (males and females separately) for 1970-1991 in greater detail than in table 78. The separate analysis of the age composition of the male and female sockeye of the Ozernaya R. is associated with the methodological aspects of forecasting the abundance of the sockeye of this local stock (Selifonov, 1975).

Our study of the correlation between the average length of the freshwater and sea periods of life in the sockeye of Kuril L. on the basis of long-term data has not produced well-defined reliable results, though reliable rank correlations have at times been observed for certain periods (7-8 years) (results not presented in this book).

The age structure of the Kamchatka R. sockeye of the early and late runs caught with sea trap nets and river drift nets during 1978-1989 is shown in tables 30 and 31 (Appendix). As indicated by our first attempts to study the inter-annual variability in the average length of the freshwater and sea periods of the Kamchatka R. sockeye, we still do not have enough material for well-defined statistically reliable results, and therefore we must continue to gather new material.

The data on the age composition of the Kamchatka R. sockeye requires further explanation.

First of all, we must keep in mind that the method used by us since 1978 to determine the age of the Kamchatka R. sockeye (Bugayev, 1987) is fundamentally different from the one used by earlier researchers (Somov, 1930; Lagunov, 1940; Krogius, 1970; Simonova, 1978) due to the fact that the biological characteristics of the Kamchatka R. sockeye were unknown prior to our investigations (Bugayev, 1981, 1981a, 1983a, 1984, 1984b, 1986, etc.). Therefore, our age determination data (Bugayev, 1987) cannot be correlated with those of our predecessors (Somov, 1930; Lagunov, 1940; Krogius, 1970; Simonova, 1978).

Due to the differences in the growth rhythm, the rate of sclerite formation and the rate of formation of supplementary zones of adjacent sclerites (ZAS) on the scales of some stocks and groups of sockeye, the age of the fish caught beyond the spawning grounds can be determined only after the stock or group to which these individuals belong has been determined. The method for identifying the sockeye stocks and groups differentiated in the Kamchatka R. watershed is described in our earlier papers (Bugayev, 1983c, 1986a).

The data presented in table 78 apply to the age composition of fish caught in trap nets at sea. As we have shown earlier (Bugayev, 1987; Bugayev, 1987a), the age composition of the fish from these catches does not reflect the age structure of the reproductive part of the stock, due to the fact that the Kamchatka R. watershed has local stocks and groups of sockeye that differ in the length of their freshwater period, their biological characteristics and the dynamics of their spawning migration. This occurs because the fishery does not remove individual stocks and groups of sockeye uniformly, which alters the age structure of the river's entire sockeye stock (Bugayev, 1987).

In order to obtain reliable information on the age composition of spawned out fish, we must gather material at the spawning grounds, and this material must include fish measurements and samples of scales and otoliths (Clutter, Whitesel, 1956). However, it is extremely difficult to carry on annual surveys of this type in the Kamchatka R. watershed which covers an area of about 56,000 km². Russian salmon researchers usually judge the age composition of the reproductive part of a stock by the age characteristics of the fish from catches, which, as a rule, meets forecasting requirements. In some cases, information on the age composition of spawned out fish is obtained from material gathered above the commercial fishery zone (the sockeye of lakes Kuril and Dalneye), though we do know that the age composition of the Kvichak R. sockeye (Iliamna L.), estimated on the basis of sockeye scale samples taken above the commercial fishery zone and at the spawning grounds, also differs during certain years (Koo, Smith, 1960). Up to 1977 (inclusively), when studying the population dynamics of the Kamchatka R. sockeye, the age of the reproductive part of the stock was judged on the basis of samples taken from the catches of the domestic fishery (Simonova, 1978).

After processing material gathered throughout the Kamchatka R. watershed in 1976-1978, we noted that the duration of the freshwater period of the Kamchatka R. sockeye from the catches did not correspond to that of the reproductive part of the stock. The years 1976 and 1977 were particularly remarkable in this respect; based on the catches (weighted data). The return of adult sockeye from underyearling smolts amounted to about 14 % in 1976, and 20 % in 1977. In reality, the percentage of spawned out fish returning after migrating downstream as underyearlings amounted to 49 % in 1976, and 43 % in 1977 (Bugayev, 1983c, 1987). Due to resorption of the scale margin in spawners caught in the vicinity of the spawning grounds, we were unable to determine the duration of the sea period of their life cycle, as a result. We could not correlate it with that of the spawned out and mature fish from the catches.

We believe that one of the causes of this inconsistency between age composition calculated on the basis of the catches and age composition based on the abundance ratio of the spawned out stocks and groups is that, due to the nonsimultaneous

placement of trap nets and the frequently changing intensity of net fishing, irregular removal of nonsimultaneously running stocks and groups of sockeye by the fishery occurs, and the fish of these stocks and groups are characterized by their own specific age, "S" by individuals of age 0.3; "E", "V", "N" and "K" by individuals of age 1.3, and "D" by individuals of age 2.3 (Bugaev, 1983c, 1987; Bugaev, 1987, 1987a).

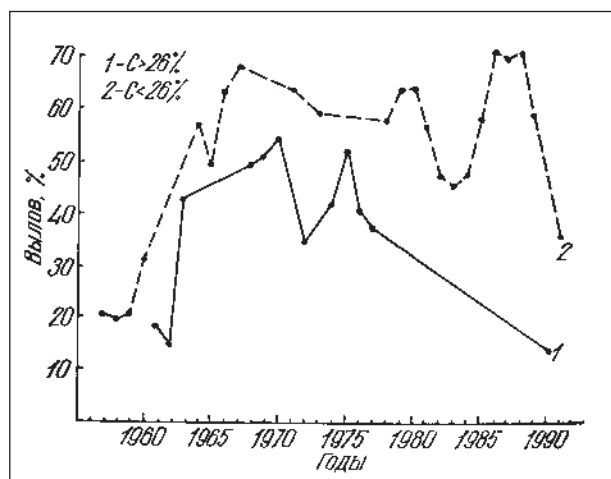


Fig. 105. Removal of Kamchatka R. sockeye by the USSR fishery, of the total number of sockeye spawners approaching the mouth of the river (depending on the abundance of sockeye from group "S"). Y-axis – removals, %; X-axis – years.

1 – ratio of group "S" > 26 %, 2 – ratio of group "S" < 26 %.

Another factor that influences the removals of sockeye stocks and groups of the Kamchatka R. watershed is their ratio in the overall sockeye stock of this river. For instance, the data in fig. 105 indicate that during the years of high abundance of group "S" fish (more than 26 % of the total abundance of sockeye spawning in the Kamchatka R. watershed) (Bugaev, 1984; fig. 2), the percentage of the total removals of sockeye decreases. In this case, we can attribute the lower rate of exploitation of the sockeye to the fact that the sea trap nets in this situation, because of the migratory characteristics of the fish, probably do not fish off the migrating individuals as well as they should. This is confirmed by the fact that the relative removals of the sockeye with river nets average 57 % (43 % in the Kamchatka Bay) over a number of years when the percentage of group "S" individuals is greater than 26 %, and they average only 33 % (67 % in the Kamchatka Bay) when group "S" individuals constitute less than 26 %, i.e. despite the higher rate of exploitation in the river, the total removals of the Kamchatka R. sockeye in the years of a high incidence of group "S" individuals still decreases.

Finally, the discrepancy between the age composition of fish from the catches and that of the reproductive part of the stock is due to the inconsistency of the methods used to gather biological statistics prior to 1978, i.e. sampling was irregular and not year-round. The fish were caught without taking the fishing gear into account (fishing gear not indicated), and the age composition was not determined separately for sea trap nets and river drift nets. Since 1978, the method of collecting samples has been greatly improved by eliminating all the above-mentioned shortcomings.

In the ensuing situation, when there were practically no long-term data on the age of the reproductive part of the sockeye stock of the Kamchatka R. (data that was needed to forecast the numbers of this stock), we proposed a method (Bugaev, 1982a, 1987) which would enable us to reconstruct in basic terms the age composition of the adult fish at the spawning grounds for a number of years.

Based on long-term data, 70-80 % of the sockeye of the Kamchatka R. spend 3 years at sea (Lagunov, 1940; Birman, 1967; Simonova, 1978; Konovalov, 1980; Mosher, 1972; table 75). Proceeding from this, we can tentatively accept 3 years as being the period of time spent by the sockeye at sea/ As a result, we can say that the age of the mature fish of group "S" is equal to 0.3, that of groups "E", "V", "N" and "K" 1.3, and the age of groups "A" and "D" 2.3. Having determined the abundance ratio of the adult fish of spawned out stocks and groups (based on A. G. Ostroumov's aerial survey data covering the period from 1957 and up to the present), we derived the age structure of the reproductive part of the stock for this period of time (Bugaev, Ostroumov, 1986; table 13).

Reconstructed data on the age composition of the reproductive part of the sockeye stock of the Kamchatka R. are now being successfully used to forecast the abundance of its spawnings runs (Bugaev, Ostroumov, 1986; Bugaev, 1987a).

The sockeye age determination results presented in table 78 can be used for analysis of the population dynamics of the Asian sockeye stocks.

10.2. Size-weight characteristics

The body length and weight of spawners from the Asian sockeye stocks in question (fig. 1) are given in table 79. As a whole, the size of the Asian sockeye (even in combined material for a number of years) displays a correlation with the geographical latitude at which the river estuary inhabited by the sockeye is located (figs. 106 and 107). The coefficient of rank correlation between the size of the fish and the latitude of the river estuary was examined in two variants, i.e. with the Urumpet R. (Iturup Is.) taken into account, which made the total number of rivers equal to 35 ($r_s=0.599$, $P<0.01$ for males;

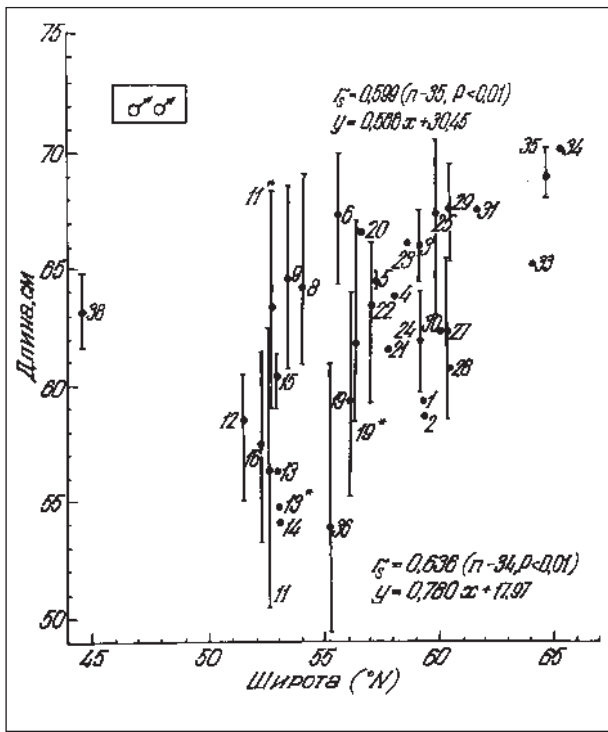


Fig. 106. Variation of body length in males of the Asian sockeye, depending on the latitude at which the mouth of the river is located. Y-axis – body length, cm; X-axis – latitude, °N. Areas marked as in fig. 1. In sockeye of stocks 11, 13 and 19, late individuals are marked with an asterisk, and early individuals are left without.

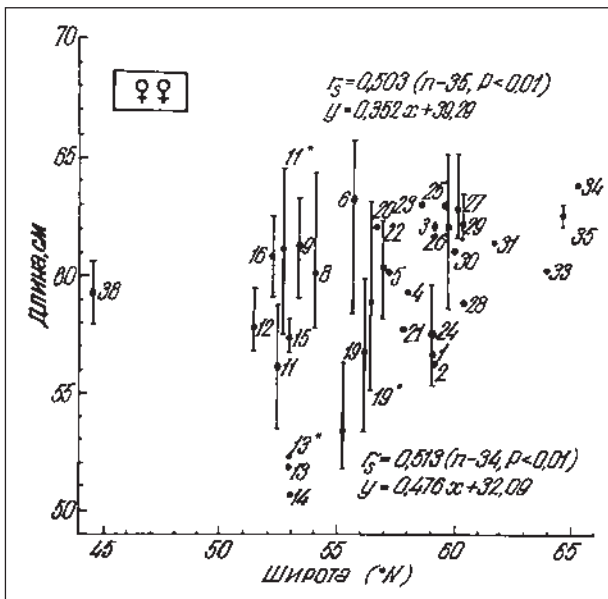


Fig. 107. Variation of body length in females of the Asian sockeye, depending on the latitude at which the mouth of the river is located. Y-axis – body length, cm; X-axis – latitude, °N. Areas marked as in fig. 1. In sockeye of stocks 11, 13 and 19, late individuals are marked with an asterisk, and early individuals are left without.

$r_s=0.503$, $P<0.01$ for females), and without the Urumpet R., making the total number of rivers 34 ($r_s=0.636$, $P<0.01$ for males, $r_s=0.513$, $P<0.01$ for females).

We did have some data on the size of the sockeye from Sopochnoye L. (Iturup Is.), but we did not include these data in figs. 106 and 107, because for the spawners displayed intense breeding colours at the time. Furthermore, because the samples contained spawners of the freshwater form of the sockeye (kokanee) in addition to the anadromous form, it was not quite clear whether it would be feasible to include the kokanee for size comparison, or not. On the Kamchatka Peninsula, kokanee are encountered only in waters where, for some unspecified reason, the anadromous form of the sockeye is not found (Kurenkov, 1977, 1979; Ostroumov, 1977, 1985). The freshwater and anadromous forms of the sockeye are encountered simultaneously in Sopochnoye L. (Ivankov, 1968, 1984). This is not unusual for some stocks of the American sockeye (Ward, Larkin, 1964; Foerster, 1968; McDonald, Hume, 1984; Burgner, 1991).

Due to the fact that we did not have any data on the weight of the fish in one very important case (table 79), we did not analyze the changes in the body weight of the individuals in relation to the latitude at which the river estuary was located. Since the length and weight of a sexually mature sockeye are in good correlation with each other (Mathisen, 1965), one can expect the body weight of Asian sockeye spawners to manifest the same relationships as depicted in figs. 106 and 107.

For the sockeye of Bristol Bay (Alaska), researchers have already demonstrated how the abundance of the local sockeye stocks of this area affects the changes in the size of the individuals, i.e. with an increase in abundance, the length and weight of the body decrease (Rogers, 1980).

Table 79. Body length and weight of adult Asian sockeye

Watershed	Year	Males				Number of fish
		Body length, cm		Body weight, kg		
		Range	Average	Range	Average	
Okhota R.	1983	51.7-66.6	59.48 ± 0.66	1.77-3.95	2.718 ± 0.098	33
Kukhtuy R.	1983	52.5-66.2	58.83 ± 0.45	1.82-3.35	2.464 ± 0.054	45
Palana R.	1983	54.0-74.0	64.64 ± 0.31	1.60-4.10	2.879 ± 0.043	144
Palana R.	1990	60.0-72.5	67.72 ± 0.51	2.24-3.97	3.176 ± 0.085	29
Tigil R.	1981	55.0-69.0	64.06 ± 1.23	1.61-3.80	2.886 ± 0.172	16
Khairyuzova R.	1984	55.0-71.0	64.32 ± 0.23	2.68-4.26	3.490 ± 0.034	123
Khairyuzova R.	1986	55.0-71.0	65.03 ± 0.51	2.09-4.75	3.684 ± 0.084	34
Khairyuzova R.	1989	58.5-69.0	64.57 ± 0.40	2.42-4.24	3.533 ± 0.077	28
Icha R.	1986	67.0-74.0	70.17 ± 0.33	3.11-4.53	3.656 ± 0.070	24
Icha R.	1989	66.0-74.0	68.20 ± 0.29	3.43-4.42	3.834 ± 0.040	44
Vorovskaya R.	1965	57.5-77.5	69.29 ± 0.60	1.85-5.05	3.473 ± 0.093	50
Vorovskaya R.	1989	45.0-67.5	61.05 ± 0.86	1.86-4.42	3.014 ± 0.122	28
Vorovskaya R.	1990	49.0-67.0	62.43 ± 0.34	1.60-4.30	3.208 ± 0.049	81
Kikhchik R.	1931	55.0-65.0	60.87 ± 0.61	2.03-3.91	3.085 ± 0.103	24
Kikhchik R.	1989	53.0-76.0	68.77 ± 0.62	1.81-5.10	3.986 ± 0.119	35
Bolshaya (early sockeye)	1978-1989	50.6-62.6	56.43 ± 1.25	1.44-2.78	2.239 ± 0.131	9
Bolshaya (late sockeye)	1978-1989	59.2-68.5	63.65 ± 0.95	2.67-3.80	3.257 ± 0.115	11*
Ozernaya R.	1978-1989	55.2-60.6	58.72 ± 0.41	2.25-3.15	2.839 ± 0.074	12*
Avacha R.	1988	49.0-70.0	60.62 ± 0.46	0.73-3.24	1.981 ± 0.062	77*
Avacha R.	1989	45.0-70.0	61.52 ± 0.36	0.96-3.51	2.460 ± 0.040	176
Avacha R.	1990	40.0-67.0	59.14 ± 0.39	0.62-3.48	2.262 ± 0.049	98
Listvenichnay R.	1980	24.0-66.0	53.40 ± 2.09	0.20-4.20	2.520 ± 0.219	35
Listvenichnay R.	1984	40.5-71.0	61.61 ± 2.34	0.85-4.80	3.197 ± 0.298	18
Kamchatka (early sockeye)	1978-1989	55.3-64.1	59.36 ± 0.84	2.31-2.95	2.623 ± 0.065	12*
Kamchatka (late sockeye)	1978-1989	58.6-67.4	61.99 ± 0.87	2.46-3.47	2.938 ± 0.083	11*
Stolbovaya R.	1984	52.0-73.0	66.75 ± 0.50	1.86-5.07	3.568 ± 0.081	52
Malamvayam R.	1983	47.0-70.0	61.89 ± 0.85	1.06-3.88	2.560 ± 0.102	44
Khailyulua R.	1978-1989	59.4-65.9	63.47 ± 0.76	2.95-3.72	3.503 ± 0.103	9*
Ivashka R.	1966	36.0-76.0	66.32 ± 1.26	0.85-5.65	3.992 ± 0.181	41
Karaga R.	1988	45.6-70.0	59.77 ± 0.48	1.00-5.21	2.912 ± 0.080	112
Karaga R.	1989	57.0-70.5	64.26 ± 0.24	2.40-4.60	3.320 ± 0.038	119
Tymlat R.	1973	57.0-77.0	68.24 ± 0.65	2.10-4.65	3.565 ± 0.083	45
Kichiga R.	1981	57.0-75.0	66.56 ± 0.42	2.13-5.15	3.840 ± 0.070	57
Kichiga R.	1982	45.0-71.0	63.10 ± 0.84	1.05-4.92	3.563 ± 0.136	29
Kichiga R.	1989	64.0-76.0	70.00 ± 0.81	3.00-5.02	3.909 ± 0.149	20
Kichiga R.	1990	57.5-79.5	70.89 ± 0.53	2.03-6.13	3.387 ± 0.099	41
Avyavayam R.	1985	45.0-76.0	58.69 ± 0.82	1.15-5.48	2.569 ± 0.111	112
Avyavayam R.	1986	50.0-77.0	65.62 ± 0.60	1.60-5.40	3.675 ± 0.092	105
Avyavayam R.	1989	45.0-76.0	62.93 ± 1.09	1.10-5.60	3.210 ± 0.140	95
Kultushnaya R.	1983	35.5-73.0	60.96 ± 1.87	0.35-4.30	2.572 ± 0.218	23
Apuka R.	1980	63.0-78.0	67.95 ± 0.79	3.01-4.92	3.624 ± 0.121	29
Apuka R.	1985	48.5-73.0	65.52 ± 0.84	1.29-5.49	3.513 ± 0.134	50
Apuka R.	1989	47.5-78.0	67.90 ± 0.68	1.40-6.10	3.912 ± 0.105	76
Apuka R.	1990	56.0-78.8	69.76 ± 0.82	1.92-5.40	4.134 ± 0.137	36
Ananapylgen R.	1980	38.0-75.0	62.41 ± 1.06	0.47-4.10	2.672 ± 0.117	68
Ukalayat R.	1989	62.0-73.5	67.77 ± 0.26	2.78-5.37	4.152 ± 0.061	68
Tumanskaya R.	1928	53.0-73.0	66.40 ± 0.55	1.40-4.85	3.521 ± 0.085	63
Achchen R.	1975	64.5-74.0	70.43 ± 0.90	–	–	14
Sarannaya R.	1990	34.0-63.0	51.52 ± 1.15	0.50-3.80	2.171 ± 0.0428	58
Sarannaya R.	1991	32.0-63.0	49.50 ± 0.92	0.55-3.95	2.012 ± 0.096	115
Urumpet R.	1990	59.0-71.0	64.77 ± 0.48	2.14-3.90	2.950 ± 0.068	49

I. B. Birman (1985) writes about the possibility of food competition between the sockeye and the pink salmon in the ocean, which suggests that the abundance of the pink salmon may influence the size and weight characteristics of the sockeye. The influence of pink salmon numbers on the size of the sockeye from the Ozernaya R. was noted by F. V. Krogius (1960) who showed that, during the years of high abundance of the Western Kamchatka pink salmon (odd-numbered years), the ocean growth rate of the sockeye from the Ozernaya R., and Dalneye L. (Paratunka R.) at sea was lower than in the years of lower abundance (even-numbered years). However, she was unable to show any reliable correlations with the abundance of the pink salmon.

There is reason to believe that the differences observed in the size of the Ozernaya sockeye of the even- and odd-numbered years may be regulated to a considerable extent by genetic factors as well (Krogius, 1960; Foerster, 1968; Ricker, 1972). The possibility of this is corroborated by the observations carried out with the sockeye of the Fraser R. where the annual differences in the body weight of the fish are not related to the abundance of the sockeye population, but, as the researchers suggest (Killick, Clemens, 1963), are the result of hereditary factors. More evidence of the possible influence of hereditary factors

Watershed	Year	Females				Number of fish
		Body length, cm		Body weight, kg		
		Range	Average	Range	Average	
Okhota R.	1983	47.7-61.5	55.93 ± 0.41	1.38-2.89	2.251 ± 0.047	66
Kukhtuy R.	1983	49.4-62.3	56.49 ± 0.44	1.32-4.20	2.274 ± 0.062	55
Palana R.	1983	50.0-74.0	62.22 ± 0.21	1.60-3.90	2.539 ± 0.025	154
Palana R.	1990	57.5-67.0	62.18 ± 0.60	2.00-3.03	2.512 ± 0.069	19
Tigil R.	1981	51.0-69.0	59.45 ± 0.85	1.20-3.41	2.195 ± 0.100	22
Khairyuzova R.	1984	54.0-67.0	59.97 ± 0.16	2.08-3.90	2.791 ± 0.023	169
Khairyuzova R.	1986	52.0-66.0	61.00 ± 0.30	1.95-3.77	3.000 ± 0.047	62
Khairyuzova R.	1989	54.0-63.0	59.58 ± 0.38	2.21-3.30	2.773 ± 0.050	24
Icha R.	1986	60.0-69.0	65.89 ± 0.43	2.11-3.75	3.212 ± 0.061	27
Icha R.	1989	62.0-69.0	65.74 ± 0.38	3.07-4.00	3.482 ± 0.041	47
Vorovskaya R.	1965	58.5-69.5	64.46 ± 0.32	1.85-3.55	2.876 ± 0.051	49
Vorovskaya R.	1989	52.0-64.5	57.83 ± 0.46	1.74-3.61	2.497 ± 0.064	36
Kikhchik R.	1990	50.0-69.0	57.85 ± 0.28	1.64-3.20	2.467 ± 0.031	103
Kikhchik R.	1931	51.7-65.0	59.14 ± 0.46	1.87-3.75	2.871 ± 0.074	39
Kikhchik R.	1989	53.0-69.0	63.44 ± 0.52	1.89-3.90	3.126 ± 0.073	40
Bolshaya R. (early sockeye)	1978-1989	53.5-58.7	56.22 ± 0.49	1.87-2.28	2.138 ± 0.050	9*
Bolshaya R. (late sockeye)	1978-1989	57.6-64.6	61.19 ± 0.72	2.45-3.17	2.845 ± 0.059	11*
Ozernaya R.	1978-1989	56.8-59.5	57.94 ± 0.23	2.27-2.75	2.607 ± 0.045	12*
Avacha R.	1988	50.0-67.0	56.82 ± 0.45	1.28-3.28	2.028 ± 0.057	71
Avacha R.	1989	51.0-65.0	58.23 ± 0.31	1.24-3.10	2.053 ± 0.036	131
Avacha R.	1990	52.0-68.0	57.03 ± 0.35	1.28-3.89	1.974 ± 0.047	112
Listvenichnaya R.	1980	64.0-68.0	59.04 ± 1.11	2.20-4.00	3.817 ± 0.137	12
Listvenichnaya R.	1984	58.0-66.0	62.62 ± 0.34	2.25-3.80	3.131 ± 0.053	31
Kamchatka R. (early sockeye)	1978-1989	53.4-60.0	56.67 ± 0.60	2.11-2.45	2.217 ± 0.027	12*
Kamchatka R. (late sockeye)	1978-1989	55.2-63.3	58.92 ± 0.72	2.17-2.71	2.242 ± 0.047	11*
Stolbovaya R.	1984	57.0-70.0	62.06 ± 0.33	1.77-3.69	2.860 ± 0.053	63
Malamvayam R.	1983	52.0-64.0	57.77 ± 0.37	1.43-3.00	2.072 ± 0.044	41
Khailyulya	1978-1989	58.2-62.0	60.24 ± 0.41	2.58-3.08	2.914 ± 0.059	9*
Ivashka R.	1966	55.0-72.0	63.12 ± 0.47	2.25-4.65	3.327 ± 0.065	50
Karaga R.	1988	46.5-63.0	55.44 ± 0.40	1.20-3.40	2.258 ± 0.055	106
Karaga R.	1989	52.0-69.0	59.72 ± 0.19	1.60-4.00	2.640 ± 0.026	156
Tymlat R.	1973	57.0-69.0	63.11 ± 0.46	1.43-3.60	2.955 ± 0.061	40
Kichiga R.	1981	56.0-68.0	60.82 ± 0.34	2.00-3.94	2.949 ± 0.054	44
Kichiga R.	1982	55.0-64.0	58.65 ± 0.46	2.18-3.69	2.773 ± 0.080	23
Kichiga R.	1989	59.5-71.0	64.00 ± 0.56	2.10-3.65	2.899 ± 0.071	26
Kichiga R.	1990	58.5-73.5	62.25 ± 0.46	2.28-4.41	2.850 ± 0.062	46
Aviavayam R.	1985	53.0-68.0	62.03 ± 0.50	1.54-3.45	2.814 ± 0.069	35
Aviavayam R.	1986	55.0-68.0	61.69 ± 0.16	2.00-4.00	2.951 ± 0.022	190
Aviavayam R.	1989	60.0-72.0	65.29 ± 0.39	2.60-4.80	3.275 ± 0.067	53
Kultushnaya R.	1983	45.0-69.0	58.87 ± 0.87	1.30-3.00	2.235 ± 0.092	27
Apuka R.	1980	57.0-66.0	62.25 ± 0.50	2.83-3.74	3.187 ± 0.057	22
Apuka R.	1985	56.5-67.0	61.59 ± 0.31	2.11-3.46	2.837 ± 0.042	52
Apuka R.	1989	57.0-69.0	62.58 ± 0.31	2.38-4.19	3.097 ± 0.054	56
Apuka R.	1990	59.0-70.0	63.55 ± 0.27	2.14-4.15	2.976 ± 0.050	66
Ananapylgen R.	1980	54.0-69.0	61.33 ± 0.39	1.47-3.60	2.411 ± 0.050	75
Ukalayat R.	1989	55.5-70.0	61.50 ± 0.25	2.17-4.78	3.150 ± 0.044	82
Tumanskaya R.	1928	51.0-69.0	60.43 ± 0.27	1.55-4.00	2.657 ± 0.040	112
Achchen R.	1975	35.0-68.0	62.14 ± 1.24	–	–	25
Sarannaya R.	1990	45.0-56.0	52.24 ± 0.34	1.40-2.70	2.046 ± 0.040	55
Sarannaya R.	1991	45.0-59.0	51.81 ± 0.48	1.15-3.20	2.084 ± 0.057	80
Urumpet R.	1990	57.0-66.0	60.62 ± 0.36	1.82-3.10	2.377 ± 0.045	51

*Average value of multi-year data; in the "Range" column are given the parameters of fluctuation of mean yearly values; in the "Number of fish" column, number of observations years.

on the size of adult sockeye at certain spawning grounds (groups of spawning grounds) is provided by the data available on the sockeye spawners of the Kamchatka R. (Konovalov, 1980; Bugaev, Ostroumov, 1990) and Kuril L. (Krokhin, Krogus, 1937; Bugaev, 1976), in the watershed of which practically all the sockeye of the Ozernaya R. reproduce. The possibility of the size and weight characteristics of the Bristol Bay sockeye being influenced by genetic factors is not rejected by D. Rogers either (1980), but this author believes that the interannual differences in the length and weight of the sockeye are influenced mainly by fish abundance (Rogers, 1980).

So far, the most representative data on the size and weight of sockeye spawners is available only for the sockeye of the Ozernaya R. (Kuril L.); for many years now, they have been collected at the weir of the Kamchatka branch of TINRO, located at the outfall of the Ozernaya R.

The length and weight of the Ozernaya sockeye for the period 1970-1991 are given in tables 80 and 81. The population dynamics of the sockeye and the pink salmon from the principal areas of their reproduction on the Kamchatka Peninsula is depicted in fig. 108.

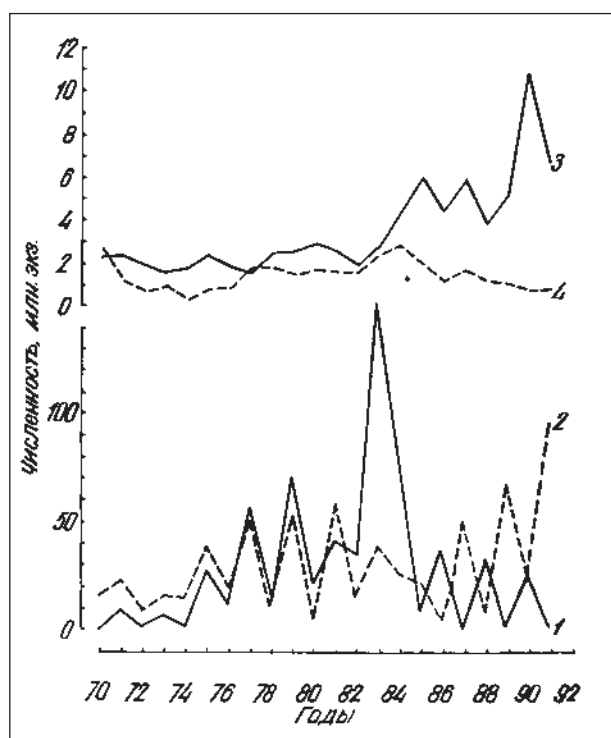


Fig. 108. Interannual variability in the abundance of some pink salmon and sockeye stocks of the Kamchatka Peninsula during 1970-1991. Y-axis – abundance, mill. specimens; X-axis – years.

1 – pink salmon of Western Kamchatka (abundance of the mature part of the stocks);
 2 – pink salmon of Northeastern Kamchatka (abundance of the mature part of the stocks);
 3 – sockeye of the Ozernaya R. (abundance of the mature part of the stock);
 4 – sockeye of the Kamchatka R. (run to the mouth of the river).

Our analysis of the relationship between the body length of male and female individuals of the most abundant age groups (2.1, 2.2, 2.3, 2.4, 3.2, 3.3) and the numbers of the pink salmon and sockeye for the period 1970-1991 has in some cases shown statistically reliable correlations (table 82). The highest number of reliable body length correlations was noted with the abundance of the Ozernaya sockeye. In all the cases, all of the statistically reliable Spearman's coefficients of rank correlation were negative. This indicates that an increase in the abundance of the sockeye and the pink salmon leads to a decrease in the size of the sexually mature fish.

After the Western Kamchatka pink salmon reached a very high level of abundance and the spawning grounds became overcrowded in 1983, the numbers of the even- and odd-numbered year-classes of the Western Kamchatka pink salmon began to change in 1985 and have continued to do so up to the present day. As a result, the numbers of the Western Kamchatka and Eastern Kamchatka stocks of the pink salmon began to fluctuate in the opposite phase (fig. 108). Taking this factor into account, we grouped all of our material into two periods, 1970-1984 and 1985-1991.

The results of our analysis of the effect of pink salmon and sockeye abundance at sea on the length of the Ozernaya sockeye during 1970-1984 and 1985-1991 are presented in table 83. As we can see from this table, in all the cases where there are statistically reliable or almost reliable correlations, we note negative coefficients of rank correlation.

For the period 1970-1984, the highest body length correlations are noted with the abundance of the Western Kamchatka pink salmon, and slightly lower ones with the abundance of the Ozernaya R. and Kamchatka R. sockeye. No significant correlations between body length and the abundance of the Eastern Kamchatka pink salmon were noted in any of the cases.

As we look at the very short observation period of 1985-1991, we note reliable correlations between the length of age 2.2 individuals and the abundance of both the Western Kamchatka pink salmon, and the Eastern Kamchatka pink salmon, a negative correlation being noted for the first, and a change from a negative to a positive correlation for the second. We attribute this change to the changes that have occurred in the even- and odd-numbered year-classes of the Western Kamchatka pink salmon since 1985 (fig. 108). Considering the existence of food competition between the sockeye and the pink salmon at sea (Birman, 1985), one can assume that this probably altered the competitive food relations between these salmonid species. Figs. 109-111 depict some of the relationships recorded in table 83.

As we analyze the body weight of the Ozernaya sockeye in relation to the abundance of the pink salmon and the sockeye in the above-mentioned areas for 1970-1984 and 1985-1991 (table 84), we note that the results obtained from this analysis are in many cases analogous to the ones derived by us earlier in our analysis of body length (table 83). This is due to the significant correlation of the length and weight characteristics of the sockeye (Mathisen, 1965). Nevertheless, we should emphasize that, in some cases, the correlation between the body length of the sockeye and the numbers of the pink salmon and the sockeye in the sea manifests itself more clearly when the length is analyzed (table 84), and in other cases when the body weight is analyzed (table 84). Figs. 112 and 113 illustrate some of the relationships indicated in table 83. The differences observed in the significance of Spearman's coefficients of rank correlation when the length and weight of the fish is compared with the abundance of the salmon at sea can be attributed to the interannual fluctuations in their fatness.

It is important to note that high coefficients of rank correlation are typically noted for individual age groups, and not for all the age groups combined, and often for salmon of different species (pink and sockeye) and different areas (tables 83 and 84). This is most likely associated with the partial overlapping of the foraging grounds of different age groups of the Ozernaya

Table 80. Average body length of adult Ozernaya R. sockeye (M. M. Selifonov, KottINRO archives; data of Soviet-Japanese Fishery commission), cm

Year	1.1		1.2		1.3		2.1		2.2		2.3		2.4		3.1		3.2		3.3		3.4		Average		
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
1970	-	-	-	-	41.1	58.0	55.2	60.2	-	63.0	-	58.1	56.0	61.5	60.8	-	-	-	-	61.5	60.8	-	-	60.0	59.0
1971	-	-	-	-	40.8	56.9	55.6	61.0	64.7	61.0	63.5	57.2	55.6	64.8	62.0	-	-	-	-	64.8	62.0	-	-	60.4	58.5
1972	-	-	-	-	41.8	57.9	56.4	61.7	68.0	63.0	64.2	60.0	57.4	64.6	62.0	-	-	-	-	64.6	62.0	-	-	62.0	59.1
1973	-	-	-	-	43.5	56.1	55.4	63.7	63.0	62.8	63.7	58.3	55.8	64.2	63.0	46.4	58.3	55.8	64.2	63.0	63.0	-	-	61.8	59.9
1974	-	-	-	-	42.8	58.0	56.0	61.1	62.0	60.8	63.0	60.7	56.1	64.2	62.4	-	60.7	56.1	64.2	62.4	62.4	-	-	61.7	59.0
1975	-	-	-	-	41.2	60.6	56.0	64.3	66.7	60.5	64.3	58.8	57.0	65.0	61.8	-	58.8	57.0	65.0	61.8	61.8	-	-	61.9	59.0
1976	-	-	-	-	42.7	57.7	56.6	64.0	64.5	62.8	64.0	57.5	56.7	-	-	-	57.5	56.7	-	-	-	-	-	61.1	59.5
1977	-	-	-	-	39.9	57.4	54.8	62.2	63.6	62.6	65.7	58.5	55.1	64.2	62.6	-	58.5	55.1	64.2	62.6	62.6	-	-	63.3	59.8
1978	40.0	-	53.0	58.0	40.2	56.8	55.9	64.6	-	-	64.6	58.6	56.7	63.9	60.7	45.3	58.6	56.7	63.9	60.7	-	-	59.5	59.5	
1979	36.5	-	60.5	59.0	38.9	54.7	53.5	59.6	64.5	64.0	63.4	57.5	54.8	63.6	60.1	40.9	57.5	54.8	63.6	60.1	-	64.5	55.2	56.8	
1980	-	-	53.8	62.0	39.8	55.7	53.9	62.4	-	62.8	60.6	38.5	57.0	54.9	62.0	38.5	57.0	54.9	63.6	62.0	-	64.0	58.9	57.5	
1981	-	-	-	59.4	37.3	55.8	54.1	63.3	62.2	61.6	63.0	60.0	60.0	53.6	63.0	-	60.0	53.6	63.0	62.0	-	-	60.0	58.0	
1982	-	-	-	-	39.2	54.7	53.3	60.3	62.4	61.8	63.6	56.8	54.1	63.5	60.9	40.1	56.8	54.1	63.5	60.9	-	62.0	57.6	57.4	
1983	-	-	-	57.0	34.0	52.1	51.3	61.6	62.6	-	58.1	52.7	50.7	61.0	58.6	35.9	52.7	50.7	61.0	58.6	-	-	58.6	57.0	
1984	-	-	-	-	37.0	53.4	53.6	62.0	62.5	-	58.8	54.9	53.4	62.0	59.3	41.0	54.9	53.4	62.0	59.3	-	-	59.9	58.3	
1985	-	-	-	58.0	41.0	55.2	62.9	59.7	69.5	61.8	62.9	56.1	55.1	62.4	59.5	-	56.1	55.1	62.4	59.5	-	-	60.6	58.8	
1986	37.8	-	53.3	62.5	40.6	56.0	55.0	63.0	62.5	60.0	63.0	53.3	53.5	67.3	44.5	53.3	53.5	67.3	60.6	63.6	-	-	59.1	58.4	
1987	-	-	50.5	47.2	38.8	54.4	52.3	59.3	62.1	58.3	62.6	55.9	53.6	60.3	-	55.9	53.6	60.3	57.1	57.1	-	-	58.6	57.4	
1988	-	-	49.5	58.8	37.6	55.1	54.5	59.6	62.8	-	62.3	54.5	54.2	63.4	38.5	54.5	54.2	63.4	60.7	60.7	-	-	58.8	58.4	
1989	-	-	-	-	40.0	53.2	52.8	59.6	64.9	61.5	62.9	54.4	54.6	62.8	39.0	54.4	54.6	62.8	60.2	60.2	-	-	57.8	57.8	
1990	38.5	-	47.5	63.6	41.3	55.6	54.3	60.8	64.8	61.9	63.8	60.8	54.3	64.6	-	57.3	54.3	64.6	61.8	61.8	-	-	63.0	59.0	
1991	-	-	46.7	49.0	38.7	53.3	53.3	58.2	62.5	60.8	61.6	54.5	2.5	62.6	44.1	54.5	2.5	62.6	58.4	58.4	-	-	57.4	56.0	
Average 1970-1991	38.2	-	51.3	52.7	39.9	55.8	54.5	60.2	64.2	61.7	63.2	56.9	54.8	63.4	41.3	56.9	54.8	63.4	60.7	60.7	-	63.5	59.9	58.4	

Table 81. Average body weight of adult Ozernaya R. sockeye (M. M. Seifonov, KoTINRO archives; data of Soviet-Japanese Fishery commission), kg

Year	1.1		1.2		1.3		2.1		2.2		2.3		2.4		3.1		3.2		3.3		3.4		Average	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1970	—	—	—	—	—	—	1.02	2.24	2.24	2.24	2.82	3.22	—	3.10	—	—	2.50	2.33	3.20	2.70	—	—	2.65	2.35
1971	—	—	—	—	—	—	0.85	2.33	2.20	2.33	2.88	3.32	3.33	2.95	—	2.44	2.17	3.51	3.10	3.10	—	—	2.58	2.57
1972	—	—	—	—	—	—	0.98	2.56	2.30	3.04	3.04	3.50	4.10	3.30	—	2.72	2.30	3.50	3.10	3.10	—	—	1.18	2.80
1973	—	—	—	—	—	—	1.06	2.23	2.12	3.23	2.84	3.23	3.78	3.27	1.20	2.46	2.21	3.25	3.27	3.27	—	—	2.99	2.74
1974	—	—	—	—	—	—	1.00	2.50	2.18	3.10	2.82	3.10	2.95	3.00	—	2.70	2.26	3.40	3.03	3.03	—	—	2.93	2.70
1975	—	—	—	—	—	—	0.90	2.83	2.23	3.26	2.80	3.26	3.52	3.20	—	2.60	2.44	3.27	2.85	2.85	—	—	3.06	2.56
1976	—	—	—	—	—	—	1.00	2.57	2.40	3.22	2.97	3.40	3.40	2.98	—	2.46	2.38	—	—	—	—	—	2.79	2.68
1977	—	—	—	—	—	—	0.72	2.25	1.89	3.45	2.94	3.45	2.86	2.96	—	2.33	1.92	—	—	—	—	—	3.08	2.60
1978	0.70	—	—	—	—	—	0.85	2.35	2.18	3.62	2.96	3.62	—	—	1.22	2.45	2.25	3.43	3.00	3.00	—	—	3.10	2.71
1979	0.60	—	—	—	—	—	0.77	2.01	1.83	3.24	2.65	3.24	3.20	—	0.85	2.30	2.00	3.37	2.66	2.66	—	—	2.25	2.27
1980	—	—	—	—	—	—	0.83	2.33	2.09	3.29	2.82	3.29	—	3.25	0.70	2.49	2.13	—	3.53	3.53	—	—	2.82	2.50
1981	—	—	—	—	—	—	0.70	2.46	2.09	3.48	2.89	3.48	2.75	3.07	—	2.85	2.08	3.35	2.75	2.75	—	—	3.15	2.72
1982	—	—	—	—	—	—	0.80	2.24	2.03	3.54	2.93	3.54	3.15	3.15	—	2.54	2.02	3.46	3.01	3.01	—	—	2.65	2.56
1983	—	—	—	—	—	—	0.55	1.83	1.70	3.06	2.50	3.06	3.02	—	0.64	1.86	1.59	3.10	2.54	2.54	—	—	2.67	2.38
1984	—	—	—	—	—	—	0.60	2.08	2.04	3.33	2.77	3.19	3.19	—	1.00	2.27	2.01	3.34	2.86	2.86	—	—	3.02	2.71
1985	—	—	—	—	—	—	0.97	2.38	2.31	3.38	2.85	3.38	4.55	3.27	—	2.51	2.27	3.39	2.84	2.84	—	—	3.11	2.75
1986	0.75	—	—	—	—	—	1.14	2.45	2.22	3.41	2.95	3.41	3.37	3.02	1.20	2.14	2.11	4.02	3.11	3.11	—	—	2.89	2.74
1987	—	—	—	—	—	—	0.85	2.21	1.96	3.38	2.86	3.38	3.27	2.78	—	2.40	1.99	3.01	2.45	2.45	—	—	2.87	2.60
1988	—	—	—	—	—	—	0.74	2.67	2.21	3.37	2.91	3.37	3.25	—	0.75	2.14	2.15	3.59	3.00	3.00	—	—	2.88	2.74
1989	—	—	—	—	—	—	0.88	2.03	1.92	3.34	2.85	3.34	3.74	2.98	0.75	2.11	2.01	3.24	2.81	2.81	—	—	2.66	2.60
1990	0.75	—	—	—	—	—	0.98	2.30	2.15	3.58	3.02	3.58	3.78	3.29	—	2.54	2.18	3.82	3.14	3.14	—	—	3.07	2.79
1991	—	—	—	—	—	—	0.75	1.99	2.00	3.09	2.64	3.09	3.30	2.92	1.15	2.22	1.87	3.22	2.55	2.55	—	—	2.50	2.44
Average 1970-1991	0.70	—	—	—	—	—	0.86	2.32	2.10	3.34	2.85	3.34	3.40	3.11	0.94	2.41	2.12	3.38	2.92	2.92	—	—	2.86	2.61

Table 82. The significance of rank correlation coefficient in the analysis of the effect of the abundance of adult pink and sockeye on the body length of adult sockeye in the Ozernaya R. in 1970-1991

Age	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye
Males				
2.1	$r_s = -0.532^*$, a = -0.046, b = 41.25	$r_s = -0.396$ –	$r_s = -0.431^*$, a = -0.000103, b = 40.27	$r_s = -0.490^*$, a = -0.000183, b = 42.33
2.2	$r_s = -0.255$ –	$r_s = -0.431^*$, a = -0.033, b = 56.86	$r_s = -0.657^{**}$ a = -0.000374; b = 57.14	$r_s = -0.237$ –
2.3	$r_s = -0.022$ –	$r_s = -0.135$ –	$r_s = -0.557^{**}$ a = -0.000143, b = 63.72	$r_s = -0.281$ –
2.4	$r_s = -0.217$ (n = 19)	$r_s = -0.098$ (n = 19)	$r_s = -0.031$ (n = 19)	$r_s = -0.178$ (n = 19)
3.2	$r_s = -0.384$	$r_s = -0.122$	$r_s = -0.670^{**}$	$r_s = -0.226$
3.3	$r_s = -0.085$ (n = 20) –	$r_s = -0.419$ (n = 20) –	$r_s = -0.356$ (n = 20) –	$r_s = -0.586^*$ (n = 20), a = -0.00135, b = 65.24
Total age groups	$r_s = -0.111$	$r_s = -0.216$	$r_s = -0.416$	$r_s = -0.245$
Females				
2.2	$r_s = -0.270$ –	$r_s = -0.509^*$, a = -0.030; b = 55.43	$r_s = -0.536$, a = -0.000213, b = 55.24	$r_s = -0.327$ –
2.3.	$r_s = -0.184$ –	$r_s = -0.425$ –	$r_s = -0.689^{**}$ a = -0.000191, b = 60.88	$r_s = -0.280$ –
2.4	$r_s = 0.082$ (n = 18)	$r_s = -0.202$ (n = 18)	$r_s = -0.359$ (n = 18)	$r_s = 0.223$ (n = 18)
3.2	$r_s = -0.384$ –	$r_s = -0.408$ –	$r_s = -0.628^{**}$ a = 0.000299, b = 55.79	$r_s = -0.235$ –
3.3	$r_s = -0.147$ (n = 21) –	$r_s = -0.488^*$ (n = 21) a = -0.033; b = 61.70	$r_s = -0.703^{**}$ (n = 21) a = -0.000266, b = 61.62	$r_s = -0.337$ (n = 21) –
Total age groups	$r_s = -0.224$ –	$r_s = -0.398$ –	$r_s = -0.546^*$, a = -0.000124, b = 58.78	$r_s = -0.165$ –

Note. In instances where “n” – number of compared pairs are not indicated, in all instances n=22; “a” and “b” – regressive equation coefficients $Y=ax + b$, where “x” – fish abundance in mill. specimens; “Y” – body length, cm. *P< 0.05; **P < 0.01.

sockeye at sea, which was pointed out earlier (Selifonov, 1989). Donald Rogers (1980) has also noted a variable degree of size-weight correlation in different age and sex groups of the Bristol Bay sockeye, depending on its abundance.

We do not deny that the rate of growth and. Consequently, the size and mass of the Ozernaya sockeye are also influenced by hereditary factors. However, based on the results of this study, we must admit that environmental factors (in this case the abundance of the pink salmon and sockeye populations) as a whole have a greater effect than hereditary factors on the growth rate and definitive size of the fish of the Ozernaya sockeye stock.

The available data suggest that the abundance of the Western Kamchatka pink salmon also influences the size of the sockeye from the Bolshaya R., which is located slightly north of the Ozernaya R. As we can see from fig. 114, the average minimum sizes of male individuals of the early form of the sockeye from the Bolshaya R. for all the age groups were noted in 1983, the year of the highest numbers of the Western Kamchatka pink salmon. Analysis of this diagram shows that the minimum sizes of male fish of the late form do not coincide with the maximum abundance of the Western Kamchatka pink salmon in 1983.

The length of female individuals of the early and late forms of the Bolshaya R. sockeye (graph not included) also showed no decrease in the size of female fish in 1983.

The effect of extreme levels of abundance of the Western Kamchatka pink salmon on the the size of the early form of the sockeye from the Kamchatka and Khailyulya rivers can be inferred on the basis of the data in fig. 115, which indicate that the smallest fish were noted in 1983. The abundance of the Western Kamchatka pink salmon does not have the same effect on the size of the male individuals of the late form of the Kamchatka R. sockeye (fig. 115).

The length of female individuals of the early form of the Kamchatka R. sockeye and the early and late sockeye of the Khailyulya R. (graph not included) also showed a decrease in 1983, but the females of the late form of the Kamchatka R. sockeye did not show the same decrease in body size (on the contrary, a certain increase in size was noted).

The above analysis of the size-weight characteristics of the Ozernaya sockeye in relation to the abundance of salmons at sea has shown that the investigations carried out with individual age groups are more informative. Unfortunately, we could not analyze the size of the sockeye from the Bolshaya R. in the individual age groups, and had to use combined data, for the available archival material on the age structure of the Bolshaya R. sockeye was, in our opinion, unreliable in some cases. So far, nothing

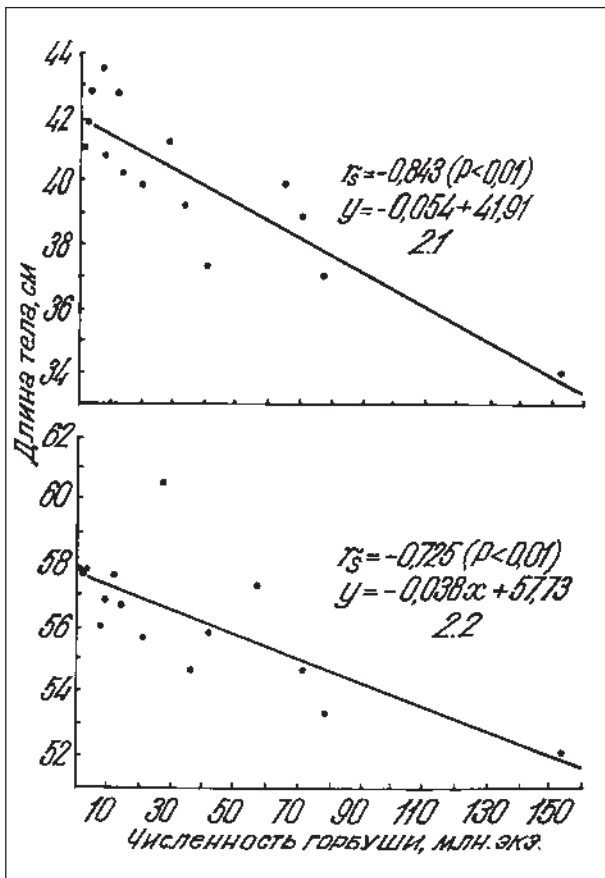


Fig. 109. Dependence of the body length in Ozernaya R. sockeye males of age 2.1 and 2.2 on the abundance of pink in Western Kamchatka during 1970-1984. Y-axis – body length, cm; X-axis – abundant of pink, mill. specimens.

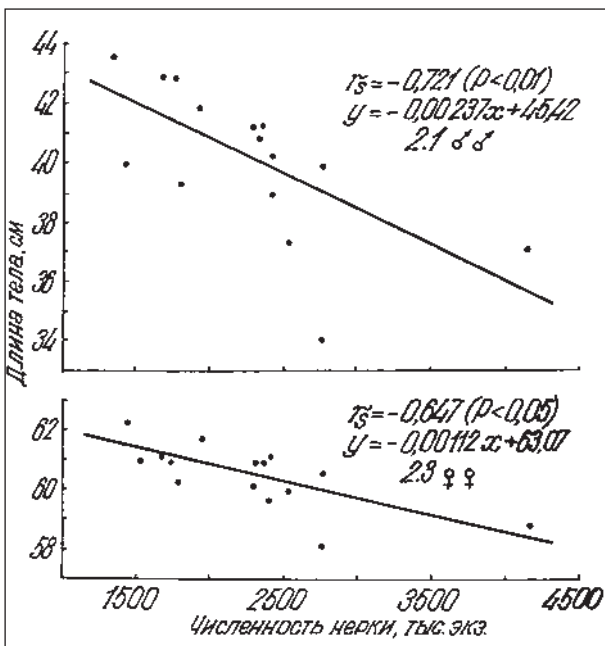


Fig. 110. Dependence of the body length in Ozernaya R. sockeye males of age 2.1 and females of age 2.3 on the abundance of the mature part of the Ozernaya sockeye stock in the ocean during 1970-1984. Y-axis – body length, cm; X-axis – abundance of sockeye, thou. specimens.

definite can be said about the influence of the abundance of the Eastern Kamchatka pink salmon on the size of the Bolshaya R. sockeye, as the series of sockeye observations carried out in this area is limited and data on individual years are insufficient.

The results of the above analysis of the available data indicate that the abundance of the pink salmon of both Western and Northeastern Kamchatka influences the definitive size of the mature sockeye of the Ozernaya R. (more so does than the abundance of the sockeye of the Ozernaya and Kamchatka rivers). This is the result of the effect of its abundance on the growth rate at sea, which in turn influences the survival rate of the fish at sea prior to the onset of sexual maturity.

The influence of the abundance of the pink salmon should be taken into account when analyzing the dynamics of abundance and compiling fishery forecasts for the sockeye of the Ozernaya R. One can assume that the increase in the abundance of the Ozernaya sockeye observed in the middle and up to the end of the 1980s and through to the beginning of the 1990s (Selifonov, 1988; latest fishery statistics) is, in addition to the effect of the natural and artificial fertilization of the Kuril L. (Problems of Fertilization..., 1988), partially due to the sudden drop in the abundance of the Western Kamchatka pink salmon

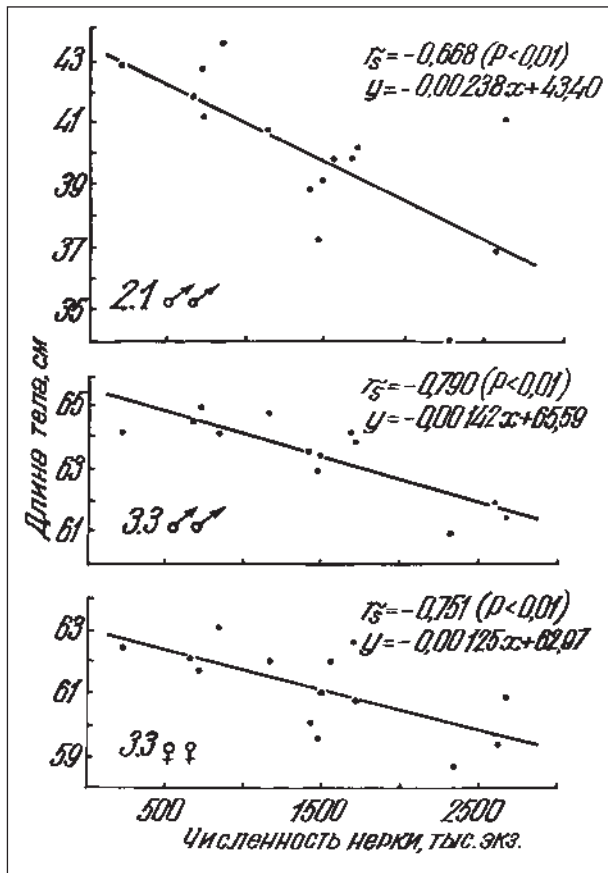


Fig. 111. Dependence of the body length in Ozernaya R. sockeye males of age 1.2 and 3.3 and females of age 3.3 on the abundance of the sockeye runs to the mouth of the Kamchatka R. during 1970-1984. Y-axis – body length, cm; X-axis – abundance of sockeye, thou. specimens.

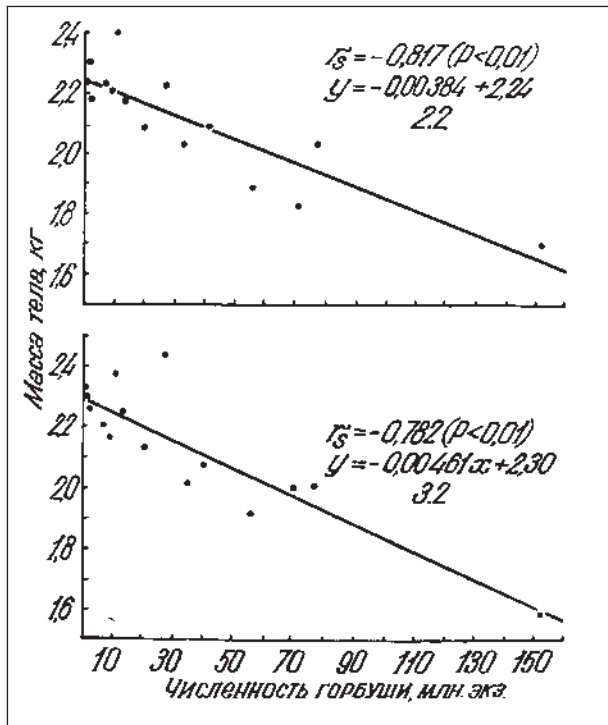


Fig. 112. Dependence of the weight of Ozernaya R. sockeye females of age 2.2 and 3.2 on the abundance of pink in Western Kamchatka during 1970-1984. Y-axis – body weight, kg; X-axis – abundance of pink, mill. specimens.

during this particular period (fig. 198). Proceeding from this fact, one might conclude that the next increase in the abundance of the Western Kamchatka pink salmon will coincide with a certain decrease in the numbers of the Ozernaya sockeye. However, the effect of a high abundance of pink salmon on the northeastern coast of the Kamchatka Peninsula, which is currently fluctuating in antiphase with the pink salmon of Western Kamchatka, can complicate the situation, and therefore an additional series of observations must be conducted here.

M. M. Selifonov (tables 32 and 33. Appendix) indicates that, for the Ozernaya sockeye as a whole, a size and weight increment dependence is observed during the spawning migrations in the later samples as compared with the earlier ones.

For the sockeye of the Kamchatka R. where distinctly different seasonal races of the sockeye exist, both the males and

Table 83. The significance of rank correlation coefficient in the analysis of the effect of the abundance of adult pink and sockeye on the body length of adult sockeye in the Ozernaya R. in 1970-1984 and 1985-1991

Age	1970-1984				1985-1991			
	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye
Males								
2.1	$r_s = -0.843^{**}$, a = -0.054, b = 41.91	$r_s = -0.482$ – –	$r_s = 0.721^{**}$, a = -0.00237, b = 45.42	$r_s = -0.668^{*}$, a = -0.00238; b = 43.40	$r_s = 0.162$ – –	$r_s = -0.214$ – –	$r_s = 0.500$ – –	$r_s = 0.090$ – –
2.2	$r_s = 0.725^{**}$, a = -0.038, b = 57.73	$r_s = -0.229$ – –	$r_s = -0.561^{*}$, a = -0.00156, b = 59.95	$r_s = -0.505$ – –	$r_s = -0.829^{*}$, a = 0.056, b = 53.78	$r_s = -0.821^{*}$, a = -0.030, b = 55.86	$r_s = 0.000$ – –	$r_s = 0.252$ – –
2.3	$r_s = -0.221$ – –	$r_s = -0.071$ – –	$r_s = -0.586^{*}$, a = -0.00101, b = 65.75	$r_s = -0.386$ – –	$r_s = -0.336$ – –	$r_s = -0.414$ – –	$r_s = 0.180$ – –	$r_s = 0.036$ – –
2.4	$r_s = -0.396$, (n = 12)	$r_s = -0.203$, (n = 12)	$r_s = -0.186$, (n = 12)	$r_s = -0.382$, (n = 12)	$r_s = 0.018$ –	$r_s = -0.072$ –	$r_s = -0.144$ –	$r_s = 0.027$ –
3.2	$r_s = -0.508$ – –	$r_s = -0.102$ – –	$r_s = -0.427$ – –	$r_s = -0.563^{*}$, a = -0.00180, b = 60.36	$r_s = -0.145$ – –	$r_s = 0.126$ – –	$r_s = 0.703$ – –	$r_s = 0.027$ – –
3.3	$r_s = -0.420$, (n = 13)	$r_s = -0.276$, (n = 13)	$r_s = -0.497$, (n = 13)	$r_s = -0.790^{**}$, (n = 13), a = 0.00142, b = 65.59	$r_s = 0.775$ – –	$r_s = -0.536$ – –	$r_s = -0.250$ – –	$r_s = -0.414$ – –
Total age groups	$r_s = -0.465$ – –	$r_s = -0.046$ – –	$r_s = -0.631^{*}$, a = -0.00113, b = 62.70	$r_s = -0.509$ – –	$r_s = -0.595$ – –	$r_s = -0.679$ – –	$r_s = 0.179$ – –	$r_s = 0.252$ – –
Females								
2.2	$r_s = -0.719^{**}$, a = -0.030, b = 55.85	$r_s = -0.363$ – –	$r_s = -0.470$ – –	$r_s = -0.651^{*}$, a = -0.00127, b = 56.58	$r_s = 0.779^{*}$, a = 0.050, b = 53.11	$r_s = -0.750$, a = -0.025, b = 54.91	$r_s = -0.143$ – –	$r_s = 0.342$ – –
2.3	$r_s = -0.541^{*}$, a = -0.020, b = 61.21	$r_s = -0.436$ – –	$r_s = -0.647^{*}$, a = -0.00112, b = 63.07	$r_s = -0.487$ – –	$r_s = 0.627$ – –	$r_s = -0.649$ – –	$r_s = 0.072$ – –	$r_s = 0.055$ – –
2.4	$r_s = -0.109$ (n = 12)	$r_s = -0.141$, (n = 12)	$r_s = 0.067$, (n = 12)	$r_s = 0.296$ (n = 12)	$r_s = 0.290$, (n = 6)	$r_s = -0.086$, (n = 6)	$r_s = 0.600$ (n = 6)	$r_s = -0.290$, (n = 6)
3.2	$r_s = -0.749^{**}$, a = -0.037, b = 56.49	$r_s = -0.481$ – –	$r_s = -0.491$ – –	$r_s = -0.575^{*}$, a = -0.00143, b = 57.23	$r_s = 0.127$ – –	$r_s = -0.342$ – –	$r_s = 0.162$ – –	$r_s = 0.327$ – –
3.3	$r_s = 0.581^{*}$ (n = 14) a = -0.023; b = 61.98	$r_s = -0.417$ (n = 14) – –	$r_s = -0.563^{*}$, (n = 14), a = -0.00137^{*}, b = 64.29	$r_s = -0.757^{**}$, a = 0.00125, b = 62.97	$r_s = 0.703$ – –	$r_s = -0.536$ – –	$r_s = -0.143$ – –	$r_s = -0.378$ – –
Total age groups	$r_s = -0.543^{*}$, a = -0.015; b = 59.07	$r_s = -0.271$ – –	$r_s = -0.647^{*}$, a = 0.000689, b = 60.12	$r_s = -0.258$ – –	$r_s = 0.582$ – –	$r_s = -0.631$ – –	$r_s = 0.126$ – –	$r_s = 0.127$ – –

Note. In instances where “N” – the number of compared pairs is not indicated: for 1970-1984 – n=15, 1985-1991 – n=7. Other values as per table 82. *P < 0.05; **P < 0.01.

Table 84. The significance of rank correlation coefficient in the analysis of the effect of the abundance of adult pink and sockeye on the body weight of adult sockeye in the Ozernaya R. in 1970-1984 and 1985-1991

Age	1970- 1984				1985-1991			
	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye
Males								
2.1	$r_s = -0.911^{**}$, $a = -0.00609$, $b = 1.192$	$r_s = -0.568^*$, $a = -0.011$, $b = 1.255$	$r_s = -0.611^*$, $a = -0.000331$, $b = 1.734$	$r_s = -0.568^*$, $a = -0.000462$, $b = 1.636$	$r_s = 0.342$ — —	$r_s = -0.393$ — —	$r_s = 0.214$ — —	$r_s = 0.144$ — —
2.2	$r_s = -0.651^*$, $a = 0.00467$, $b = 2.510$	$r_s = -0.270$ — —	$r_s = -0.279$ — —	$r_s = -0.413$ — —	$r_s = 0.811^*$, $a = 0.012$, $b = 2.097$	$r_s = -0.964^{**}$, $a = -0.00655$, $b = 2.547$	$r_s = -0.571$ — —	$r_s = 0.451$ — —
2.3	$r_s = 0.109$	$r_s = -0.155$	$r_s = 0.123$	$r_s = 0.116$	$r_s = 0.500$	$r_s = -0.613$	$r_s = 0.162$	$r_s = 0.236$
2.4	$r_s = -0.545$ (n = 12) — —	$r_s = -0.594^*$, (n = 12), $a = -0.015$, $b = 3.740$	$r_s = -0.224$, (n = 12) — —	$r_s = -0.497$, (n = 12) — —	$r_s = -0.018$ — — —	$r_s = 0.000$ — — —	$r_s = 0.536$ — — —	$r_s = 0.054$ — — —
3.2	$r_s = -0.558^*$, $a = 0.00437$, $b = 2.619$	$r_s = -0.340$ — —	$r_s = -0.275$ — —	$r_s = -0.531^*$, $a = -0.000177$, $b = 2.717$	$r_s = 0.018$ — —	$r_s = 0.018$ — —	$r_s = 0.775$ — —	$r_s = 0.073$ — —
3.3	$r_s = 0.297$ (n = 13) —	$r_s = -0.483$, (n = 13) —	$r_s = -0.027$, (n = 13) —	$r_s = -0.478$, (n = 13) —	$r_s = -0.901^*$, $a = 0.021$, $b = 3.137$	$r_s = -0.786^*$, $a = 0.00787$, $b = 3.779$	$r_s = -0.214$ — —	$r_s = -0.072$ — —
Total age groups	$r_s = -0.048$	$r_s = -0.104$	$r_s = -0.036$	$r_s = -0.150$	$r_s = 0.559$	$r_s = -0.714$	$r_s = 0.107$	$r_s = 0.451$
Females								
2.2	$r_s = -0.817^{**}$, $a = -0.00384$, $b = 2.237$	$r_s = -0.438$ — —	$r_s = -0.290$ — —	$r_s = -0.460$ — —	$r_s = 0.775$, $a = 0.00621$, $b = 2.011$	$r_s = -0.786^*$, $a = -0.00361$, $b = 2.252$	$r_s = -0.107$ — —	$r_s = 0.451$ — —
2.3	$r_s = -0.441^{**}$	$r_s = -0.369$	$r_s = -0.477$	$r_s = -0.272$	$r_s = 0.645$	$r_s = -0.667$	$r_s = -0.144$	$r_s = -0.036$
2.4	$r_s = -0.014$, (n = 12)	$r_s = -0.259$, (n = 12)	$r_s = 0.266$, (n = 12)	$r_s = -0.126$, (n = 12)	$r_s = 0.725$, (n = 6)	$r_s = -0.600$, (n = 6)	$r_s = 0.314$, (n = 6)	$r_s = -0.087$, (n = 6)
3.2	$r_s = -0.782^{**}$, $a = -0.00461$, $b = 2.302$	$r_s = -0.450$ — —	$r_s = -0.314$ — —	$r_s = -0.504$ — —	$r_s = 0.523$ — —	$r_s = -0.643$ — —	$r_s = 0.035$ — —	$r_s = 0.306$ — —
3.3	$r_s = -0.537$, (n = 14) — —	$r_s = -0.746^{**}$, (n = 14), $a = 0.00973$, $b = 3.213$	$r_s = -0.290$, (n = 14) — —	$r_s = -0.449$ — —	$r_s = 0.829^*$, $a = 0.014$, $b = 2.614$	$r_s = -0.679$, $a = 0.00608$, $b = 3.082$	$r_s = -0.036$ — —	$r_s = -0.198$ — —
Total age groups	$r_s = -0.279$	$r_s = -0.238$	$r_s = -0.213$	$r_s = -0.354$	$r_s = 0.587$	$r_s = -0.655$	$r_s = -0.145$	$r_s = 0.183$

Note. In instances where “n” – number of compared pairs are not indicated: for 1970-1984 – n=15, 1985-1991 – n=7; “a” and “b” – regressive equation coefficients $Y=ax + b$, where “x” – fish abundance in mill. specimens; “Y” – body weight, kg. *P< 0.05; **P < 0.01.

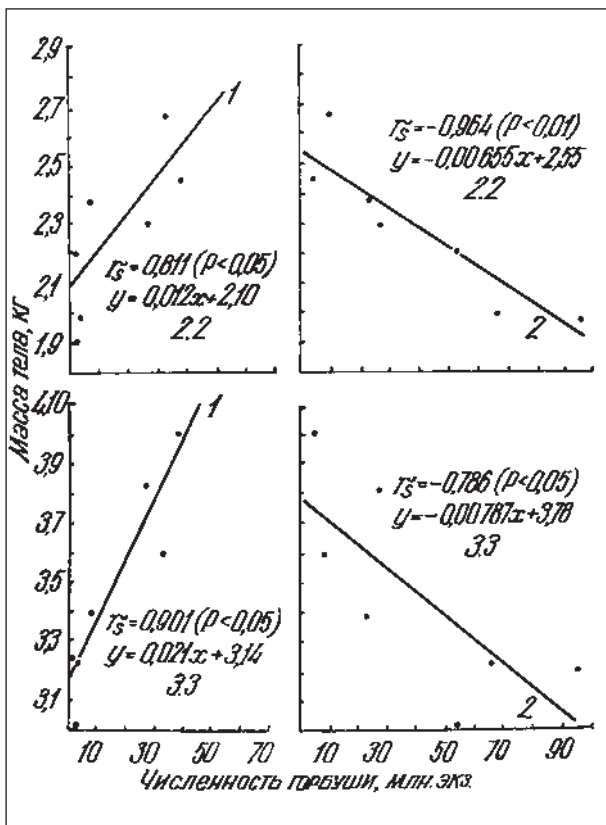


Fig. 113. Dependence of the weight of Ozernaya R. sockeye males of age 2.2 and 3.3 on the abundance of pink salmon in Western and Northeastern Kamchatka during 1985-1991. Y-axis – body weight, kg; X-axis – abundance of pink salmon, mill. specimens. 1 – Western Kamchatka, 2 – Northeastern Kamchatka.

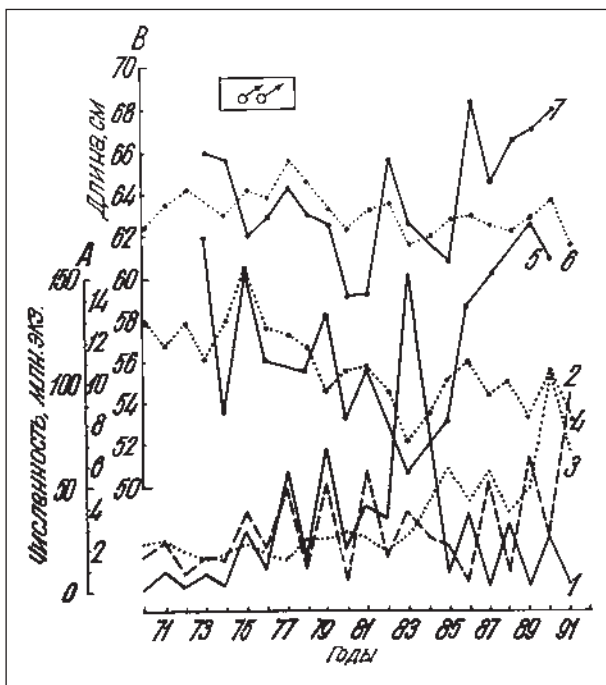


Fig. 114. Interannual variability in the abundance of pink salmon and sockeye, and the body length of male sockeye from some stocks of the western part of the Kamchatka Peninsula. Y-axis – abundance (A), mill. specimens, and body length (B), cm; X-axis – years. 1 – abundance of pink salmon in Western Kamchatka; 2 – abundance of pink salmon in Northeastern Kamchatka; 3 – abundance of Ozernaya R. sockeye; 4 – body length of Ozernaya R. sockeye of age 2.2; 5 – body length of early sockeye of the Bolshaya R. (total age groups combined); 6 – body length of Ozernaya R. sockeye of age 2.3; 7 – body length of late sockeye of the Bolshaya R. (total age groups combined).

the females of the late migration have a larger body size and weight than the early-migrating individuals (tables 34 and 35, Appendix).

The research data on the size of the adult sockeye of the Kamchatka R. are determined to a great extent by the fishing gear that was used to catch the fish (figs. 116 and 117). As we can see from the diagrams, the body length characteristics derived from drift net samples are nearly always greater than from samples taken with trap nets at sea. This is due to the fact that the Ust-Kamchatsk Fish Cannery receives fish caught incidentally in chinook salmon nets which have a much larger mesh size than nets used specifically for catching sockeye. It is impossible to separate the fish caught in chinook nets from those caught in sockeye nets at the fish cannery. It would probably be possible to utilize the combined data from the river drift nets in Kamchatka R. main river bed and from the sea trap nets if the sockeye came strictly from sockeye nets. Proof of this are the data on the chum salmon caught in the Kamchatka R. watershed in August when fishing with chinook nets was no longer being carried on (Nikolayeva, Zavarina, 1991).

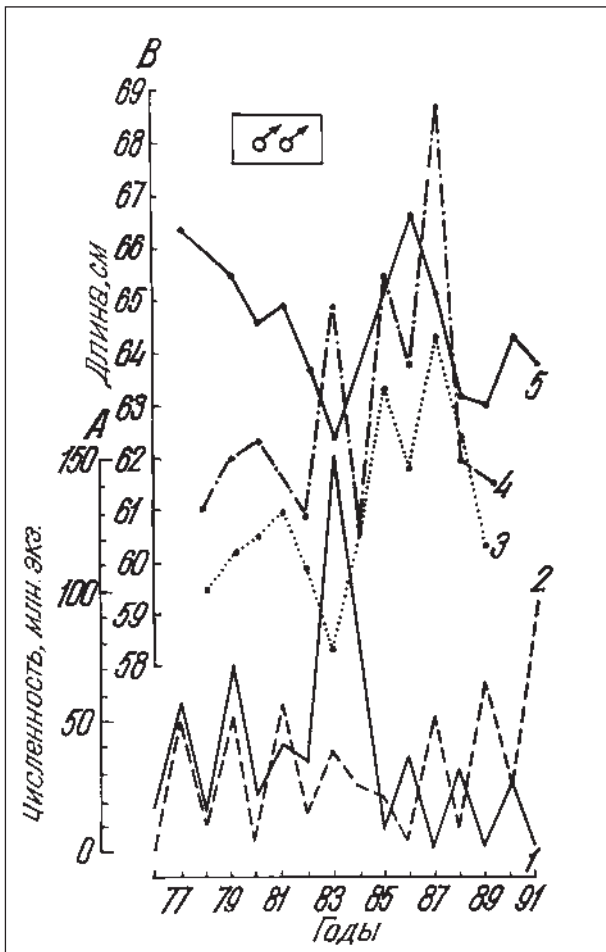


Fig. 115. Interannual variability in the abundance of pink salmon and sockeye, and the body length of male sockeye from some stocks of the eastern part of the Kamchatka Peninsula. **Y-axis – abundance (A), mill. specimens, and body length (B), cm; X-axis – years.**

- 1 – abundance of pink salmon in Western Kamchatka;
- 2 – abundance of pink salmon in Northeastern Kamchatka;
- 3 – body length of early Kamchatka R. sockeye of age 1.3, cm;
- 4 – body length of late Kamchatka R. sockeye of age 1.3, cm;
- 5 – body length of Khailyulya R. sockeye of age 1.3, cm;

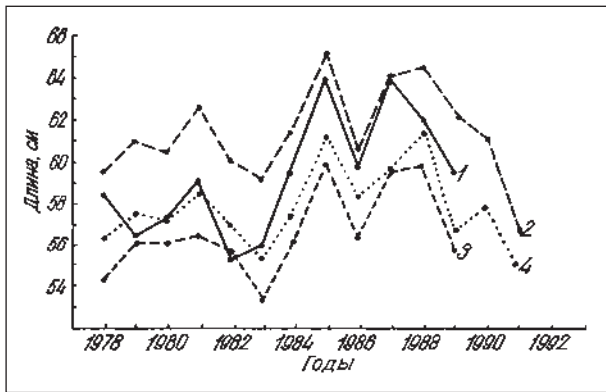


Fig. 116. Average length of mature early-running Kamchatka R. sockeye caught with different types of fishing gear during 1978-1991.

- Y-axis – body length, cm; X-axis – years.**
- 1 – males, marine trap net; 2 – males, river drift nets; 3 – females, marine trap net; 4 – females, river drift nets.



Fig. 117. Average length of mature late-running Kamchatka R. sockeye caught with different types of fishing gear during 1978-1991.

- Y-axis – body length, cm; X-axis – years.**
- 1 – males, marine trap net; 2 – males, river drift nets; 3 – females, marine trap net; 4 – females, river drift nets.

We used biostatistical data from sea trap nets as the standard data for studying the interannual growth variability of the Kamchatka R. sockeye. We do not have any data for 1990-1991 due to the fact that trap nets were not set up at sea because of a low abundance of sockeye from the Kamchatka R.

The data on the size of the Kamchatka R. sockeye prior to 1978 (Simonova, 1978) cannot be correlated to our own data, due to the fact that they were processed by our predecessors without the fishing gear and landing periods taken into account.

The length and weight of individuals from local sockeye groups and stocks of the Kamchatka R. watershed (fig. 2) are given in tables 36 and 37 (Appendix). Analysis of these tables shows that the fish of group "S" have the largest size and weight in the Kamchatka R. watershed.

The length and weight of mature individuals of the early and late seasonal races of the sockeye of the Bolshaya R, and the sockeye of the Khailyulya R. (without subdivision into age groups) are given in tables 38-40 (Appendix).

The average length and weight of fish from the most abundant age groups of the Kamchatka R. sockeye (tables 41-44, Appendix) and a number of other stocks of the Asian sockeye are presented in tables 45-48 (Appendix).

Tables 49-52 (Appendix) present the variation range and average length of spawners from a number of Asian sockeye stocks with the same duration of the freshwater period, but a different duration of the sea period in the life cycle. These data can prove useful in some cases when determining the age of sockeye, particularly the length of the sea period.

10.3. Fecundity and maturity coefficients

Our study of fecundity in the Asian sockeye on the basis of our own data and the literature has shown that the absolute fecundity of the female fish depends primarily on their size (fig. 118, table 85).

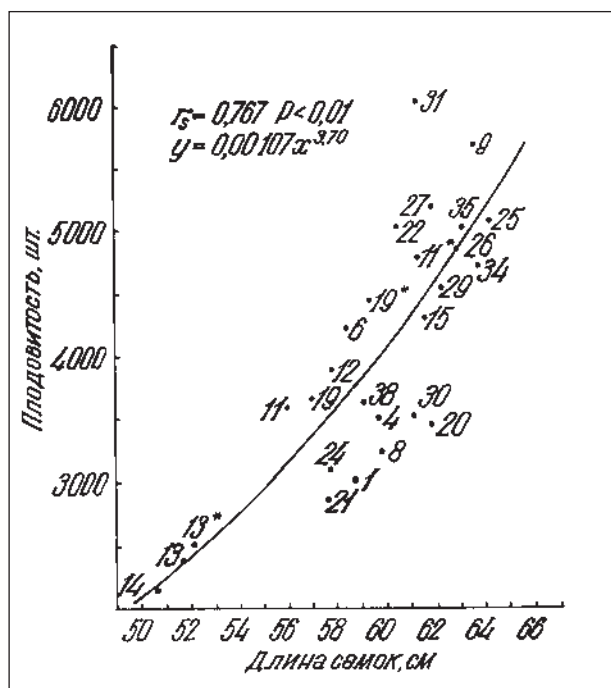


Fig. 118. Length of females and fecundity of the Asian sockeye.
Y-axis – fecundity, no. of eggs; X-axis – body length of females, cm.
Areas marked as in fig. 1.
In the sockeye of stocks 11, 13 and 19, late runners are marked with an asterisk, and early runners are not.

Table 53 (Appendix) presents the absolute fecundity of female individuals from the most frequently encountered age groups in the Asian sockeye, as well as the fecundity for all the age groups in certain stocks of this region (table 54, Appendix).

As indicated above, the size of the Ozernaya R. sockeye appears to be correlated to the abundance of certain stocks of the pink and sockeyes on the Kamchatka Peninsula. In connection with this, we correlated the fecundity of the females of the Ozernaya sockeye (table 86) to the abundance of the Western Kamchatka and Eastern Kamchatka pink salmon, as well as the sockeye of the Ozernaya and Kamchatka rivers for the periods 1970-1984 and 1985-1991 (table 87). As we can see from this table, significant correlations exist in some cases.

The series of observations on the fecundity of the Kamchatka R. sockeye is considerably smaller than for the Ozernaya sockeye; therefore, we cannot yet analyze fecundity in relation to the abundance of the pink and sockeye.

Table 55 (Appendix) gives us an idea of the absolute fecundity of Kamchatka R. female sockeye from trap-net catches of early- and late-migrating individuals at sea, and table 56 (Appendix) shows us the fecundity of these individuals by age groups (data combined for 1978-1989). Table 57 (Appendix) characterizes the interannual variability of female fecundity in the principal age groups of the sockeye, and table 58 (Appendix) that of individual sockeye second order stocks and their groups in the Kamchatka R. watershed.

Table 85. Absolute fecundity of stocks of female Asian sockeye

Watershed	Years	Body length, cm		Fecundity, number		Number of fish	Notes
		Range	Average	Range	Average		
Uega R.(Okhota R. watershed)	1968	–	58.94	1892-3533	3011	53	Nikulin, 1975
Tigil R.	1981	51.0-69.0	59.79 ± 0.93	2025-6318	3514 ± 259	19	Our data
Icha R.	1929	–	58.50	–	4218	–	Pravdin, 1940
Vorovskaya R.	1965	58.5-69.5	64.46 ± 0.32	1344-5647	4277 ± 178	49	Our data
Vorovskaya R.	1989	52.0-64.5	57.82 ± 0.51	1225-6390	2899 ± 193	31	Our data
Vorovskaya R.	1990	50.0-69.0	57.85 ± 0.28	1148-4547	2569 ± 70	102	Our data
Kikhchik R.	1989	57.0-69.0	63.85 ± 0.57	3567-9240	5676 ± 235	27	Our data
Bolshaya R. (early sockeye)	1979-1989	53.5-58.71	56.09 ± 0.53	2963-4534	3602 ± 183	8*	Our data
Bolshaya R. (late sockeye)	1980-1989	57.60-64.63	61.46 ± 0.86	3814-5815	4770 ± 191	9*	Our data
Osernaya R.	1978-1989	56.80-59.50	57.94 ± 0.23	3731-4192	3878 ± 47	12*	See table 86
Dalneye L. (early sockeye)	No	46.0-58.0	51.94 ± 0.09	1100-3750	2360 ± 60	268	Krogius et al., 1987
Dalneye L. (early sockeye)	No	42.0-64.0	52.29 ± 0.05	950-3400	2500 ± 56	500	Krogius et al., 1987
Blizhneye L. (late sockeye)	No	42.0-60.0	50.80 ± 0.06	950-3350	2132 ± 63	300	Krogius et al., 1987
Avacha R.	1988	51.0-63.0	60.00 ± 1.59	2568-5388	4287 ± 400	7	Our data
Avacha R.	1989	55.0-62.0	59.86 ± 1.01	2574-4906	3535 ± 296	7	Our data
Avacha R.	1990	63.0-68.0	65.20 ± 0.86	4147-6419	5079 ± 389	5	Our data
Kamchatka R. (early sockeye)	1978-1989	54.40-59.97	57.09 ± 0.62	3156-4524	3633 ± 124	10*	Our data
Kamchatka R. (late sockeye)	1978-1989	57.19-63.25	59.30 ± 0.68	3711-5350	4422 ± 155	10*	Our data
Stolbovaya R.	1984	57.0-70.0	62.03 ± 0.33	1572-9716	3453 ± 147	62	Our data
Malamvayam R.	1983	52.0-64.0	57.77 ± 0.37	1263-5412	2870 ± 135	41	Our data
Khailyulya R.	1977-1988	60.00-61.78	60.65 ± 0.26	4719-5311	5036 ± 83	7*	Our data
Karaga R.	1988	51.5-61.5	56.20 ± 0.60	2028-5016	3591 ± 180	20	Our data
Karaga R.	1989	52.8-63.0	59.74 ± 0.34	750-5376	2606 ± 180	34	Our data
Tymlat R.	1973	57.0-69.0	64.36 ± 1.27	2420-9710	5092 ± 584	11	Our data
Kichiga R.	1981	56.6-63.0	60.14 ± 0.43	3375-7240	4927 ± 186	22	Our data
Kichiga R.	1989	59.0-71.0	64.00 ± 0.56	2955-5700	4554 ± 130	26	Our data
Kichiga R.	1990	58.0-73.5	66.13 ± 0.45	2947-7743	5107 ± 161	45	Our data
Avyavayam R.	1985	53.6-68.0	62.09 ± 0.52	2910-6885	5195 ± 174	33	Our data
Apuka R.	1980	57.0-66.0	61.96 ± 0.54	2360-4036	3282 ± 121	19	Our data
Apuka R.	1985	56.5-67.0	61.59 ± 0.31	2333-6328	4653 ± 135	52	Our data
Apuka R.	1989	57.0-69.0	62.62 ± 0.30	2430-8481	5212 ± 184	57	Our data
Apuka R.	1990	59.0-70.9	63.53 ± 0.30	2135-8964	5187 ± 196	59	Our data
Ananapylgen R.	1980	54.0-69.0	61.29 ± 0.39	1584-9840	3538 ± 153	73	Our data
Ukalayat R.	1989	55.0-70.0	61.50 ± 0.25	4590-7253	6043 ± 66	82	Our data
Seutakan R.	1976	59.0-72.5	63.92	3214-5300	4750	53	Chereshnev, 1981
Achchen R.	1972	56.0-71.0	63.11	3400-8400	5033	111	Chereshnev, 1981
Urumpet R.	1967	49.0-67.0	58.00 ± 0.41	2035-5076	3635 ± 51	113	Ivankov, 1984
Urumpet R.	1990	57.0-66.0	60.52 ± 0.37	2871-4832	3627 ± 61	48	Our data

*Average value of multi-year data; in the “Range” column are given the parameters of fluctuation of average yearly values; in the “Number of fish” column, number of observations years.

As we analyze the coefficients of maturity in the spawners of the Asian sockeye, we note that this index is highly variable, for it depends on the date and place of the catch. Therefore, a comparative study of the maturity coefficients in individuals from different bodies of water is hardly worthwhile. Nevertheless, the maturity coefficients of individuals caught at approximately the same time and in the same areas (regularly from year to year) may be of some value.

Apart from other factors, the coefficients of maturity also depend on the age of the fish, i.e. individuals with a lower sea age (smaller size) usually have higher coefficients of maturity than those with a higher sea age (larger size). This is clearly illustrated by the maturity coefficients of the sockeye of Kuril L. (table 59, Appendix) and the Kamchatka R. (table 60, Appendix).

Table 61 (Appendix) shows the interannual variability of the mean coefficients of maturity for some stocks of the Asian sockeye without age differentiation, and table 62 (Appendix) shows the same in greater detail for the sockeye of the Kamchatka R.

Table 63 (Appendix) gives the mean coefficients of maturity for individuals of local sockeye second order stocks and their groups of the Kamchatka R., caught in trap nets at sea (based on 1978-1989 data).

Section 11. Population dynamics of local stocks of the Asian sockeye

The highest abundance of the Asian sockeye is noted on the Kamchatka Peninsula where approximately 90-95 % of all the Asian sockeye is caught in some years in the watersheds of the Kamchatka R, and Ozernaya R. (Kuril L.) alone (Levanidov et al., 1970; Lagunov, 1975; Ostroumov, 1975a; Catches of Pacific Salmon..., 1989).

Table 86. Absolute fecundity of female Ozernaya R. sockeye (Selifonov, 1975; M. M. Selifonov, KoTINRO archives), number of eggs

Year	Age								Average
	1.2	1.3	2.2	2.3	2.4	3.2	3.3	3.4	
1970	–	–	3400	3780	–	3320	3500	–	3388
1971	–	–	3600	4000	–	3760	3980	–	4089
1972	–	–	3700	3995	4300	3760	4500	–	3987
1973	–	–	3600	3950	4500	3650	4200	–	3736
1974	–	–	3400	4000	4900	3700	–	–	3864
1975	–	–	3719	3760	–	4160	3810	–	3705
1976	–	–	3860	4440	3700	3890	–	–	3990
1977	–	–	3545	3960	4676	3261	4380	–	3841
1978	–	–	3469	4315	–	3671	4275	–	4020
1979	–	3947	3470	4031	–	3800	4188	4337	3731
1980	–	–	3377	3938	–	3427	5227	–	3741
1981	–	3451	3011	3912	–	3265	3794	–	3700
1982	–	–	3406	4476	4783	3054	4233	–	3984
1983	–	–	3222	4068	–	2893	3997	–	3950
1984	–	–	3147	3877	–	2989	4016	–	3816
1985	–	4012	4084	4277	4146	3731	4244	–	4192
1986	–	–	3668	4167	3666	3352	4474	4572	4050
1987	2862	3335	2990	4125	3277	3069	3321	–	3693
1988	–	4227	3720	3901	2421	4060	–	–	3896
1989	–	–	3205	3911	5026	3027	4102	–	3760
1990	–	3861	3217	3918	4580	3147	3329	–	3656
1991	2748	–	3099	3936	3773	2910	3898	–	3672
Average 1970-1991	2805	3805	3450	4033	4134	3450	4077	4454	3839

Table 87. The significance of rank correlation coefficients in the analysis of the effect of the abundance of adult pink and sockeye on the fecundity of female Ozernaya R. sockeye

Age	1970-1984			
	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye
2.2	$r_s = -0.406$ –	$r_s = -0.132$ –	$r_s = -0.603^*$, a = -0.194, b = 3905	$r_s = -0.610^*$, a = -0.185, b = 3725
2.3	$r_s = 0.089$	$r_s = -0.177$	$r_s = -0.193$	$r_s = -0.120$
3.2.	$r_s = -0.459$ –	$r_s = -0.131$ –	$r_s = -0.266$ –	$r_s = -0.736^*$, a = -0.378, b = 4046
3.3	$r_s = 0.049$, n = 13 –	$r_s = -0.571^*$, n = 13, a = 9.17, b = 4416	$r_s = -0.159$, n = 13 –	$r_s = -0.143$ –
Total age groups	$r_s = -0.121$	$r_s = -0.386$	$r_s = -0.119$	$r_s = -0.175$

Age	1985-1991			
	West Kamchatka pink	North-East Kamchatka pink	Ozernaya R. sockeye	Kamchatka R. sockeye
2.2	$r_s = 0.685$	$r_s = -0.750$	$r_s = -0.286$	$r_s = -0.360$
2.3	$r_s = 0.054$	$r_s = -0.214$	$r_s = 0.250$	$r_s = 0.631$
3.2	$r_s = 0.703$ –	$r_s = 0.893^*$, a = -9.39, b = 3697	$r_s = -0.464$ –	$r_s = 0.523$ –
3.3	$r_s = 0.522$, n = 6	$r_s = -0.543$, n = 6	$r_s = -0.543$, n = 6	$r_s = 0.290$, n = 6
Total age groups	$r_s = 0.342$	$r_s = 0.643$	$r_s = -0.607$	$r_s = 0.775$

Note. In instances where “n” – number of compared pairs are not indicated: for 1970-1984 – n=15, 1985-1991 – n=7; “a” and “b” – regressive equation coefficients $Y=ax + b$, where “x” – fish abundance in million units; “Y” – fecundity, number of eggs. *P < 0.05; **P < 0.01.

Tables 64 and 65 (Appendix) give the Kamchatkan catches of the sockeye for 1957 through 1991 (including the catches of secondary fisheries), and table 66 (Appendix) gives the abundance of adult fish that spawned out in the waters of the Kamchatka Region during the period 1957-1991 (by areas).

Fig. 119 depicts the dynamics of abundance of the Kamchatka R. and Ozernaya sockeye for the period 1957-1991, for which correlative data on the abundance of the sockeye of these rivers are available. Prior to 1957, due to the lack of data on the abundance of spawned out adult individuals in the Kamchatka R. watershed, it did not make as much sense to compare the abundance of the sockeye of these rivers. As we can see from fig. 119, the sockeye of the Ozernaya R. was the most abundant in Asia during this period.

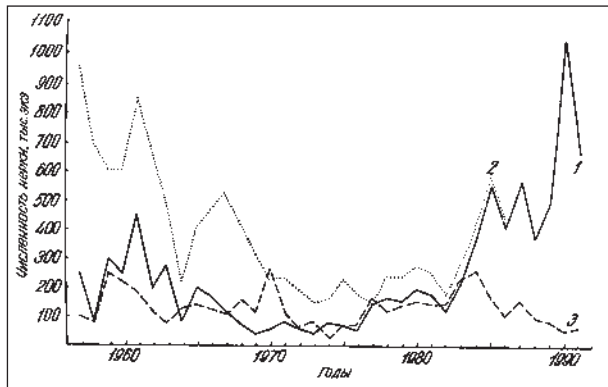


Fig. 119. Abundance of the sockeye of the Ozernaya and Kamchatka rivers in 1957 through 1991. Y-axis – abundance of spawners, thou. specimens; X-axis – years.
 1 – run of the Ozernaya R. sockeye to the mouth of the river (after removals by the Japanese fishery), thou. specimens;
 2 – abundance of the mature part of the sockeye stock of the Ozernaya R. in the ocean, thou. specimens;
 3 – run of the Kamchatka R. sockeye to the mouth of the river (after removals by the Japanese fishery), thou. specimens.

The major stocks of the Asian sockeye have been researched quite well, and are now being monitored (Selifonov, 1986, 1988, 1988a; Bugaev, Ostroumov, 1986; Bugaev, 1987a). The fishery has also shown an interest in the management of small stocks and sub-stocks, which means that it is now time to study their population dynamics. Let us examine the dynamics of sockeye abundance on the Kamchatka Peninsula from the most abundant and best researched stocks to the least abundant and most poorly researched ones.

11.1. Sockeye of the Ozernaya R.

The first conclusions regarding the population dynamics of the Ozernaya sockeye were arrived at by F. V. Krogius and Ye. M. Krokhin (1956, 1956a), after which T. V. Yegorova continued the investigations (Yegorova et al., 1961; Yegorova, 1964, 1966, 1968, 1975).

M. M. Selifonov has spent many years studying the current population dynamics of the Ozernaya sockeye (1975, 1978, 1983, 1986, 1988, 1988; 1982; 1987, 1987a, 1989). Therefore, this section of the book is devoted to reviewing the work of this author.

The stocks of the Ozernaya R. sockeye are evaluated on the basis of three indices, i.e. the high seas fishery, the catches of the home fishery and the spawning migrations of adult fish (Selifonov, 1986, 1988, 1988a).

The Japanese high seas fishery began to develop in 1952, and by 1955-1957 Japanese fishing vessels were already harvesting a maximum 10,000,000-20,000,000 sockeye annually. The sea catches of sockeye dropped in the years that followed, and have continued to decline.

The Ozernaya sockeye stands out in the overall high seas catches of this species by the structure of its scales, which is dependent on its spatial and temporal distribution (Selifonov, 1975).

At the time the Japanese fishery was getting underway, the Ozernaya sockeye stock was in satisfactory condition. In 1957-1958, about 6,000,000-7,000,000 sockeye was being harvested. Later, as the total stock of this species diminished, so did the catches, and by 1972 the take had dropped to 1,351,000 fish (table 88). After 1972, the Japanese side provided limited data on their fishing operations, and therefore the numbers of the Ozernaya sockeye were calculated by analogy with the previous years. Nevertheless, we can say with certainty that about 300,000-500,000 sockeye have been harvested annually over the past years (Selifonov, 1975, 1978, 1982, 1983, 1986, 1987a, 1988, 1988a, 1989).

On the western coast of the Kamchatka Peninsula, the largest salmon catch (from 1909 to 1991) was observed in 1928; it amounted to 306,000 tons, including 39,000 tons of sockeye. In 1929 and 1930, 37,000 tons of sockeye was harvested on the western coast of the peninsula during each of these years. There is no question that up to 20,000-22,000 tons of Ozernaya sockeye was harvested during these years. During the 1930s, the catches decreased approximately 2-fold, the take of the USSR amounting to 2000-4000 tons, and that of Japanese concessions to 6000-7000 tons annually. After the suspension of Japan's concessionary fishing in 1945, the USSR began to harvest from 4000 to 8000 tons annually (table 89). With the organization of Japan's high seas salmon fishery in 1952, the coastal landings of the USSR began to decline in the years that followed, and an excessively high rate of high seas exploitation brought the Ozernaya sockeye population to the point of depression. At the end of the 1960s through the 1970s, the off-shore landings varied from 74 to 997 tons.

The introduction of a 200-mile economic zone in 1977 and a fishery ban on a vast area of the northwestern part of the Pacific Ocean in 1978, as well as the implementation from 1981 of an extensive program for increasing the productivity of

Table 88. Catches of various local sockeye stocks by Japanese vessels (Selifonov, 1995), thou. specimens

Year	Total Japan catch	Ozernaya R.	Other Asian stocks	American stocks	Immature sockeye	Ratio of total catch, %	
						Ozernaya R.	Other Asian stocks
1952	740	740	–	–	–	100.0	–
1953	1600	1600	–	–	–	100.00	–
1954	3748	3200	–	–	–	85.38	–
1955	12164	5700	–	–	–	46.86	–
1956	9634	4000	–	–	–	41.52	–
1957	20096	7100	3433	8411	1152	35.33	17.08
1958	12025	6200	2800	2425	600	51.56	23.28
1959	9125	3080	3015	1300	1730	33.75	33.04
1960	12879	3600	3208	3650	2421	27.95	24.91
1961	12998	4000	2431	5800	767	30.77	18.70
1962	10590	4426	3674	700	1790	41.79	34.69
1963	8909	3529	2371	650	2352	39.54	26.63
1964	7097	1370	2657	650	2420	19.30	37.44
1965	12038	2030	2145	6000	1863	16.86	17.82
1966	7254	2954	2200	700	1400	40.72	30.33
1967	10579	4066	1940	700	3873	38.43	18.34
1968	9161	3386	1665	700	3410	36.96	18.17
1969	8402	2812	661	2000	2929	33.47	7.87
1970	9873	1741	1505	3000	3627	17.63	15.24
1971	6550	1472	1554	600	2994	22.47	23.72
1972	6895	1351	1139	200	4205	19.59	16.52

Kuril L., promoted an increase in the stocks of the Ozernaya sockeye. The off-shore removals increased accordingly, reaching 14.400 tons in 1990 (table 89).

The adult fish that enter the Ozernaya R. to spawn are counted at a weir located 700 m from the outfall of the river. This counting fence is set up at the beginning of July, and dismantled at the beginning of September. Some of the adult fish pass through before the fence is put up (about 10,000-30,000 individuals, depending on the magnitude of the run), and some of the sockeye pass through after it is taken down (from 30,000 to 100,000).

During observations from 1940 to 1991, the number of spawners changed from 260,000 to 6,000,000 individuals (table 89).

After the suspension of Japan's concessionary fishing operations, a sufficient number of adult fish could reach the spawning grounds, and the status of the Ozernaya sockeye population improved. With the development of Japan's high seas fishery, the number of adult fish entering the river to spawn dropped somewhat during the first decade. However, prolonged excessive exploitation of the sockeye in the ocean led to a sudden drop in the sockeye stocks and consequently to a long-term shortage of spawners. The state of depression lasted for nearly 20 years. Only the above-mentioned special measures were able to restore the stock and increase the number of spawners.

In the course of the entire period of observations on the Ozernaya sockeye stock (1940-1991), the numbers of the mature part of the stock varied extensively from a low 1,440,000 individuals to a high 10,583,000 (table 89).

During this period, the Ozernaya sockeye was fished off at different rates. From 1940 to 1944, the removals of the sockeye were quite high due to Japanese concessions operating simultaneously with the home fishery. In the period that followed and up to 1952, only the USSR fished for sockeye. However, whereas only about 33% of the total numbers of the stock was removed at the beginning of this period, 64-75 % was removed at the end of it. Both of these periods are characterized by a high abundance of the sockeye population. As we have mentioned earlier, the Japanese high seas salmon fishery began to develop in 1952, and by 1954 the removals of sockeye already exceeded 90 % of the stock. A period of extreme overexploitation of the Ozernaya sockeye began, with the removals fluctuating from 70 to 90 %. At the beginning of this period, the numbers of the sockeye were still at a high level, but from 1964, a period of depression of the Ozernaya sockeye stock set in. The numbers of the mature part of the population dropped to 1,440,000 individuals in 1977.

This type of situation could not but cause anxiety over the fate of the population, and therefore strict limitations on sockeye fishing at sea were introduced in 1977 and 1978. Furthermore, measures for increasing the productivity of Kuril L. were begun in 1981. As a result of these measures, the numbers of the population were restored. The rate of exploitation was reduced to 33-63 %.

In addition to being exploited by the domestic coastal fishery, the stock of Ozernaya sockeye was highly exploited by the high seas fishery, which affected its numbers significantly. In turn, the changes in abundance then affect the reproductive success of the stock. Because of this, it is necessary to determine the number of spawners in order to maintain the productive resources of the stock at the optimal level under the conditions of the highest possible and sustainable yields. This is extremely important, as fertilization measures to increase the fish productivity and the numbers of the sockeye population have been conducted on Kuril L. since 1981.

Data on the abundance of spawners and offspring of the sockeye for 1940-1976 have been used for this. The method of least squares was used to plot the reproduction curves (Ricker, 1954; Andreyev, 1969).

Table 89. Catch and escapement of *Ozernay R. sockeye* (Selifonov, 1975; M. M. Selifonov, KoTINRO archives)

Year	USSR catch		Escapement, thou. specimens	Adult fish abundance, thou. specimens	Total catch USSR and Japan, %
	Tons	Thou. specimens			
1934	1950	—	—	—	—
1935	337	—	—	—	—
1936	1866	—	—	—	—
1937	2878	—	—	—	—
1938	4144	—	—	—	—
1939	2938	—	—	—	—
1940	1453	680	650	5950	89.08
1941	910	410	500	3940	87.31
1942	1704	580	500	4700	89.36
1943	2989	1390	3200	8170	60.83
1944	3510	1550	850	4120	79.37
1945	2776	2050	4190	6270	33.17
1946	6203	2300	1700	4000	57.50
1947	4032	1600	3200	4800	33.33
1948	4167	2000	750	2750	72.73
1949	7704	3400	4200	7600	44.74
1950	8090	2930	960	3890	75.32
1951	6018	4300	2400	6700	64.18
1952	7497	3650	2350	6740	65.13
1953	4257	2360	1200	5160	76.74
1954	3208	1400	320	4920	93.50
1955	1832	800	500	7000	92.86
1956	3149	1300	1200	6500	81.54
1957	2561	1100	1400	9600	88.54
1958	579	300	500	7000	92.86
1959	2075	900	2100	6080	65.46
1960	2052	900	1550	6050	74.38
1961	5165	2000	2500	8500	70.59
1962	3763	1200	800	6426	87.56
1963	2346	780	500	4809	89.60
1964	594	500	300	2170	86.18
1965	1946	1000	1000	4030	75.19
1966	1456	700	1000	4654	78.51
1967	1070	500	700	5266	86.71
1968	173	100	650	4136	84.28
1969	74	30	370	3212	88.48
1970	468	180	380	2301	83.49
1971	997	330	550	2352	76.62
1972	336	150	450	1951	76.93
1973	393	150	260	1519	83.11
1974	798	340	460	1687	72.73
1975	446	175	530	2344	77.39
1976	365	140	400	1753	77.18
1977	181	660	750	1440	49.92
1978	707	245	1450	2420	40.08
1979	497	220	1350	2415	44.10
1980	1297	500	1500	2773	45.91
1981	1646	550	1250	2540	50.79
1982	1241	457	750	1794	58.19
1983	1336	518	1650	2752	40.04
1984	2687	930	2750	4161	33.91
1985	6261	2130	3420	5881	41.85
1986	4953	1752	2350	4320	46.60
1987	7989	2680	3000	5680	47.18
1988	4637	1650	2050	3700	44.59
1989	6751	2472	2500	4972	49.72
1990	14432	4583	6000	10583	43.31
1991	10809	4179	2500	6679	62.57

The research covers a space of time when the numbers of the mature part and recruitment of the sockeye were at their highest and lowest (the mature part of the population amounted to 9,600,000 individuals in 1957, and 1,500,000 in 1973; the recruitment amounted to 9,300,000 individuals for the 1959 spawning season, and 1,200,000 for 1969). This space of time was subdivided into three periods according to the year-classes. The first period (A1) covered 1940-1948, the second period (A2) 1949-1958), and the third period (A3) 1959-1969. Only a coastal fishery existed during the first period, the number of spawning adults averaged 1,700,000 (from 500,000 to 4,200,000), and the average annual abundance of offspring was at the 5,000,000 level. The second period was characterized by the start of intensive high seas fishing by Japan; the average

abundance of spawning sockeye dropped to 1,500,000 individuals, and the abundance of offspring increased to 6,600,000 individuals. During the third period, intensive high seas fishing continued. In addition to this, the removals of immature fish increased considerably, the number of spawners dropped to one million individuals, and, at the same time, the returns of the sockeye fishery dropped to an average 3,400,000 individuals (Selifonov, 1978a).

The following formulas for plotting reproduction curves were derived for the three periods:

$$(A1) R_1 = 7.283E * e^{-0.3832E};$$

$$(A2) R_2 = 13.51E * e^{-0.6122E};$$

$$(A3) R_3 = 7.359E * e^{-0.6073E},$$

where "R" denotes the abundance of offspring (millions of individuals), and "E" the number of parents (millions of individuals).

Using these formulas, we plotted the reproduction curves (fig. 120), and the characteristic points on these curves (table 90).

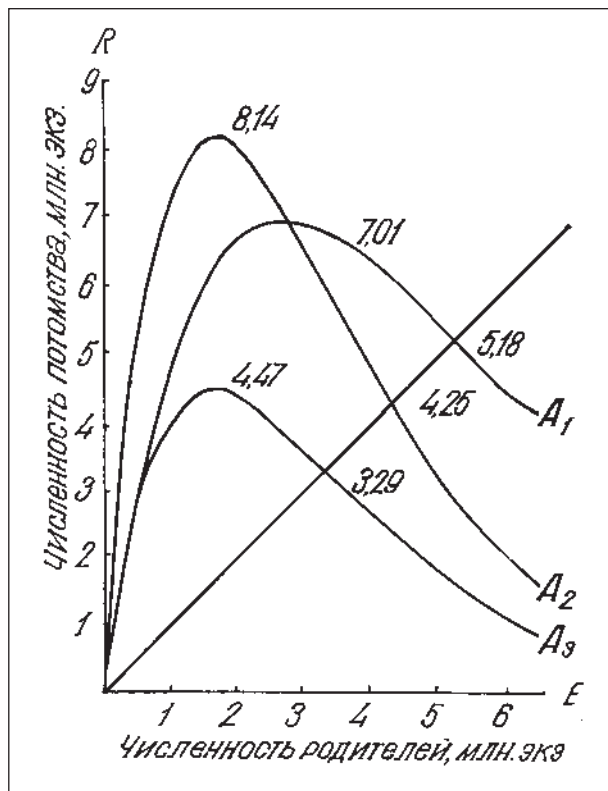


Fig. 120. Reproduction curves of the Ozernaya R. sockeye for the first (A1), second (A2) and third (A3) periods (explained in text) (Selifonov, 1988a). Y-axis – abundance of offspring, mill. specimens; X-axis – abundance of parents, mill. specimens.

For A1, the abundance of spawners was $E_m=7,010,000$ individuals. For A2, the number of spawning sockeye dropped by one million, and the maximum recruitment amounted to 140,000 individuals. For A3, the same number of spawners as in A2 produced a much smaller recruitment (nearly half the size). The third period was characterized not only by a high rate of exploitation, but also by a high percentage (up to 50 %) of removals of immature fish in the ocean, which was not noted for A2. Therefore, an extremely high rate of exploitation and high removals of immature fish were the main causes of the drop in the reproductive success of the Ozernaya sockeye (Selifonov, 1978a).

Table 90. Characteristic points on the production curve for various abundance levels (per period) of Ozernaya R. sockeye (Selifonov, 1988a), mill. specimens

Period	E_r	R_m	E_0	R_0	$R_n = E_n$	Catch ratio, %
A1	2.61	7.01	1.90	4.8	5.18	62.5
A2	1.68	8.14	1.35	6.7 3.1	4.25	76.9
A3	1.65	4.47	1.10		3.25	79.3

Note. R_m – maximum progeny resulting from optimum brood stock E_0 ; $R_n = E_n$ – point of intersection of the production curve with the point of diminishing returns.

During the different periods, the highest possible yields also changed in accordance with the highest recruitments. Naturally, when the removals exceed a certain limit, the abundance of the population and the size of the catches decrease. It has been established that, with optimal occupation of the spawning grounds, not more than 70 % of the mature part of a stock should be removed by the fishery (Ricker, 1963; Zasosov, 1969). Only then can we ensure a steady recruitment and a rational sustainable yield (Menshutkin, Kislyakov, 1968; Ricker, 1969; Selifonov, 1988a).

According to the observations of T. V. Yegorova et al. (1961), 2,500,000-3,500,000 spawners is the optimal number for the reproduction of the Ozernaya sockeye, for the recruitment in this case will amount to 6.000.000-10.000.000 individuals. According to our estimates, the optimal figure suggested by these authors is too high. For instance, the spawning of 2,500,000-4,200,000 (an average of 3,500,000) individuals produces 4,200,000-8,500,000 (an average of 6,700,000) offspring. The highest recruitment of 5.800.000-9.400.000 (an average of 7.800.000) individuals was produced by the spawning of 1,600,000 adult fish.

A. G. Ostroumov (1970), watershed his calculations on the size of the spawning areas in the Ozernaya R. watershed, feels that the spawning of 2,500,000 adult fish will not result in the overcrowding of the spawning grounds. These assumptions were made at the time when the numbers of the sockeye stock were being maintained at a fairly high level. They began to diminish from the beginning of the 1960s. V. V. Menshutkin and Yu. Ya. Kislyakov (1968) came to the conclusion that a stock can lose its commercial value if the number of steady spawners drops below one million individuals.

According to M.M. Selifonov (table 90), the optimal number of spawners lies between 1,350,000 and 1,900,000. This level of escapement of fish to the spawning grounds can ensure a high level of the Ozernaya sockeye stocks and a catch of 4,800,000-6,700,000 fish (12,000-16,000 tons).

We should note that the Ozernaya sockeye stock can be increased by fertilizing Kuril L., which can result in better conditions for the survival of the young during the foraging period. As for the number of spawners, it would not be to the purpose to exceed the suggested optimum, as the success of spawning is restricted by the size of the spawning areas (Selifonov, 1978a).

Proceeding from the data in table 89, one can say that an excessive number of adult fish passed through to the spawning grounds during 1984-1991. If we go by the lower optimal limit (1,350,000 individuals), we can say that an extra 13,400,000 individuals (or 37,000 tons) escaped past the fishery during this period. If we go by the upper optimal limit (1,900,000 individuals), then an additional 9,400,000 sockeye (or 25,000 tons) could have been taken. Therefore, it is recommended that all the fish above the optimal occupation level of the spawning grounds be subjected to removal.

11.2. Sockeye of the Kamchatka R.

The catch statistics for the sockeye of the Kamchatka R. from the beginning of the 20th century and up to the present are presented in fig. 121.

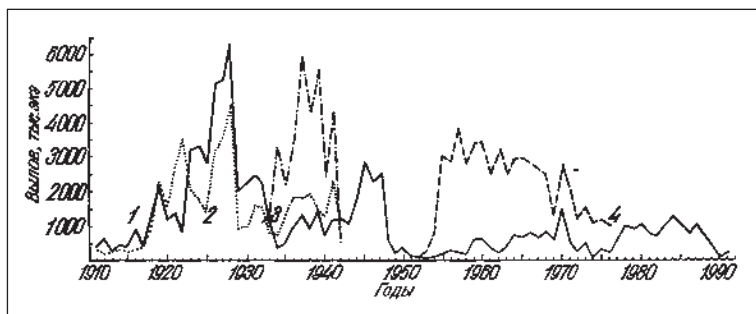


Fig. 121. Commercial exploitation of the Kamchatka R. sockeye. Y-axis – removal, thou. specimens; X-axis – years.

- 1 – removal by the USSR (Russia prior to 1917);
- 2 – offshore removal by Japan (INPFC, 1979);
- 3 – removal by Japan in Kamchatka Gulf (INPFC, 1979);
- 4 – high seas fishing by Japan (Simonova, 1978).

Compared with the sockeye of the Ozernaya R., the dynamics of the sockeye population of the Kamchatka R. has been researched to a much smaller extent, due to the fact that aerial surveys of the abundance of spawned out adult sockeye in the watershed of this river were begun only in 1957 (Ostroumov, 1962, 1964, 1972, 1975a, etc.). Table 91 gives the number of spawned out adult sockeye and the removals of Kamchatka R. sockeye by the USSR (Russia prior to 1917) against the total number of individuals approaching the river estuary.

N. A. Simonova (1978) gave us our first picture of the population dynamics of the Kamchatka R. sockeye. However, a biological study of certain local stocks and groups of the sockeye and more accurate age determination of sockeye from the Kamchatka R. (Bugaev, 1983c) led to the revision of all the research related to this question.

As we have shown earlier (Bugaev, 1983c, 1986a; section 8.1), a series of local second-order stocks and their groups of the sockeye (fig. 2), which have their own specific population dynamics, can be differentiated and identified in the Kamchatka R. watershed (Bugaev, 1983b; Bugaev, Ostroumov, 1986; Bugaev, 1986b; Bugaev, 1987a).

At the present time, it is difficult to study the population dynamics of the year-classes of Kamchatka R. sockeye, due to the lack of estimates on its removal by Japan's high seas fishery.

It is even more difficult to study the abundance of sockeye year-classes at the level of individual local stocks and groups, because we must first estimate their removals by both the Japanese and the USSR fisheries.

Annual estimation of the removal of local stocks and groups of Kamchatka R. sockeye by the USSR fishery was begun in 1978, and is still being carried on (table 92). On the basis of these conclusions, we extrapolated the removal of Kamchatka R. second order stocks and their groups of the sockeye by the Russian fishery in the data for 1957-1977. We do not have any estimates on the removal of individual stocks and groups of the Kamchatka R. sockeye by Japan's high

Table 91. Catch and escapement of Kamchatka *R. sockeye*

Year	USSR catch		Escapement, thou. specimens	Run, thou. specimens	Catch ratio, %
	Tons	Thou. specimens			
1957	559	212	800	1012	20.9
1958	403	153	600	753	20.3
1959	1417	537	2000	2537	21.2
1960	1803	683	1500	2183	31.3
1961	916	347	1500	1847	18.8
1962	479	181	1000	1181	15.3
1963	894	339	450	789	43.0
1964	1905	722	550	1272	56.8
1965	1877	711	725	1436	49.5
1966	2156	817	475	1292	63.2
1967	1938	734	350	1084	67.7
1968	2064	782	800	1582	49.4
1969	1559	591	575	1166	50.7
1970	3810	1443	1225	2668	54.1
1971	1280	485	425	910	53.3
1972	615	233	440	673	34.6
1973	1336	506	350	856	59.1
1974	249	94	130	224	42.0
1975	994	377	335	732	51.5
1976	789	299	435	734	40.7
1977	1678	636	1060	1696	37.5
1978	2617	987	720	1707	57.8
1979	2246	906	515	1421	63.8
1980	2647	1010	560	1570	64.3
1981	2232	836	640	1476	56.6
1982	1792	711	790	1501	47.4
1983	2619	1052	1265	2317	45.4
1984	3401	1260	1361	2621	48.1
1985	2861	1015	741	1756	57.8
1986	2209	764	305	1069	71.5
1987	2948	1092	465	1557	70.1
1988	1785	732	293	1025	71.4
1989	1460	531	361	892	59.5
1990	241	83	511	594	14.0
1991	569	228	398	626	36.4

Note. Catches calculated taking into account sockeye caught by G.P.H. from 1973. Japanese marine catches were not included.

seas fishery.

At the given stage of research, as we examine how the spawning grounds are occupied by adult sockeye, we shall introduce corrections only for Japan's total catch of sockeye, and disregard the corrections for the removals of the Kamchatka R. stock of the sockeye and its integral part at sea (Bugaev, 1987a).

The runs of the sockeye to the mouth of the Kamchatka R. in our early research (Bugaev, Ostroumov, 1986; Bugaev, 1987a) and in this book are estimated against the value of the mean total annual catch of sockeye by Japan's fishery during 1978-1983, which amounted to about 5000 tons over this period of time. In the case where Japan's actual catch during certain years was greater, we increased the data on the run of mature fish to the Kamchatka R. estuary by the corresponding number of times, and vice versa. The possibility of allowing this has been proven by the forecasts of Kamchatka R. sockeye (Bugaev, 1986b; Bugaev, Ostroumov, 1986; Bugaev, 1987a).

The abundance of specific local stocks and groups of the sockeye was estimated by means of the formula (Bugaev, 1987a) $N^* = NC/(1-u)C^*$, where

N^* – denotes the estimated abundance (return) of a stock or group to the mouth of the Kamchatka R. during the year in question (thou. fish);

N – the actual abundance of a stock or group at the spawning grounds according to the data of aerial surveys during the year of observations (thou. fish);

C^* – the average catch of sockeye by Japan's high seas fishery during 1978-1983 (thou. tons);

C – the total catch of sockeye by Japan's high seas fishery during a given spawning year (thou. tons);

u – the percentage of removals from a stock or group by Russian fishermen to the number of sockeye approaching the mouth of the Kamchatka R. during a given year.

When analyzing the returns, we used the following estimated age of sexual maturation: 0.3 for "S"; 1.3 for "E", "V" and "N"; 2.3 for "A" and "D". We did not examine stock "K" in this respect, due to the low numbers of its spawners. The "parent-offspring" relationship depending on the temperature conditions of a particular year has already been examined for the sockeye of the Kamchatka R. watershed. Based on the air temperatures in the study area during the warmest period of the year (June-August), all the years were classified as "warm" (above the long-term average) or "cold" (below the long-term average) (Bugaev, 1983b; Bugaev, 1987a). In the majority of cases, the strongest correlations were noted

Table 92. Catch ratio of second order stocks and their groups of Kamchatka *R. sockeye* by USSR fisheries in 1979-1989 (from total fish entering river mouth), %

Stock, group	1978	1979	1980	1981	1982	1983	1984
“E”	49.0	59.9	63.0	55.0	47.1	45.9	45.2
“A”	73.9	60.1	70.6	59.7	44.6	40.5	52.8
“C”	45.1	63.3	49.9	41.4	29.6	34.8	26.5
“B”	77.8	65.9	45.2	62.2	43.4	61.6	61.0
“D”	54.1	70.3	65.5	52.1	43.5	39.8	50.9
“H”	44.4	36.5	50.1	49.3	17.9	13.3	33.3

Stock, group	1985	1986	1987	1988	1989	Average 1978-1989
“E”	58.0	77.1	77.5	75.6	56.3	59.1
“A”	61.9*	71.4	64.5	80.3	64.3	62.1
“C”	25.8	48.7	56.2	47.3	38.5	42.3
“B”	58.9	59.5	74.8	62.6	64.9	61.4
“D”	33.2	72.8	70.3	71.4	58.2	56.8
“H”	64.9	75.5	62.5	86.1	66.2	50.0

*Taking into account a special fishery at the stream joining Azabach L, and the Kamchatka R. (not including the fishing effort for stock “A” – 41.8 %).

between the numbers of returning adults and the air temperature at Ust-Kamchatsk during the summer the adult fish spawned (beginning of egg incubation), and not during winter egg incubation, alevin and fry development or fingerling growth in summer. Furthermore, the cold years were found to be more beneficial for the local stocks and groups, the young of which, after migrating downstream from the spawning grounds, foraged permanently or for a certain length of time in shallow lakes, side channels or in the brackish Nerpichye L. (“S”, “E”, “N”); the warm years proved to be more favourable for the stocks reproducing in the watershed of the large and deep lakes Azabach and Dvukhyurtochnoye (“A”, “D”). For the local group “V”, the young of which feed and grow in the vicinity of the spawning grounds during the first summer, the incubation temperatures in summer hardly have any effect on the level of reproduction (Bugaev, 1983b; Bugaev, 1987a).

In addition to temperature effects on reproduction, the stock “A” sockeye of Azabach L. may have been affected by fertilization of the lake by volcanic ash resulting from volcanic eruptions (Kurenkov, 1975; Bugaev, 1986b; Bugaev, 1987a).

Over the past few years, due to increased observations, we managed to check some of our earlier correlations (Bugaev, 1986b; Bugaev, Ostroumov, 1986; Bugaev, 1987a). Let us now examine the most important ones.

As we can see from fig. 122, in both cases ($t \leq 0.1^\circ\text{C}$ and $t > 10.1^\circ\text{C}$ – long-term average of the mean temperature of the air in June–August near the town of Ust-Kamchatsk), the abundance of the returning fish of group “E” (fig. 2) during 1962-1985 (brood years 1957-1979) increased in direct proportion to the abundance of parent fish. This points to the fact that the abundance of offspring during these years did not yet reach the level at which the reproductive success begins to diminish. However, from 1980 and up to 1986 (brood years), during which the abundance of spawned out adults (B) was at a low level, the reproductive success of group “E” sockeye dropped significantly (fig. 123) in comparison with the preceding period (A).

We attribute the observed decrease in the reproductive success of group “E” (fig. 123) primarily to the deterioration of competitive interrelations of this group with the sockeye stock reproducing in the Azabach L. watershed (stock “A”), as well as to the change in the species composition of the fish foraging in this watershed where, instead of the sockeye, the freshwater form of the threespine stickleback has begun to predominate (Bugaev, 1988; table 37), and is a serious food competitor of juvenile sockeye (Burgner et al., 1969; Markovtsev, 1972; O’Neil et al., 1987; section 8.5.3).

In the Azabach L. watershed, overcrowding of the spawning grounds by stock “A” sockeye was observed in 1982 through 1985 (Bugaev, 1986b); as a result, the reproductive success of this stock declined drastically (fig. 124, E). At approximately the same time, beginning in 1985 (Bugaev, 1992a), the numbers of the anadromous form of the threespine stickleback dropped sharply in the Kamchatka R. watershed, causing the numbers of the freshwater form to increase (Bugaev, 1988; table 37). The combined effect of these two factors probably led to a significant drop in the abundance of primarily stock “A” individuals (fig. 124) and at the same time affected those of group “E” (fig. 123), the young of which feed and grow in Azabach L. together with the young of stock “A”. This is also corroborated by the simultaneous decrease in the size of the stock “A” and group “E” smolts migrating to the sea from Azabach L. (table 25).

As we can see from fig. 124, in the case where Azabach L, was not fertilized (A), the reproductive success of stock “A” sockeye began to decline significantly at the point where the numbers of spawned out adult fish reached 100,000 individuals, and dropped to a very low level with a further increase in their numbers (E). In the case where the lake was fertilized (fig. 124, B and C), despite the decrease in reproductive success at an abundance level exceeding 100,000 spawners, the reproductive success of stock “A” remained fairly high.

Considering the fact that a negative reliable correlation exists between the rate of return of stock “A” and group “E” individuals during certain (cold) brood years (Bugaev, 1987a), one should take a conservative approach to the increase in

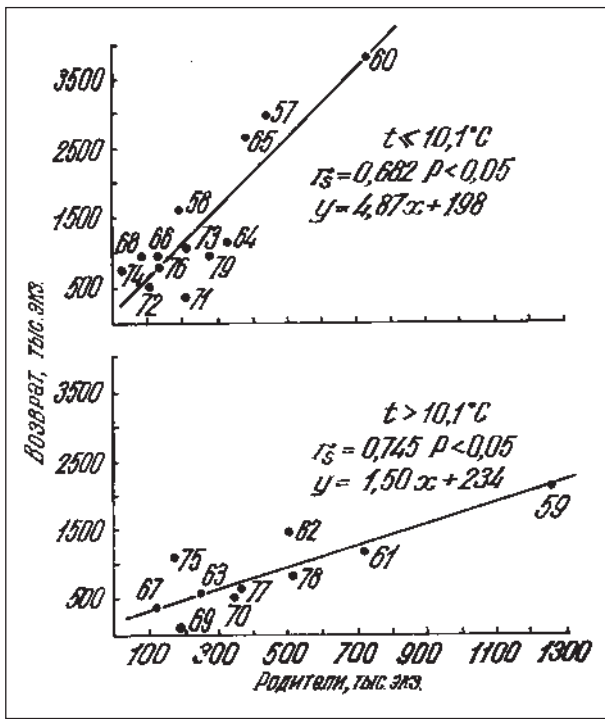


Fig. 122. Abundance of the group "E" sockeye run to the mouth of the Kamchatka R., depending on the abundance of spawned out parents (Bugaev, 1987a, with addenda). Y-axis – return, thou. specimens; X-axis – parents, thou. specimens. Figures near dots denote the year of spawning of the parents.

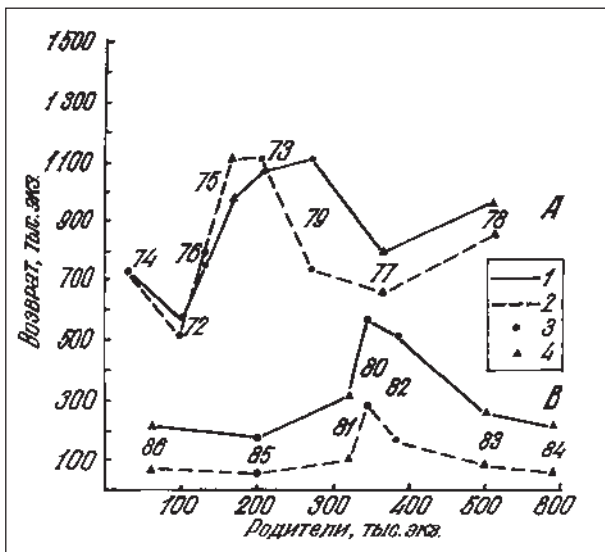


Fig. 123. Abundance of the group "E" sockeye run to the mouth of the Kamchatka R., depending on the abundance of parents spawning in 1972-1986. Y-axis – return, thou. specimens; X-axis – parents, thous. specimens.

A – period of normal reproductive success;
 B – period of low reproductive success;
 1 – actual return of mature fish to the mouth of the Kamchatka R.;
 2 – estimated return of mature fish to the mouth of the Kamchatka R. (with the sockeye removal by the Japanese fishery at sea equal to 5000 tons);
 3 – cold brood years;
 4 – warm brood years.
 Figures near dots denote the year of spawning of the parents.

stock "A" abundance by artificial fertilization of Azabach L., as it can lead to a drop in the reproductive success of the more numerous group "E". At the first stage, we must ensure an annual reduction of this stock's spawners to below 100,000 individuals (preferably even to 40,000-60,000 individuals). Then, having waited for 7-8 year-classes to return in order to get reliable data (based on the results obtained), we can proceed with experiments on artificial fertilization of Azabach L. The optimal escapement level of sockeye spawners to the Azabach L. watershed can be achieved only by specialized fishing in the Azabachye side channel.

We have already shown (Bugaev, 1987a) that, up to the brood year of 1969 (inclusively), there was a highly reliable correlation between the rate of return of stock "A" and the abundance of *Cyclops scutifer* in October ($r=0.935$; $P<0.01$). However, due to the fact that zooplankton sampling was not carried out in Azabach L. during 1970-1980, this type of correlation cannot be considered with the present returns of the sockeye because of the short series of observations carried out. We now have data on the returns of year-classes for which zooplankton abundance data are available only from 1986 and up to the present (a mere 7 years, including the 1992 return).

In connection with this and considering the existence of a correlation between the growth of juvenile sockeye and the abundance of zooplankton (section 8.7.2), we determined the rate of return of stock "A" and group "E" sockeye in relation to the size of the smolts. As we can see from fig. 125, a strong reliable correlation exists between the length of the group "E" sockeye smolts migrating from Azabach L. In the smolts of stock "A", the correlation between the rates of return and the size of the smolts is not statistically reliable as yet.

The available data on the rate of return of group "S" individuals (Bugaev, 1987a; fig. 126) also give grounds for assuming that the eruption of the Bezymyanni volcano in 1956 had a favourable effect on the reproductive level of group "S".

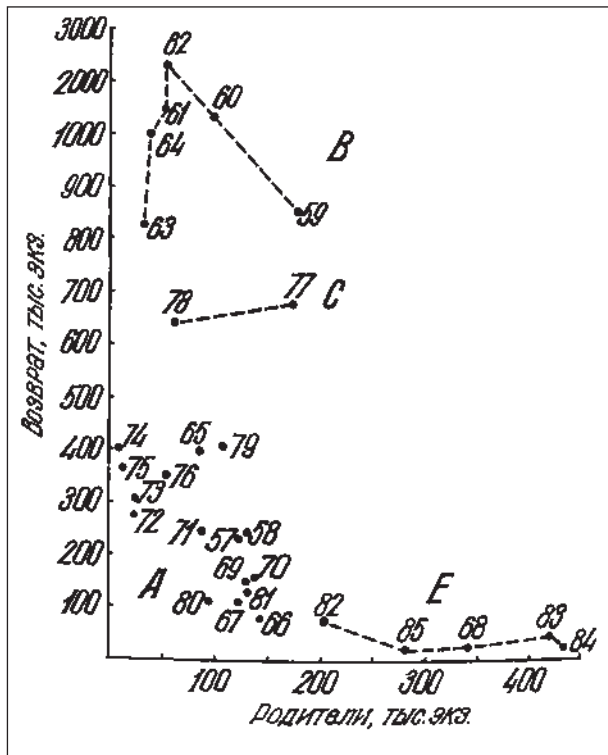


Fig. 124. Abundance of the stock "A" sockeye run to the mouth of the Kamchatka R., depending on the abundance of spawned out parents (after Bugaev, 1986a, with addenda). Y-axis – return, thou. specimens; X-axis – parents, thou. specimens.

A – year-classes foraging after low and normal occupation and slight overcrowding of spawning grounds in the Azabach L. watershed (reproduction not affected by the eruption of volcanos);

B – year-classes in which reproduction was affected by the eruption of the Bezmyannyi volcano in 1956;

C – year-classes in which reproduction was affected by the eruption of the Tolbachik volcano in 1975;

E – year-classes returning after significant overcrowding of spawnings grounds in the Azabach L. watershed.

Figures near dots denote the year of spawning of the parents.

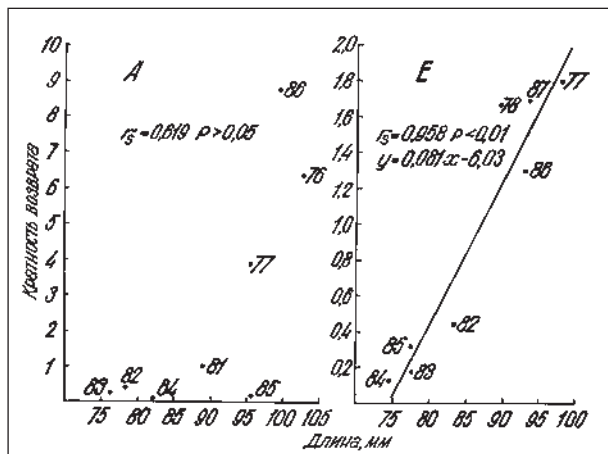


Fig. 125. Rate of returns (abundance of returning individuals/abundance of spawned out individuals) of sockeye spawners of stock "A" and group "E", depending on the length of their smolts. Y-axis – number of returns; X-axis – body length of smolts, mm.

A – stock "A", E – group "E".

Figures near dots denote the year of spawning of the parents.

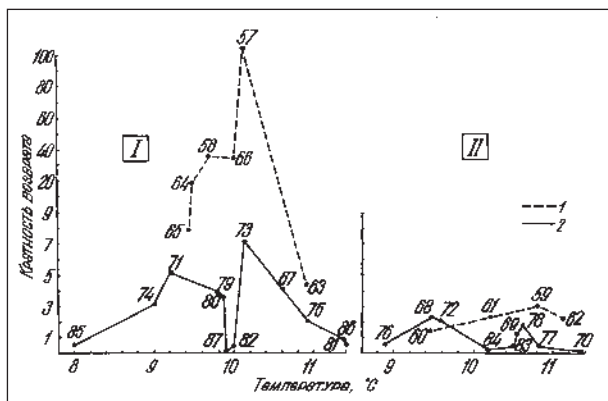


Fig. 126. Rate of returns (abundance of returning individuals/abundance of spawned out individuals) of sockeye spawners of group "S", depending on the mean air temperature in June–August in Ust-Kamchatsk (Bugaev, 1987a, with addenda). Y-axis – number of returns; X-axis – average temperature of the air in June–August in Ust-Kamchatsk, °C.

I – abundance of spawners under 180,000; II – abundance of spawners over 180,000.

1 – year-classes in which reproduction was affected by the eruption of the Bezmyannyi volcano in 1956; 2 – the rest of the year-classes.

Figures near dots denote the year of spawning of the parents.

Considering that extensive ashfalls occurred in the Kamchatka R. valley and particularly in the area of the Kamakovskaya lowland during the eruption of the Bezmyannyi volcano in 1956 (Kurenkov, 1975; Ostroumov, 1984) and that the young of group "S" migrates through this area as underyearlings mainly in June (Bugaev, Karpenko, 1983; Bugaev, 1984) when zooplankton develops in these lakes for a short time (Kurenkov, 1967), the increase in the rate of returns just from the spawning of individuals in the first years after volcanic eruption can be attributed solely to the effect of natural fertilization of the lakes in the Kamakovskaya lowland by volcanic ash. The eruption of the Bezmyannyi volcano had a much smaller effect on the fish of the other stocks and groups migrating downstream to the sea via the lakes of the Kamakovskaya lowland. First of all,

the juveniles of stock "D" and groups "E" and "V" migrate through this area having a larger size (50-120 mm on the average) than the underyearlings of group "S" (average 30 mm). It is a known fact that the smaller the juveniles, the greater the effect of their environment on their survival rate (Nikolsky, 1974a). Secondly, the fish of groups "E" and "V" migrate through the Kamakovskaya lowland area in July–August when the plankton from the floodplain lakes is already being washed out by high water (Kurenkov, 1967).

The question arises, why did the eruption of the Bezmyannyi volcano in 1956 affect the reproduction of group "S", and the eruption of the Tobachik volcano in 1975, which affected the reproductive level of stock "A" (fig. 124), did not (Fig. 126). This might be explained by the following.

The ashfall in the Kamchatka R. valley in 1956 was much more abundant than in 1975, and also the Bezmyannyi volcano is located much closer to the Kamakovskaya lowland as compared with the Tolbachik volcano. An interesting point is that an increase in the numbers of returning group "S" individuals is already evident in the first years following the eruption of the Bezmyannyi volcano (fig. 126), while the increase in stock "A" returns is noted only several years later (Kurenkov, 1975). Considering that eruptions similar to the one in 1956 are very rare and it is still premature to speak of special fertilization of the Kamchatka R. valley, particularly the lakes of the Kamakovskaya lowland, we should base our forecasts of group "S" abundance strictly on the year-classes reproducing years after the eruption (those not affected by natural fertilization).

As we can see from fig. 126, group "S" sockeye manifest a lower level of reproductive success (a low rate of return) at air temperatures of about 10°C. Therefore, the most unfavourable brood years for the sockeye of this group are those with moderate temperatures, in addition to the extremely warm and extremely cold brood years.

Analysis of the population dynamics of stock "D" sockeye has shown that the returns drop after the numbers of adult fish in the Dvukhyrtochnoye L. watershed exceed 20,000. We attribute this to the shortage of breeding areas for sockeye spawners in the watershed of this lake.

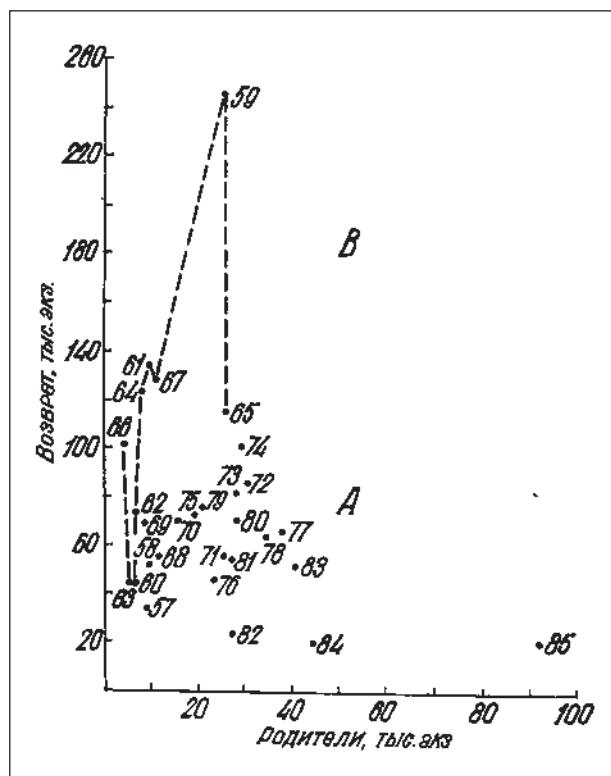


Fig. 127. Abundance of the stock "D" sockeye run to the mouth of the Kamchatka R., depending on the abundance of spawned out parents.

Y-axis – return, thou. specimens; X-axis – parents, thou. specimens.

A – year-classes in which reproduction was not affected by the eruption of volcanos;

B – year-classes in which reproduction was affected by the eruption of the Bezmyannyi volcano in 1956.

Figures near dots denote the year of spawning of the parents.

The population dynamics of secondary sockeye stocks and groups ("V", "N") of the Kamchatka R. watershed, was examined by us earlier (Bugaev, 1987a). There have been no significant specifications made regarding population dynamics since the publication of our last paper in which this was discussed (Bugaev, 1987a). Therefore, the population dynamics of the above-mentioned structural components of the Kamchatka R. sockeye is not being examined at this time.

We currently have only a rough idea of the "optimal" abundance of adult fish for the sockeye of the Kamchatka R. Summing up the concepts on "optimal" and high abundance for the local sockeye stocks and groups of our day. We found that the "optimal" population of spawning grounds for the entire stock of the Kamchatka R. sockeye is equal to 1,400,000 individuals during cold brood years, and 2,025,000 during warm ones (Bugaev, 1987a).

The theoretical return from this number of spawners (without the year-classes affected by the ashfall from the Bezmyannyi and Tolbachik volcanoes) will be 5,600,000 and 3,580,000 individuals respectively. With the "optimal" escapement taken into account, the USSR (Russian since 1992) catch of Kamchatka R. sockeye will be at the level of 4,200,000 and 1,555,000 individuals, or 10,500 and 3,900 tons (average 7.200 tons). This level of removals approximates the long-

term average catch of Kamchatka R. sockeye in 1932 through 1947, which was equal to 6,200 tons (Ostroumov, 1964).

Knowing that the maximum landings of Kamchatka R. sockeye used to reach 20,000 tons, the only conclusion we come to is that the theoretical "optimal" abundance of adult fish is still very far from the actual optimum for the entire sockeye stock of the Kamchatka R. This is due primarily to the fact that, since 1957, the abundance of spawned out adult sockeye has never reached the optimal level for the most numerous "E" group in the Kamchatka R. watershed; it approximated this level to some extent only in some cases. As far as we know, this is also true of the individuals of groups "S" and "V" (Bugaev, 1987a).

Naturally, it will be practically impossible to ensure the optimal abundance of spawners for all the sockeye stocks and groups of the Kamchatka R. watershed simultaneously; therefore, we must strive to accomplish this for at least the main (most numerous) ones. Let us examine the principles by which the abundance of the main local sockeye stocks and groups of this watershed is regulated.

Fishing for Kamchatka R. sockeye by USSR (Russian) fisheries is carried out with trap nets in the Kamchatka Gulf and with drift nets in the Kamchatka R. The 1965-1980 catch statistics for the Kamchatka R. sockeye indicate that an average 46.9 % of the total catch was taken with nets, which proves that efficient fishing with nets can serve as an important factor in the regulation of the abundance of this sockeye stock.

The spawning migration of the Kamchatka R. sockeye occurs from the beginning of June to the end of July. Approximately 80 % of the season's total catch of sockeye is taken in June. The specialized sockeye net fishery (if it is allowed) does not operate the whole month of June because a chinook salmon is likely to be caught with it during this period. By and large, the following is how the sockeye net fishery operates in the Kamchatka R.

At the beginning of the chinook run, large-meshed chinook nets are used to catch Kamchatka R. salmon, and sockeye are taken incidentally at this time. At the peak of the sockeye run to the river, usually on June 10-15th, most fishermen switch to nets with a smaller mesh, and then mostly sockeye are caught. After several days of fishing at the peak of the sockeye run, when 50-60 % of the recommended catch is in, restrictions are placed on the specialized sockeye net fishery (usually from June 21st to 30th) in order to prevent overfishing. Archival data indicate that this procedure was followed from the 1930s-1940s up to 1980. In 1981-1985, the sockeye net fishery was regulated to take the population dynamics of groups "S" and "E" into account. Later, due to the drop in abundance from 1986 to the present (the causes of which are discussed above), the specialized net fishing for the Kamchatka R. sockeye was terminated.

Analysis of the Kamchatka R. sockeye catches in relation to temperature conditions (warm or cold summer) did not reveal any significant difference in the number of fish caught to the total number of sockeye approaching the mouth of the Kamchatka R. However, we have found that the rate of exploitation of the Kamchatka R. sockeye by the domestic fishery depends on the percentage of group "S" individuals. In the case where group "S" sockeye are numerous and constitute more than 26 % of the total number of spawned-out adult fish, the total removal of Kamchatka R. sockeye drops (fig. 105).

Considering that the reproductive success of group "S" individuals is 2.2-3.1 or more times lower than that of group "E" (in year-classes where the reproductive success was not affected much by the eruption of the Bezymyanni volcano in 1956), we feel that it is more efficient to allow a higher escapement of group "E" individuals, than group "S" (Bugaev, 1987a). The necessity of this fishing strategy becomes even greater in view of the fact that the spawning grounds of group "E" sockeye have never been adequately occupied from year to year since 1957.

Mass migration is not characteristic of group "S" individuals, and their entry into the river is more prolonged. Therefore, group "S" sockeye do not "attract" the attention of fishermen, especially as chinook salmon are particularly plentiful at this time. Fishing pressure can be diverted by changing net fishing times in the river. The problem of regulating trap net catches of group "S" sockeye has not been resolved as yet.

As we have shown earlier (Bugaev, 1987a), an average of about 70 % of the season's total catch of sockeye with drift nets is taken from June 10th to 30th, and therefore regulation of net fishing for sockeye of groups "E" and "S" and stock "A" should be carried out during this period. The occurrence of stock "A" individuals in the catches at the beginning of the run (June 1st-10th) is somewhat higher on the average than during the peak (June 10-30th). In view of the low abundance of Kamchatka R. sockeye and the higher numbers of a chinook salmon prior to June 10th, it would not be feasible to conduct specialized fishing for the sockeye prior to its mass migration. During the main run of the Kamchatka R. sockeye (June 10-30th), the proportion of stock "A" individuals is usually lower (Bugaev, 1987a). However, due to the fact that Azabach L. is situated in the commercial fishing zone, the possibility of catching stock "A" sockeye at the mouth of the Azabachye side channel is quite real. Taking this into account, we must consider the whole situation of fishery regulation from the point of view of differentiated removal of strictly group "E" and "S" individuals (Bugaev, 1987a). Fishing pressure can be shifted from group "E" to group "S" by starting the specialized net fishery roughly 2-4 days after the mass migration begins, instead of at the same time. This and a relatively constant level of escapement can bring about an increase in the overall production of the Kamchatka R. sockeye.

Though the losses with the old traditional system of drift net fishing in the Kamchatka R. will probably be lower than with any other system, we cannot at the present time endorse the one existing up to 1980 (inclusively) after having examined the results of the population studies.

Tables 67-72 (Appendix) characterize the frequency of occurrence of sockeye from the local stocks and groups of the Kamchatka R. in drift net catches during the spawning migration.

11.3. Secondary stocks of the sockeye

On the western and eastern coasts of the Kamchatka Peninsula, the sockeye, with the exception of the Ozernaya and Kamchatka R. stocks, is caught incidentally with other species of Pacific salmon. This is due to the fact that the sockeye occupies a special place among the Pacific salmon, for it requires lakes in which its young can feed and grow for 1-3 years. Furthermore, the young of the sockeye require not only large lakes, but also fairly deep ones (over 13-18 m deep) (Kurenkov, 1978), and such lakes are scarce on the Kamchatka Peninsula. Nevertheless, the sockeye catch in the rivers of Western and Eastern Kamchatka combined (excluding the sockeye of the Ozernaya and Kamchatka rivers) can presently yield from several hundred to more than two thousand tons annually with rational exploitation.

The sockeye of secondary Kamchatkan stocks, similar to that of the major Asian and American sockeye stocks is affected by the Japanese high seas fishery. For a number of objective reasons, the Kamchatka Branch of TINRO is still with holding from studying the removal of secondary sockeye stocks at sea. Therefore, we have examined the “parent–offspring” relationship only in the year-classes that have returned to their home rivers to spawn since 1977, when the rate of exploitation by the Japanese high seas fishery was much lower.

In view of the fact that the rate of the Japanese sockeye fishery has been declining from year to year since 1977-1978 (and unsanctioned high seas salmon fishing by Taiwanese and South Korean fishermen increasing at the same time), we are assuming that the fishing pressure on the sockeye stocks at sea have been comparatively stable from 1977 and up to the present (compared with the entire period of Japan’s high seas fishing for Pacific salmon).

Let us examine the population dynamics of the secondary stocks of the Western Kamchatkan sockeye. The overwhelming majority of the sockeye from this area, except for the stocks of the Ozernaya and Palana rivers, mature at age 1.3 (table 78).

Knowing the distribution of the trap nets at sea and the removals of sockeye by secondary procurement agencies (state fisheries) over a number of years in some of the Western Kamchatka rivers, we consider 55 % to be the average standard rate of exploitation for the Bolshaya R. sockeye, and 30 % the rate of exploitation of this species in the rest of the rivers.

The main characteristic of the Western Kamchatkan stocks of the sockeye is that their numbers usually fluctuate in one phase, i.e. the numbers in all the rivers decrease or increase simultaneously. In recent years, the numbers of the Western Kamchatkan sockeye have increased, which, in our opinion, is due to the drop in the numbers of the Western Kamchatkan pink salmon (fig. 108).

Our comparison of the fluctuations in the abundance of the Western Kamchatkan stocks of the sockeye was based on the abundance of the runs of the Ozernaya River sockeye stock to the mouth of this river (table 93, fig. 128). In our opinion, the unidirectional fluctuations in the abundance of most of the Western Kamchatkan sockeye stocks are probably caused by the unidirectional fluctuations in the survival rate of the sockeye at sea, which determine their population dynamics as a whole.

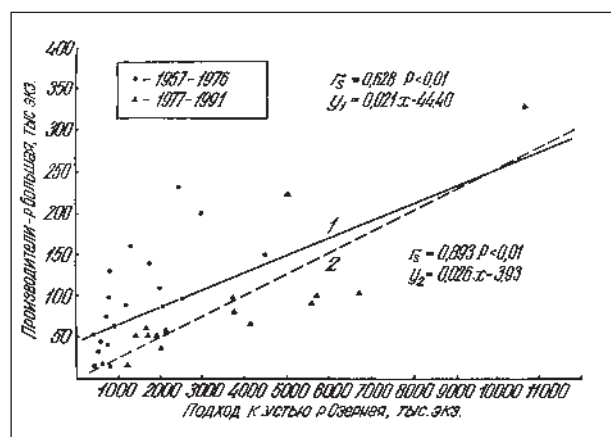


Fig. 128. Correlation between the abundance of the sockeye run to the mouth and the Ozernaya R. and the abundance of adult fish spawning in the Bolshaya R. watershed. Y-axis – abundance of adults spawning in the Bolshaya R., thou. specimens; X-axis – sockeye run to the mouth of the Ozernaya R., thou. specimens.
1 – from 1957 to 1991, 2 – from 1977 to 1991

A study of the “parent–offspring” relationship in the sockeye of individual Western Kamchatka rivers and groups of rivers has not shown that the spawning grounds in any of the areas of this region have ever been overpopulated since 1972 (1977 return). An exception to this is the sockeye of the Bolshaya R., in the watershed of which 329,500 adult fish spawned in 1988, and for which more accurate data will be available in several years time. Analysis of the brood stock figures for 1957-1976 gives no valid indication of excessive escapements (except for the sockeye of the Palana R.).

Fig. 129 characterizes the changes in the abundance of spawned out sockeye in the Bolshaya and Palana rivers in 1970 through 1991; as we can see from this diagram, restriction of the rate of exploitation by the Japanese high seas fishery since 1977-1978 has to some extent improved the escapement levels in general.

In our study of the “parent–offspring” relationship in the sockeye of Northeastern Kamchatka, we found that the overwhelming majority (70-90 %) of the fish from the rivers in this area matured at age 1.3. except for those from the Kultuchnaya R. where they mature at age 2.3 and from the Ananavayam R. where they mature at age 2.3-6.2 (table 78).

As in the case of the Western Kamchatka rivers, we do not as yet have any statistics on the sockeye catch for the individual rivers of Northeastern Kamchatka; only generalized data are available for some areas (Appendix. table 64, 65). In connec-

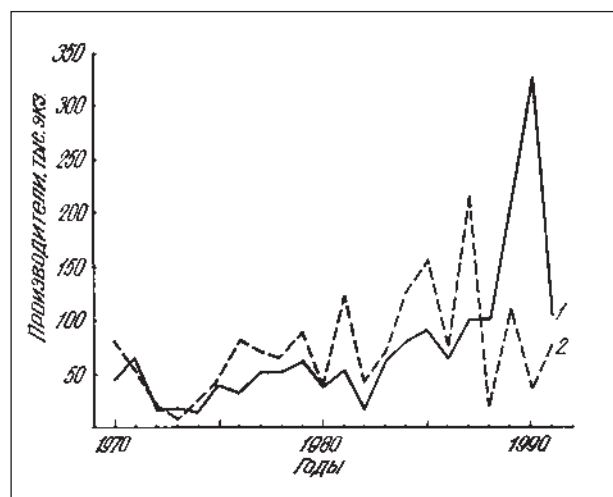


Fig. 129. Abundance of spawned out sockeye in the watersheds of the Bolshaya and Palana rivers in 1970 through 1991. Y-axis – abundance of spawners, thou. specimens; X-axis – years. 1 – Bolshaya R., 2 – Palana R.

Table 93. The significance of rank correlation coefficients in the analysis of sockeye abundance in some West Kamchatka rivers dependin on the abundance of sockeye runs in the mouth of the Ozernaya R. in 1977-1991 (by rivers and catch statistics from commercial fishery enterprises), thou. and specimens

Sockeye abundance	“Red Worker”		“October Revolution”		“October”	“Fisherman”	“Red October”	Lesnovsky G.P.H.
	Ozernaya R.	Udoshk R., Opala R., Golygina R., Koshegochek R., Yavinskaya R.	Bolshaya R.	Kikhchik R., Mukhina R., Khomutina R., Utka R.	Kolpakova R., Vorovskaya R., Udova R., Kekhta R., Kol R., Pymta R.	Saichik R., Icha R., Oblukovina R.	Utkholok R. Belogolovaya R., Moroshechnaya R.	Palana R.
Escapement	$r_s = 0.927$, $P < 0.01$, $n = 15$, $a = 0.482$, $b = 392.27$	$r_s = 0.676$, $P < 0.01$, $n = 15$, $a = 0.000471$, $b = 3.72$	$r_s = 0.893$, $P < 0.01$, $n = 15$, $a = 0.0263$, $b = -3.93$	$r_s = 0.893$, $P < 0.01$, $n = 15$, $a = 0.00402$, $b = 0.91$	$r_s = 0.883$, $P < 0.01$, $n = 15$, $a = 0.000531$, $b = 0.82$	$r_s = 0.794$, $P < 0.01$, $n = 15$, $a = 0.00451$, $b = -0.82$	$r_s = 0.549$, $P < 0.05$, $n = 15$, $a = 0.000437$, $b = 4.26$	$r_s = 0.218$, $P > 0.05$, $n = 15$ – –
Fish cannery catch	$r_s = 0.914$, $P < 0.01$, $n = 15$, $a = 0.518$, $b = -392.27$		$r_s = 0.841$, $P < 0.01$, $n = 15$, $a = 0.0472$, $b = -26.50$		$r_s = 0.591$, $P < 0.05$, $n = 15$, $a = 0.00104$, $b = 2.28$		$r_s = 0.833$, $P < 0.01$, $n = 15$, $a = 0.00253$, $b = 0.68$	$r_s = 0.475$, $P > 0.05$, $n = 15$ – –

Note. All situations covered by 15 observation years. “x” – abundance of Ozernaya R. run, thou. specimens; “Y” – abundance of sockeye on spawning grounds and land cannery catches, thou. specimens.

tion with this, we in some cases determined the abundance of the sockeye for each river on the basis of the rate of exploitation of the pink salmon (the main species caught in this area), as specialized fishing for the sockeye is not carried on in the smaller rivers, and it is usually taken along with the pink and chum salmons. Furthermore, knowing the distribution of the trap nets at sea and the catches of state fisheries over a number of years. we arrived at the following standard rate of exploitation for the sockeye in some of the rivers: 20 % in the Stolbovaya, Lebyazhya, Karaga, Vyvenka and Avyavayam rivers; a rate of exploitation equal to the one for the pink salmon of the Karaginski area (from the Stolbovaya R. to the Anapka R.) in the Ivashka and Dranka rivers; a rate of exploitation equal to the one for the pink salmon of the Olyutorski area (from the Khai-Anapka R. to the Apuka R.) in the Pakhacha and Apuka rivers.

Fig. 130 depicts the changes in the abundance of spawned out adult sockeye and the numbers of their offspring for the Karaginski area (from the Stolbovaya R. to the Anapka R.), and fig. 131 for the Olyutorski area (without the stocks of the Kultuchnaya and Ananapylgen rivers). We feel that the data provided in figs. 130 and 131 are still insufficient for passing judgement on the optimal abundance of the sockeye in these areas.

Figs. 132 and 133 characterize the changes in the numbers of spawners in some rivers and areas of N ortheastern Kamchatka in 1970 through 1991; as we can see from these diagrams, restriction of the rate of exploitation by the Japanese high seas fishery in 1977-1978 had a favourable effect on the escapement.

In other rivers of the Kamchatka Region, the numbers of the sockeye were even lower than in the ones mentioned above, and therefore they were not included in our study.

According to the data available to us, the annual removals of the sockeye in the Sarannaya R. (Bering Is.) at the present time amount to about 70-100 tons.

According to I. A. Chereshev's data (1981), the catch of sockeye in Achchen L. (Eastern Chukotka) at the beginning of the 1960s amounted to an annual 30-50 tons; the maximum catch of 206 tons was taken in 1963. After that, the catches

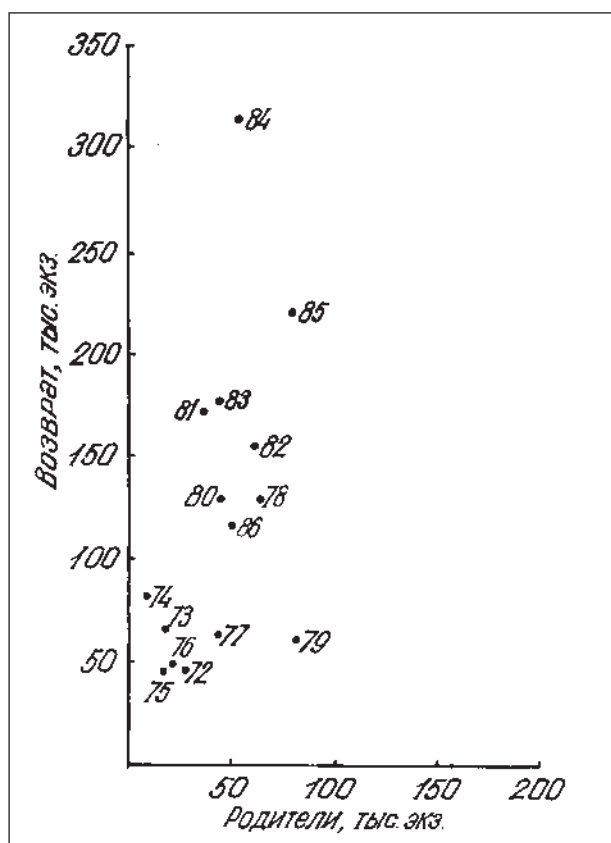


Fig. 130. Correlation between the abundance of adult sockeye spawning in the area from the Stolbovaya R. to the Anapka R. and the magnitude of the sockeye run (return) to the mouths of these rivers in 1977 through 1991. Y-axis – return, thou. specimens; X-axis – parents, thou. specimens.

Figures near dots denote the year of spawning of the parents.

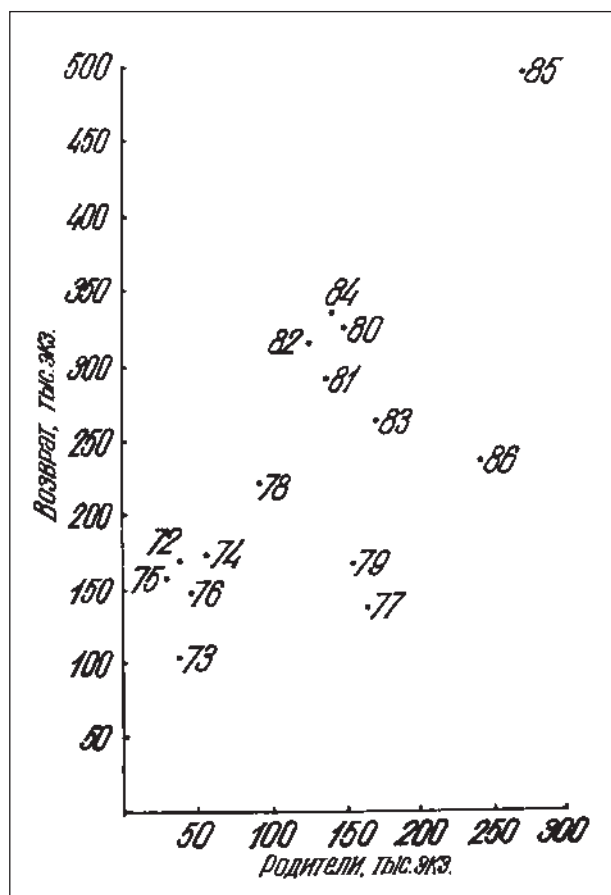


Fig. 131. Correlation between the abundance of sockeye spawning in the area from the Khai-Anapka to the Apuka R. (not including the sockeye of the Kultuchnaya R.) and the magnitude of the combined sockeye run (return) to the mouths of these rivers in 1977 through 1991. Y-axis – return, thou. specimens; X-axis – abundance of parents, thou. specimens.

Figures near dots denote the year of spawning of the parents.

began to diminish, amounting to only 3 tons in 1973. The catch of sockeye in Seutakan L. is usually much smaller than in Achchen L. (Chereshnev, 1981).

We do not have any recent statistically reliable data on the abundance of the sockeye in other parts of Asia apart from those presented above.

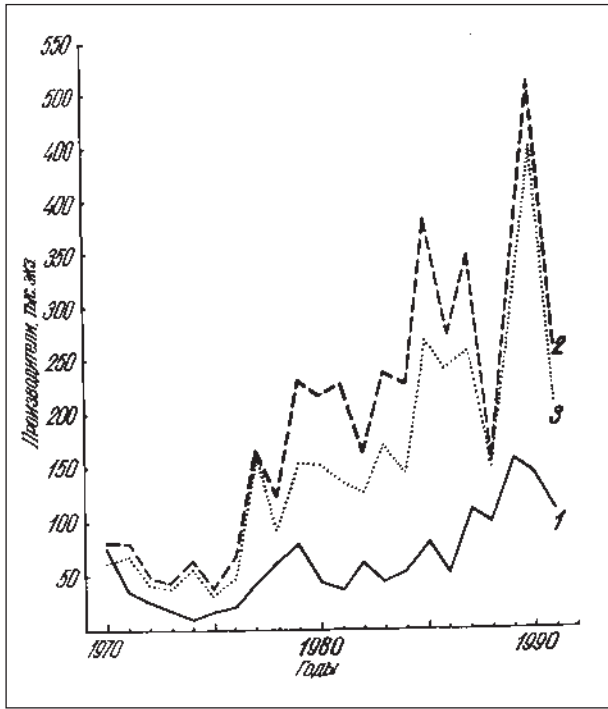


Fig. 132. Abundance of spawned out sockeye in the rivers of North-eastern Kamchatka from the Stolbovaya R. to the Apuka R. in 1970 through 1991. **Y-axis – abundance of spawners, thou. specimens; X-axis – years.**
 1 – area from the Stolbovaya R. to the Anapka R., thou. specimens;
 2 – area from the Khai-Anapka R. to the Apuka R. (including the Kultuchnaya R.), thou. specimens;
 3 – area from the Kahi-Anapka R. to the Apuka R. (without the Kultuchnaya R.), thou. specimens.

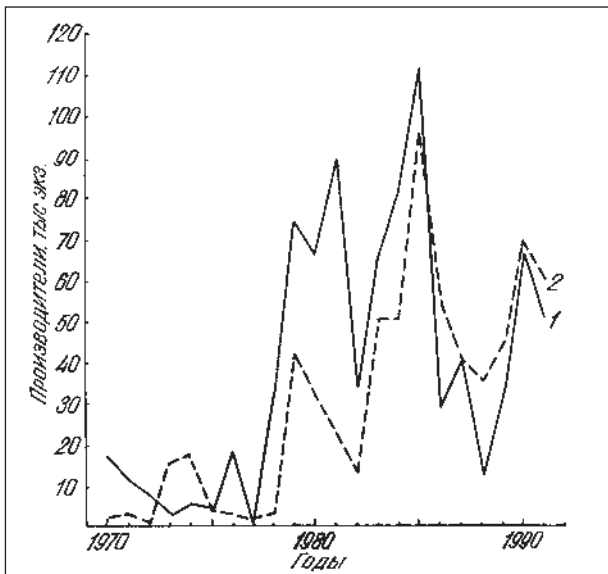


Fig. 133. Abundance of spawned out sockeye in the watersheds of the Kultuchnaya and Ananapylgen rivers in 1970 through 1991. **Y-axis – abundance of spawners, thou. specimens; X-axis – years.**
 1 – Kultuchnaya R., 2 – Ananapylgen R.

Section 12. The prospects of natural and artificial reproduction of the Asian sockeye

As we examine the problems of rational exploitation of fish populations and the prospects of their reproduction, keeping in mind, if only theoretically, the possible negative repercussions of changes in the population structure of the stocks, we must exert every possible effort to prevent situations which would greatly increase the probability of these negative consequences. At first glance, the most efficient way of solving this problem would be to avert or minimize any changes in the population structure of the stocks, but this is possible only if we refrain from exploiting the stocks and turn their habitats into reserves. Any environmental changes and any effect on the abundance of the fish stocks, be they factors reducing them (fishing), or increasing them (fish farming), affect and alter the population structure of the stocks to some extent (Mina, 1986).

Sometimes, the only way out of this situation is to evenly distribute fishing operations according to the populations comprising the stock (Altukhov, 1974; Konovalov, 1980). However, it is practically impossible to implement this type of strategy when exploiting natural populations (Larkin, 1972). At best, the component parts of a stock, which may have a fairly complex population structure, can be used as a “regulatory unit”. We are also faced with the question of whether it makes good sense to strive for the preservation of the population structure and genetic composition characteristic of a given stock under natural conditions unaffected by fishing when fishing operations are being conducted, as we strive to prevent the negative repercus-

sions of changes in the population structure of fish stocks, do we have a right to claim that all changes in population structure lead to negative consequences (Mina, 1986)?

It is important to remember that a fish stock represents a component of the ecosystem, as does each of its constituent populations. In the interests of the fishing industry, a stock should be maintained in a state that would enable it to utilize the resources of the environment to the fullest extent and to preserve its optimum composition from the economical point of view. If any of the populations of the stock disappears as a result of exploitation or the effect of other external factors, but then is replaced in the ecosystem by a new population originating from emigrants of other populations of the same stock, the newly formed population will not be genetically identical to the one existing before it. However, this does not mean that the occurring replacement will inevitably have a detrimental effect on the numbers and reproductive success of the stock as a whole. We cannot even claim that the genetic diversity of the stock will diminish as a result of this replacement. Such replacements of some populations by others, as well as the union and division of populations have occurred in the history of every stock in natural environments unaffected by fishing operations. The high reparative capacity of populations of certain species manifests itself in the process of acclimatization in new areas, when highly abundant new populations emerge from small groups of founder individuals (Mina, 1986).

The closer the system of fish stock exploitation comes to complete fishery management, the more efficient it is. The more effective the measures for improving the abundance and composition of the stocks, the less detrimental the unforeseen changes in their population structure. The negative consequences of these changes can be partially or completely compensated by the creation of conditions favourable, if not for all, then at least for some of the populations that form the stocks (Mina, 1986).

Rational utilization of the local stocks of sockeye (and other species of salmon) lies in the regulation of the escapement and the removals, which is attained by preliminary and efficient forecasts.

A well-managed salmon fishery is based on the strategy of annual optimal stocking of the spawning grounds with fish from controlled local stocks. Optimal stocking can be accomplished if the length, the areas and the methods of the fishing operations are placed under control.

The number of spawners which brings the maximum return is usually regarded as the optimum for the breeding part of the stock. The optimal abundance of spawners is determined on the basis of the historically accurate correlation between the recruitment (usually regarded as the number of new mature spawners) and the abundance of parent spawners. In practice, it is difficult to achieve a good correlation between the components. At first, a series of observations on the abundance of the breeders of the stock must be available (Ricker, 1954; Burgner et al., 1969).

Prompt correction of decisions taken is a particularly important detail of regulated fishing operations. This can help to eliminate the errors made in early forecasts. A high interannual variability in the abundance of migrations is common to the majority of local stocks of the Asian and American sockeye.

The researchers (managers) who regulate the removals and the escapement should point out the trends of practical measures supported by theoretical solutions in order to guarantee the maximum sustainable yield of rationally utilized local sockeye stocks.

First of all, we must determine in each specific case the maximum allowable abundance of spawners for each local stock, and then keep the escapement close to the optimum level. During regulated fishing operations, we must take into account the biological characteristics of the spawners, which may show that the hypothetical abundance of a run or the surmised conditions in a breeding area have to be corrected.

A researcher (manager), fully aware of the difference between theory and practice, should centre his attention mainly on the large-scale commercial fishery which removes the main part of a fish population on its way to the spawning grounds, and even allows for some overfishing if there is even the slightest danger of overpopulation of the breeding grounds. Generally speaking, both the breeding areas and the foraging grounds should be utilized to their fullest capacity. This approach is taken during regulation of the sockeye fishery in North America (Burgner et al., 1969) where this species is highly abundant (Alaska Commercial..., 1989).

The abundance of the anadromous sockeye stocks is, on the whole, directly proportional to the size (area) of the bodies of water inhabited by them and the depth of the euphotic zone which often depends on the overall depth of a particular body of water (Koenings, Burkett, 1987).

According to I. I. Kurenkov (1978), the average depth of lakes should be not less than 13-18 m. due to the fact that the young of the sockeye require a constant supply of zooplankton food throughout the year. In lakes with depths of less than 13-18 m, the abundance of zooplankton varies throughout the year. with the highest levels in summer and lower ones as the temperature drops. Smaller depths intensify these processes (Kurenkov, 1978).

As we examine and discuss the prospects of natural reproduction of the Asian sockeye. we must first proceed from the fact that the reproductive conditions for the sockeye in this region are less favourable than for the sockeye on the Pacific coast of North America where there is a large number of adequately large and deep foraging and spawning lakes, in the watershed of which abundant sockeye populations usually breed.

Taking the above-mentioned prerequisites into account, we can say that there are only two sockeye stocks in Asia, i.e. the Kamchatka R. and the Ozernaya R. stocks which account for most of the sockeye in this region. The high abundance of the Kamchatka R. sockeye can be attributed to the presence of Azabach L. where up to 50-70 % of all the young salmon of this river feed and grow, and the abundance of the Ozernaya R. sockeye to the presence of Kuril L. where practically 100 % of the sockeye of this river forages.

Theoretically, the abundance of the Asian sockeye could be increased by creating a stock of anadromous sockeye in Kronotskoye L. where a population of kokanee (freshwater form of sockeye) breeds at the present time (Krokhin, Kurenkov, 1964; Kurenkov, 1977, 1979). A small part of the young kokanee from Kronotskoye L. migrate downstream to the sea at the age of 2+ (Bugaev, Kurenkov, 1985), as indicated by the data of fig. 134. As we can see from this diagram, the downstream migrants from this lake are clearly distinguished from the Kronotskaya R. sockeye which does not originate in the lake (at least this year-class does not).

Even the creation of fishways through the rapids of the Kronotskaya R. could probably eventually initiate the mass seaward migration of kokanee, turning a part of the freshwater form into an anadromous sockeye. Together with the introduction of fertilized eggs in the lake, or anadromous sockeye spawners via fishways as well, the creation of an anadromous sockeye stock in Kronotskoye L. would increase the numbers of the sockeye on the Kamchatka Peninsula significantly (Krokhin, Kurenkov, 1964; Kurenkov, 1977, 1979).

However, this problem cannot be solved at the present time, even in perspective, due to the fact that Kronotskoye L. and the Kronotskaya R. flowing out of it are situated on the territory of the Kronotsky Reserve which holds the status of a biosphere and where all types of hunting and fish are prohibited (Naumenko et al., 1986).

In our opinion, with the shortage of lakes suitable for the reproduction of the sockeye on the Kamchatka Peninsula and Asia as a whole, this situation is clearly absurd, for it outrightly rejects economic gains. A new sockeye stock in Kronotskoye L. could very well equal that of the Kamchatka R. or the Ozernaya R. in abundance (Krokhin, Kurenkov, 1964; Kurenkov, 1979). There is no question that the kokanee population of Kronotskoye L. would diminish if a stock of anadromous sockeye were formed, but it would not cease to exist. For instance, in many of the lakes on the Pacific coast of North America, kokanee populations coexist with anadromous sockeye populations (Ward, Larkin, 1964; Foerster, 1968; McDonald, Hume, 1984; Burgner, 1991).

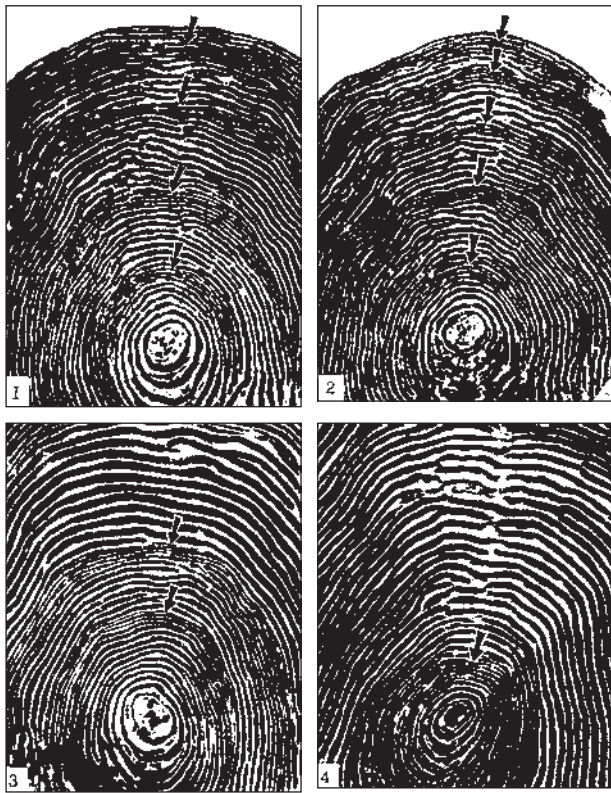


Fig. 134. Structure of the scales in the kokanee and sockeye of the Kronotskaya R. watershed.

1 – kokanee of Kronotskoye L. (Krodakyg), 4 September 1975, AC=260 mm, male, age 4+, arrows mark ZAS (annuli);
 2 – kokanee of Kronotskoye L. (Outlet), 7 September 1975, AC=255 mm, age 5+, arrows mark ZAS (annuli);
 3 – sockeye of the Kronotskaya R. (return from kokanee), 30 July 1990, AC=550 mm, female, age 2.3, arrows mark ZAS (annuli);
 4 – sockeye of the Kronotskaya R., 30 July 1990, AC=620 mm, male, age 1.3, arrow marks ZAS (annulus).

Compared with the sockeye stocks of the Kamchatka and Ozernaya rivers, the abundance of all the other secondary stocks of the Asian sockeye is not very high, but they do include a number of stocks which are now, or may eventually be of some economic importance, basically for local fisheries. We are referring primarily to the Kamchatkan sockeye of the Bolshaya, Palana, Kultuchnaya, Ananapylgen, Paratunka and Listvenichnaya rivers; the groups of rivers in the northeastern part of the Kamchatka Oblast and the Olyutorski area; some rivers on the Sea of Okhotsk coast (Kukhtuy R., Okhota R.), in the Anadyr-Navarin area and on the Chukchi Peninsula (Maynopylgen R., Tumanskaya R., Seutakan R., Achchen R.), as well as on the Commander Isls. and the Kurile Isls. (Sarannaya R. and Urumpet R. respectively).

Rational utilization of the secondary stocks of the Asian sockeye and the estimation of the optimal abundance of spawners in them are prevented primarily by the virtually total absence of catch statistics for these sockeye stocks, which is augmented by the lack of catch statistics from the Japanese high seas fishery (long-term data). The absence of data on Japanese removals also makes it difficult to carry out forecasts for the sockeye of the Kamchatka R., though statistics on the removals of sockeye by the USSR (Russian) fishery are available. The only exception here is the estimation of Ozernaya R. sockeye removals by the Japanese high seas fishery, which was carried out by M. M. Selifonov over a period of many years (Selifonov, 1975, 1988;

Selifonov, 1987a, 1989). It is possible to obtain similar estimates for the sockeye of the Kamchatka R. in the years to come, for the Kamchatka branch of TINRO has received the first scale samples from the Soviet–Japanese Fishery Commission. However, the work involved in differentiating the sockeye of the Kamchatka R. is very extensive, and this prevents us from accomplishing it in the nearest future.

The fertilization of certain lakes will increase the reproductive level of some stocks of the Asian sockeye substantially. The positive effect of fertilization, which coincided with a higher survival rate at sea, was demonstrated for the sock-eye salmon of the Ozernaya R. (Selifonov, 1986, 1988), Azabach L. which is located in the lower reaches of the Kamchatka R. (Kurenkov, 1975; Bugaev, 1986b; Bugaev, 1987a), the Kamchatka R. watershed as a whole (Bugaev, 1987a), and Listvenichnoye L. (Kurenkov, Kurenkov, 1988).

While it is possible to say that the effect of fertilization is more or less positive for the watersheds of rivers where the breeding and foraging of young sockeye are confined to a single lake (lakes Kurilskoye and Listvenichnoye), the results of fertilization appear to be more complex for the sockeye of the Kamchatka R. because of the reciprocal influence of the aboriginal (stock “A”) and transitory (group “E”) young during the foraging period in Azabach L. The increase in the numbers of the stock “A” sockeye during certain years is accompanied by a drop in the numbers of the group “E” sockeye (Bugaev, 1987a).

The problem is intensified by the presence of a population of freshwater threespine stickleback (*leiurus* morph) in the lake, as well as by the migration of the anadromous form of the same species (*trachurus* morph) to the lake to spawn and the migration of young pond smelt to forage (Bugaev, 1988, 1992a), and, as we know (section 8.5.3), these species compete with each other for food.

In connection with this, measures for the fertilization of Azabach L. should be developed cautiously.

Our primary goal in the regulation of Kamchatka R. sockeye numbers and the fertilization of Azabach L. should be the stabilization of the escapement to Azabach L. at 40,000–60,000 sockeye (a drop in reproductive success is observed if the number of spawners exceeds 100,000); this can be achieved only by building a substantial counting fence in the lower part of the Azabachye side channel and fishing out the extra individuals at that point.

Stable reduction of stock “A” sockeye numbers would create better foraging conditions in the lake for the young of group “E”, which would have an overall favourable effect on the total abundance of the Kamchatka R. sockeye, for, based on the long-term data, this group constitutes more than 40 % of all the sockeye of this river.

At the present time, the breeding grounds in the Azabach L. watershed can become overpopulated quite regularly because of a significant drop in the rate of exploitation by the Japanese high seas fishery. The time has come to examine the question of organizing fishing operations in the side channel in case of natural fertilization (by volcanic ash during the eruption of the Klyuchevskaya group of volcanoes), or artificial fertilization of Azabach L.

The current strategy for the regulation of the Ozernaya R. sockeye fishery lies in the interworkings of the latter (trap nets at sea and drift nets in the lower reaches of the river) and the escapement of the optimal number of spawners to the breeding areas of Kuril L. (Selifonov, 1978a). This can also be achieved by installing an effective up-to-date counting fence at the outfall of the Ozernaya R. and controlling the escapement of spawners to the lake (the extra fish should be caught and processed as required in the vicinity of the weir).

It is much more complicated to regulate the escapement of sockeye to the spawning grounds in the Kamchatka R. watershed as compared with the Ozernaya R. watershed. The Kamchatka is a large river, and the sockeye in it are caught together with chinook and chum.

Nevertheless, the removal of Kamchatka R. sockeye can be conducted expeditiously, without upsetting the overall regulatory fishing strategy for other salmons (chinook and chum). In our opinion, the measures for rational exploitation of the Kamchatka R. sockeye should be developed with emphasis placed on optimal reproduction of stock “A” and groups “E” and “S”, which are the most numerous and run at different times in some cases (Bugaev, 1987, 1987a; Bugaev, 1987a; section 11.2).

In the Kamchatka R. watershed, many of the young sockeye migrate downstream as underyearlings (Bugaev, 1983c, 1984, 1991a, 1992). We assumed at one time (Bugaev, 1984a) that the sudden drop in the catches (numbers) of the Kamchatka R. sockeye at the ending of the 1940s (fig. 121) was due to the salinization of Nerpichye L., which is situated in the lower reaches of the Kamchatka R. This lake underwent salinization at the beginning of the 1940s, and it has remained brackish up to the present (Kurenkov, 1967a, 1970).

In our opinion (Bugaev, 1984a), during the periods when Nerpichye L. was a freshwater lake (Kurenkov, 1967a, 1970), significantly more underyearling sockeye (compared with the present) migrated to this lake to feed and grow, for in those days it had a more consistent forage base for the young of the sockeye. As a result, the reproductive success and the catches (numbers) of the Kamchatka R. sockeye were higher (fig. 121). In connection with this, we can say that the desalinization of Nerpichye L. can also help increase the reproductive success of the Kamchatka R. sockeye. One has only to remove the dike separating the old mouth of the Kamchatka R. from the sea (located about several kilometres south of the present one). When the distance from the mouth of the side channel to the sea increases, the effect of the tides will diminish significantly, and Nerpichye L. will again become a freshwater lake (Kurenkov, 1967a, 1970).

The reproductive level of the Kamchatka R. sockeye can also be increased somewhat by improving that of the Dvukhyurtochnoye L. sockeye. Based on a whole set of investigations, we came to the conclusion that there were not enough breeding areas for the sockeye in the watershed of this lake. There is a possibility of setting up incubators here, and from these the young of the sockeye could migrate to the lake to feed and grow.

Touching on the artificial reproduction of the Asian sockeye, we must first of all emphasize that its development, as in the case of natural reproduction, will be limited by the insufficient number of lakes suitable for the feeding and growing of young sockeye.

In our opinion, it is theoretically possible to create small fish-rearing farms like the Big Lake Hatchery in Alaska on small lakes of local commercial importance; the eggs at this hatchery are incubated in an artificial environment, and the underyearlings are released into the lake where they grow until it is time to migrate downstream to the sea (Clupath, Kyle, 1990). In most of the bodies of water where the Asian sockeye is encountered, we must first conduct exploratory surveys to establish whether these lakes have breeding grounds suitable for the spawning of the sockeye. The lakes with insufficient breeding areas can be recommended for further investigation to establish whether they are suitable as foraging grounds for the young of the sockeye, or perhaps as incubator sites.

Surveys have recently been conducted to establish the possibility of creating fish-rearing farms based on populations of downstream-migrant accelerated underyearlings sockeye (Popova, Tolstyak, 1986; Klyashtorin, Smirnov, 1990; Klyashtorin et al., 1990).

We are against the creation of fish-rearing farms which base their production on populations migrating downstream as underyearlings, and release nonaccelerated underyearling sockeye into the sea. In our opinion, the seaward migration of underyearling sockeye in such populations is forced (to some extent), and it is unlikely that fish-rearing farms with this type of biotechnology for rearing sockeye will be consistently efficient. A sad example of this is the now defunct Ushkovsky Fish Hatchery which had operated in the Kamchatka R. watershed for close to 50 years.

We recommend that measures be taken to fertilize small lakes in order to increase the reproductive success of secondary local stocks of the Asian sockeye. On the Kamchatka Peninsula, these questions are now being considered by the Fertilization and Monitoring Laboratory of the Kamchatka branch of TINRO.

Finally, the numbers of the Asian sockeye can be increased by the acclimatization of kokanee (freshwater, or landlocked, sockeye) in certain lakes which are quite suitable as breeding grounds for the sockeye, but where anadromous sockeye and kokanee are not encountered at all for a number of reasons (waterfalls, no drainage). For instance, the kokanee was acclimatized in lakes Karymskoye and Klyuchevoye (the latter located in the caldera of the Ksudach volcano), and in a number of other lakes on the Kamchatka Peninsula by bringing spawners in from Kronotskoye L. In addition to adult kokanee from Kronotskoye L., underyearlings from Karymskoye L., where acclimatization of kokanee was first carried out on the Kamchatka Peninsula, were released into Tolmachevskoye L. (Bolshaya R. watershed). Kamchatkan kokanee were introduced in Nikko L. (Japan) by bringing its eggs in from the populations of lakes Kronotskoye and Karymskoye (Kurenkov, 1985; Iwata et al., 1991), acclimatized kokanee can probably serve a local food and sport fish.

SUMMARY

This book represents a generalization of long-term observations on the Asian sockeye, and is based on the 20-year results of the author's research of the species. The need for this type of generalization became apparent long ago, for researchers often could not obtain the necessary information on the biology of the Asian sockeye due to the complete absence or obsolescence of such data, and often to the incompatibility of the methods used to derive these data.

We have attempted to make maximum use of the oldest archival data available to us, and to interpret them from the positions of our own practical experience in researching the biology and population dynamics of this species. We do not lay claim to exhaustive information on all the aspects of sockeye biology in this book; we limited ourselves mainly to the study of the freshwater period of its life cycle, though we understand perfectly that the biological characteristics of the sockeye are made up of complex cause-and-effect relationships that exist between the freshwater and sea periods of this species' life cycle.

The Asian sockeye is found in greatest abundance on the Kamchatka Peninsula, where approximately 90-95% of all the Asian sockeye is harvested in some years the watersheds of the Kamchatka and Ozernaya rivers.

As a result of our study of the scale structure in the juvenile and adult sockeye, the incidence of its infection by the indicator parasite *Diphyllobothrium* sp., as well as the migrations and growth of juvenile sockeye in the Kamchatka R. watershed, we have come to distinguish the following local second-order stocks and their groups.

1. A group of local second order stocks of the tributaries in the upper and middle reaches of the Kamchatka R., the young of which migrate downstream to the sea as underyearlings ("S").

2. A group of local second order stocks of the tributaries in the upper and middle reaches of the Kamchatka R., the young of which spend their first year in the vicinity of the spawning grounds and migrate seaward the following year ("V").

3. A group of local second order stocks of the tributaries in the lower and to some extent middle reaches of the Kamchatka R., the young of which migrate as underyearlings to forage in Azabach L., and migrate seaward the following year ("E").

4. The local second order stock of Azabach L., the young of which forage together with the young of group "E", and spend mostly two winters in the lake ("A").

5. The local second order stock of Dvukhyurtochnoye L., the young of which spend mostly two years in the lake ("D").

6. The local second order stock of the brackish Nerpichye L, and a group of local stocks from the tributaries of the lower Kamchatka R., the young of which migrate to Nerpichye L. to forage (these structural components are indistinguishable in the catches); the young of the stock and group spend one winter in the lake ("N").

7. The local second order stock of Kursin L., the young of which spend mostly one year in the lake ("K").

All of these stocks and some of the groups have an early (spring) and late (summer) seasonal race of the sockeye ("E", "A", "K", "N", "D"). Some groups are represented by virtually one seasonal race, e.g. group "S" by an early race only, and "V" by a late race; as a whole, they reproduce in the same area. In the case of the sockeye, we regard the seasonal races as structural components of local sub-stocks.

Unlike the sockeye of the Kamchatka R, which spawns and forages throughout the tributaries and certain lakes of the river watershed, the sockeye of the Ozernaya R. reproduces strictly in the Kuril L. watershed. The small Etamynk L. from which the Etamynk R. flows into Kuril L. is the second spawning and foraging ground of the sockeye in the Ozernaya R. watershed, but the abundance of this species in Etamynk L. is very low and can hardly be compared with that of Kuril L. Two seasonal races of the sockeye exist in the Ozernaya R. watershed, but one of them (the early race) constitutes only about 1-2 % of the total numbers, and therefore it was believed that the sockeye of Kuril L. was homogenous in composition and had no seasonal races.

We have discussed the July–November migration of underyearling sockeye from the tributaries of the lower and middle reaches of the Kamchatka R. to Azabach L. (group "E"). The average size of the juveniles migrating in July–beginning of September is slightly smaller than of those migrating later on. In the underyearlings that migrate to the lake, a zone of adjacent sclerites, which is not an annulus, forms on the scales after their migration to the lake watershed. In Azabach L., the overwintered young of group "E" and stock "A" (all age groups) resume their growth virtually at the same time.

In the overwhelming majority of cases, the juvenile sockeye migrate downstream from Azabach L. with two zones of adjacent sclerites (ZAS) on their scales. The young of group "E" migrate downstream from the lake at age 1+ and the young of the Azabach L. stock at age 2+. The yearling smolts of group "E" have two ZAS on their scales (the first a supplementary one, and the second an annulus); the two-year-old smolts of the Azabach L. stock do not usually have supplementary ZAS. A method for identifying fish of the Azabach L. stock and group "E" among the downstream migrants has been developed on

the basis of the definition of the ZAS and, to a smaller extent, the number of sclerites in the existing zones of scale growth, as well as the incidence of infection by plerocercoids of the genus *Diphyllbothrium* and the number of gill rakers.

Unlike Azabach L. where up to 50-70 % of all the juvenile sockeye of the Kamchatka R. feeds and grows, the brackish Nerpichye L. (one of the largest lakes of NE Asia) is not a very important foraging ground for the juvenile sockeye from the tributaries of the Kamchatka R. We believe the instability of the forage base during the salinization of Nerpichye L. to be the cause of the insignificant migration of juvenile sockeye to the lake in comparison with the situation in Azabach L., Nerpichye L. belongs to the shallow lakes where depths of 4-5 m predominate. In freshwater lakes of this type, the forage base for juvenile sockeye fluctuates. Therefore, even during the freshwater periods of Nerpichye L., it probably is not a prime foraging ground for young sockeye of the Kamchatka R. watershed. However, in our opinion, the importance of Nerpichye L. as a foraging ground for juvenile sockeye from the tributaries of the Kamchatka R. increases during the freshening period.

The structure of the scales in smolts (body length) of the aboriginal (stock "A") and transitory (group "E") juvenile sockeye migrating from Azabach L., as well as the central part of the scale in adult sockeye of stock "A", which corresponds to the growth of the young during the freshwater period, undergoes regular changes that depend on the level of the forage base in the lake, the water temperature and the abundance of parent fish.

The central part of the scale in adult sockeye from Kuril L., which corresponds to the growth of the juvenile sockeye during the freshwater period (body length of smolts), changes according to the level of the forage base and water temperature in the lake. The strongest relationship is noted between the number of sclerites on the scales of age 2.2 and 2.3 individuals during the first and second years and the abundance of *Cyclops scutifer* in the lake in August–October. The latter indicates that August–October is the main period of growth for the young of the sockeye here. The relationship between the number of sclerites and the water temperature in the lake is a subordinate one. Analysis of the influence of water temperature on the spacing of the sclerites (with subdivision into years of high and low abundance of juveniles in the lake) has shown high reliable correlations with water temperature at certain depths. The interannual variability in the thermal stratification of the near-surface and abyssal waters of Kuril L. can affect the growth of juvenile sockeye. With the abundance of *Cyclops* in the lake down to a certain level, the young of the sockeye grow better with small temperature gradients, but with an increase of *Cyclops* abundance above this limit, they grow better with higher temperature gradients.

Our study of the food interrelations of the fish foraging in the pelagic zone of Azabach L. now makes it possible to draw certain conclusions regarding the factors that determine the changes in the abundance of some species of fish in the watershed of Azabach L. and the Kamchatka R. We believe that the recently observed increase in the abundance of the freshwater form of the threespine stickleback (*leiurus* morph) in Azabach L. is related to the specialized fishery of the anadromous form (*trachurus* morph) in the lower reaches of the Kamchatka R. during 1979-1984, which was stopped in 1985 due to overexploitation. Prior to overfishing, the migratory form of the threespine stickleback spawned extensively in Azabach L. Underyearlings of the migratory form (*trachurus* morph) migrate from Azabach L. to the sea in masses at the end of August–September. Underyearlings of the two forms of the threespine stickleback have a high degree of food similarity in the lake. We expect that before the specialized *trachurus* fishery got underway (this morph spawns slightly earlier than *leiurus*), the high abundance of underyearling *trachurus* suppressed and limited the numbers of *leiurus* through food competition during the first summer. This created more favourable foraging conditions for the young of the sockeye. A sharp increase in the numbers of *leiurus*, observed by us since 1984 and coinciding with the overcrowding of the spawning grounds in the Azabach L. watershed in 1982-1985, may have been one of the major causes of the decrease in the present numbers of the group "E" sockeye, which, based on the average long-term data, amounted to more than 40 % of the total numbers of the Kamchatka R. sockeye. The increase in the abundance of *leiurus* did not have the same catastrophic effect on the abundance of stock "A" sockeye because the numbers of the latter were greatly limited by the area of the spawning grounds in the Azabach L. watershed. Later, more profound and detailed research into the fish community of this river will be required as recommendations for bioamelioration are developed.

We have also discussed the methods of age determination in the sockeye, as well as methods by which the supplementary ZAS on its scales, which do not reflect the seasonal rhythm of growth of the fish, can be identified. Analysis of the periods of formation of annuli and the periods of scale initiation in young sockeye salmon from the same waters has shown that the young of the year in all the bodies of water studied resume their seasonal growth (the formation of annuli) before their scales begin to appear, or, in rare cases, the resumption of growth and scale initiation take place at the same time in underyearlings. Therefore, if the number of sclerites in the first zone of scale growth is greater than in the second, we can expect to find supplementary ZAS there.

For more accurate age determination, a knowledge of sockeye biology during the freshwater period can be helpful in some cases. Therefore, the most accurate determination of the length of time spent in fresh (brackish) waters by individuals caught at sea is possible only if we know the waters or the type of river or lake in which the fish grew, or at least its origin (Asian or American sockeye). In the sea period of their life cycle, some sockeye may develop supplementary ZAS on their scales during certain years.

We have examined the age structure of mature fish from 38 Asian stocks of the sockeye. Individuals of age 1.3 predominate in the sockeye on the western coast of the Kamchatka Peninsula, except for the sockeye of the Ozernaya and Palana rivers where spawners with two freshwater years of growth predominate (of age 2.2-2.3 and 2.3 respectively). In the sockeye on the eastern coast of the Kamchatka Peninsula, the age structure is more varied as a whole, but individuals of age 1.3 predominate in the river stocks. Most of the Kamchatka R. sockeye from the catches of the USSR (Russia) are of age 1.3, and less commonly 2.3 and 0.3. In the sockeye of the same stocks and groups, we observe differences in the age composition of the fish caught by drift nets in the river and trap nets at sea, as well as differences in the timing of the spawning migration. The age structure of fish from catches differs significantly from the age structure of the reproductive part of the sockeye stock of the Kamchatka R., which is related to the effect of the fishery on its structure. Having determined the ratio of the spawned out

stocks and groups (on the basis of aerial survey data from 1957 to the present) and knowing the age at which most of the fish attain sexual maturity, we derived the age composition of the reproductive part of the stock since 1957. The results of our research have changed the traditional concept of age structure in the sockeye of the Kamchatka R., and are now being used successfully to predict the abundance of its spawning runs. A highly unusual age composition is noted in the individuals from the Ananapylgen R. where we encounter a large number of fish with 4-6 freshwater years of growth. The age structure of the Asian sockeye can be affected by various factors (population abundance, availability of food, type of river or lake, etc.). As a whole, a negative relationship between the average duration of the freshwater and sea periods is noted for the Asian sockeye.

The changes observed in the size characteristics (analysis of weight characteristics unfeasible due to lack of material) of mature sockeye within our study areas (from Iturup Is. to Eastern Chukotka) indicated a correlation with the geographic latitude at which the river estuary inhabited by the sockeye is located.

Our analysis of the interannual variability of the body length and weight of mature male and female individuals of the Ozernaya sockeye in the most abundant age groups (2.1, 2.2, 2.3, 2.4, 3.2 and 3.3) in some cases showed reliable correlations between the abundance of the pink salmon and that of the sockeye during 1970-1991.

After the Western Kamchatkan pink salmon attained an extremely high level of abundance and the spawning grounds became overpopulated in 1983, the abundance of the even- and odd-numbered year-classes of the Western Kamchatkan pink salmon began to change in 1985, and has continued to change up to the present day. As a result, the abundance of the Western Kamchatkan stocks and the pink salmon of Northeastern Kamchatka began to fluctuate in the opposite phase. This taken into consideration we examined the interannual variability of size in the Ozernaya sockeye for two periods. For the period 1970-1984, we noted the highest negative relationships between the body length and weight of the Ozernaya sockeye and the abundance of the Western Kamchatkan pink salmon, and slightly lower values of length and weight dependence on the abundance of Ozernaya and Kamchatka R. sockeye. We did not at any time note any reliable correlations with the abundance of the Eastern Kamchatkan pink salmon, as we examine 1985, a very brief period of observations, we also note reliable correlations in some cases, both with the abundance of Western Kamchatkan pink salmon (positive), and with the abundance of Northeastern Kamchatkan pink salmon (negative). Considering the fact that the sockeye and the pink salmon are food competitors in the sea, we can assume that the change in the abundance of the even- and odd-numbered year-classes of the Western Kamchatkan pink salmon was probably responsible for the change in the food competition of these species of salmon since 1984. These data suggest that the abundance of Western Kamchatkan pink salmon has had some influence on the size of the sockeye from the Bolshaya, Kamchatka and Khailyulya rivers (material on other rivers not discussed). The absolute fecundity of the Asian sockeye depends primarily on the size of the females. The changes in fecundity are also discussed for individuals of age groups.

Analysis of the population dynamics of two major Asian stocks of the sockeye, the Ozernaya R. and Kamchatka R. stocks, has shown that the first is a highly abundant stock at the present time, while the second is at a very low level of abundance.

Over the past few years, the spawning grounds in the Ozernaya R. watershed (Kuril L.) have been continuously overpopulated. The high abundance of this stock is due to a number of factors, namely fertilization, improvement of survival conditions and reduction of the Japanese high seas fishery.

In the Kamchatka R. watershed, because of the differences in the biology of the freshwater period, the known local sockeye stocks and sub-stocks have their own specific dynamics of abundance. The overall dynamics of abundance of the Kamchatka R. sockeye is considered to be the sum of the fluctuations in the abundance of each of its components. In the Azabach L. watershed, we periodically observe the overcrowding of spawning grounds by adult sockeye, which has a detrimental effect on the population dynamics of not only stock "A", but also group "E". This is due to the fact that the individuals of stock "A" and group "E" are food competitors.

The fluctuations in the abundance of sub-stocks of the Asian sockeye on the Kamchatka Peninsula are characterized mainly by the data on the overpopulation of spawning grounds, due to the absence of fishery statistics for individual rivers.

The abundance of the sockeye sub-stocks of Western Kamchatka fluctuates synchronously with that of the Ozernaya R. sockeye, i.e. the abundance of the latter increases concurrently with the abundance of sockeye in the small rivers. Only the sockeye stock of the Palana R. is an exception to this rule.

As we examine the prospects of natural and artificial reproduction of the sockeye in Asia, we must proceed from the fact that these prospects are limited because this region does not have a great number of lakes that would be suitable for the foraging of the young prior to their downstream migration. Fertilization of certain bodies of water and rational utilization of the sockeye stocks are the resources by which the abundance of the Asian sockeye can be increased. The freshening of the brackish waters of Nerpichye L., which is not at all a difficult task, could increase the abundance of sockeye in the Kamchatka R. watershed.

The situation concerning sockeye abundance on the Kamchatka Peninsula could be altered considerably by creating a stock of anadromous sockeye using the Kronotskoye L. stock of kokanee (freshwater form of sockeye) as a base. However, the fact that Kronotskoye L. is located on the territory of the Kronotsky State Biosphere Reserve, where all hunting and fishing activity is prohibited, prevents us from doing so.

In a complex, the Asian sockeye is a component of the ecosystem of the northern part of the Pacific watershed, as is each of the components of its populations. In the interests of the fishing industry, the local stocks of the Asian sockeye should be maintained in such a way as to enable them to utilize the resources of their environment more fully and to preserve the best population structure from the economic point of view. A knowledge of the biological characteristics of the species makes it possible, at least theoretically, to visualize the negative consequences of changes to the population structure of the stocks, and to prevent situations in which the probability of these negative consequences would be particularly high.

APPENDIX

Table 1 (appendix). *Water temperature horizons in Kuril L. in 1957-1990 at the central station, May (data from Ozernovsky observation point of KoTINRO), °C*

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	1.45	1.40	1.40	1.39	1.40	1.40	1.55	2.40
1960	–	–	–	–	–	–	–	–
1961	1.92	1.90	1.91	1.82	1.92	2.00	2.00	2.00
1962	2.50	2.48	2.48	2.48	2.48	2.48	2.48	2.48
1963	–	–	–	–	–	–	–	–
1964	0.72	1.84	1.95	2.12	2.27	2.40	2.68	2.87
1965	3.10	2.90	2.90	2.90	2.90	2.90	2.80	2.80
1966	0.20	0.40	0.50	0.50	0.50	0.70	1.00	1.60
1967	2.30	2.30	2.30	2.40	2.40	2.70	2.90	3.20
1968	2.60	2.60	2.60	2.60	2.60	2.50	2.40	2.40
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–	–
1972	–	–	–	–	–	–	–	–
1973	0.50	0.10	0.30	0.50	0.70	0.80	1.20	1.50
1974	2.70	1.50	1.50	1.50	1.50	1.50	1.50	1.50
1975	2.00	1.00	1.00	1.00	1.10	1.10	1.10	1.10
1976	2.00	0.90	0.90	0.90	0.90	0.90	0.80	0.80
1977	–	–	–	–	–	–	–	–
1978	–	–	–	–	–	–	–	–
1979	0.01	0.10	0.20	0.30	0.50	0.60	1.50	2.10
1980	0.01	0.10	0.20	0.30	0.40	0.50	0.90	1.20
1981	1.70	1.60	1.60	1.60	1.70	1.70	1.80	2.70
1982	2.70	2.40	2.40	2.40	2.40	2.40	2.40	2.40
1983	–	–	–	–	–	–	–	–
1984	2.50	2.80	2.80	2.80	2.80	2.80	2.80	2.80
1985	1.40	1.90	1.90	1.90	1.90	1.90	2.25	2.70
1986	2.30	2.40	2.40	2.40	2.40	2.40	2.40	2.40
1987	–	–	–	–	–	–	–	–
1988	–	–	–	–	–	–	–	–
1989	2.30	2.10	2.10	2.10	2.10	2.10	2.10	2.10
1990	1.90	1.90	1.90	1.90	1.90	1.90	1.90	1.90

Table 2 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, June (data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	3.20	2.60	2.60	2.60	2.60	2.60	2.60	2.60
1960	4.00	3.00	3.21	2.42	3.44	3.45	3.05	3.42
1961	1.95	1.94	1.94	1.93	1.92	1.92	1.92	1.92
1962	3.40	3.20	3.20	3.20	3.10	3.10	3.10	3.10
1963	3.40	3.40	3.40	3.40	3.40	3.40	3.40	3.40
1964	–	–	–	–	–	–	–	–
1965	3.40	3.20	3.30	3.30	3.30	3.30	3.40	3.40
1966	1.40	1.20	1.20	1.20	1.20	1.20	1.30	1.90
1967	3.25	3.20	3.10	3.10	3.10	3.10	3.10	3.10
1968	3.40	3.00	3.00	3.00	3.00	3.00	3.00	3.00
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–	–
1972	1.70	1.70	1.60	1.60	1.60	1.60	1.60	1.60
1973	4.00	1.50	1.50	1.50	1.50	1.50	1.50	1.70
1974	3.20	1.90	1.90	1.90	1.90	1.90	1.80	1.80
1975	3.20	2.10	2.10	2.10	2.10	2.10	2.10	2.10
1976	2.90	1.60	1.60	1.60	1.60	1.60	1.60	1.60
1977	–	–	2.60	2.60	2.60	2.60	2.60	2.60
1978	–	–	–	–	–	–	–	–
1979	2.80	2.80	2.80	2.80	2.80	2.80	2.85	2.90
1980	3.00	2.40	2.40	2.40	2.40	2.40	2.40	2.30
1981	3.50	3.30	3.30	3.30	3.30	3.30	3.30	3.30
1982	3.50	2.90	2.90	2.90	2.90	2.90	2.90	2.90
1983	4.10	3.80	3.80	3.80	3.80	3.80	3.70	3.70
1984	3.70	3.70	3.70	3.60	3.60	3.60	3.60	3.60
1985	2.70	3.10	3.20	3.20	3.20	3.20	3.30	3.20
1986	2.90	3.40	3.40	3.40	3.40	3.30	3.30	3.30
1987	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90
1988	3.40	2.90	2.90	2.90	2.90	3.00	3.00	3.00
1989	3.10	2.70	2.70	2.80	2.80	2.80	2.80	2.80
1990	3.60	3.80	3.60	3.60	3.60	3.60	3.60	3.60

Table 3 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, July (data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	5.91	5.65	5.64	5.64	5.31	5.02	4.80	4.41
1960	3.85	3.72	3.72	3.72	3.72	3.72	3.72	3.72
1961	3.11	3.11	3.11	3.11	3.11	3.11	3.11	3.11
1962	9.41	6.58	5.08	4.90	4.48	4.22	4.05	3.97
1963	6.93	6.40	5.19	4.82	4.53	4.53	4.28	4.08
1964	4.10	4.10	4.00	4.00	3.90	3.90	3.90	3.70
1965	3.90	3.70	3.70	3.70	3.70	3.70	3.70	3.70
1966	3.10	3.30	3.30	3.30	3.30	3.30	3.40	3.40
1967	4.20	4.00	4.00	4.00	4.00	4.00	4.00	3.95
1968	4.60	3.80	3.80	3.80	3.80	3.80	3.80	3.80
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	2.50	2.50	2.50	2.50	2.50	2.50	2.50	2.50
1972	2.30	2.30	2.30	2.30	2.30	2.30	2.30	2.20
1973	3.80	2.70	2.70	2.70	2.70	2.70	2.70	2.70
1974	5.20	3.50	3.40	3.20	3.20	3.20	3.00	2.90
1975	3.80	3.60	3.30	3.20	3.00	2.90	2.90	2.90
1976	3.30	2.10	2.10	2.10	2.10	2.10	2.10	2.10
1977	–	–	3.90	–	–	3.70	3.70	3.60
1978	–	–	2.90	2.90	2.90	2.90	2.90	2.90
1979	3.60	3.60	3.60	3.60	3.60	3.50	3.50	3.50
1980	4.00	3.10	3.10	3.10	3.00	3.00	3.00	3.00
1981	6.90	5.30	5.00	4.80	4.60	4.00	3.90	3.80
1982	6.80	3.90	3.90	3.90	3.90	3.90	3.90	3.90
1983	8.60	6.80	6.00	5.70	4.70	4.50	4.35	4.30
1984	6.10	6.50	6.30	6.00	5.30	5.10	4.85	4.70
1985	3.50	3.80	3.80	3.80	3.80	3.80	3.80	3.90
1986	11.20	10.20	4.80	4.50	4.50	4.40	4.40	4.30
1987	4.60	3.70	3.60	3.60	3.60	3.60	3.70	3.80
1988	4.50	4.80	4.70	4.60	4.60	4.50	4.00	3.80
1989	5.20	4.50	4.00	3.90	3.90	3.80	3.75	3.70
1990	6.40	5.50	4.30	4.20	4.20	4.20	4.00	4.00

Table 4 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, August (data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	9.52	7.10	6.06	5.40	4.52	4.33	4.12	4.00
1960	5.58	4.50	4.49	4.49	4.49	4.20	4.19	4.15
1961	–	–	–	–	–	–	–	–
1962	8.61	8.10	7.89	7.10	6.29	4.75	4.63	3.80
1963	11.67	11.10	9.22	6.45	4.79	4.79	4.38	4.10
1964	7.10	6.70	6.50	6.30	5.90	5.30	4.40	4.10
1965	8.30	7.00	6.50	6.10	5.70	5.20	4.40	4.00
1966	5.00	4.30	4.30	4.30	4.30	4.30	4.20	4.20
1967	9.20	7.90	7.00	6.50	5.50	4.50	4.10	4.00
1968	7.90	7.25	5.70	5.64	5.65	5.15	4.20	3.95
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	5.20	4.80	4.70	4.20	4.00	3.50	2.90	2.80
1972	3.60	3.10	3.10	3.10	3.10	3.10	3.10	2.80
1973	7.40	5.20	4.40	4.00	3.70	3.70	3.30	3.00
1974	–	–	–	–	–	–	–	–
1975	8.20	6.00	5.80	5.70	5.50	5.30	4.10	3.40
1976	4.30	3.30	3.20	3.20	3.10	3.10	2.90	2.90
1977	–	–	–	–	–	–	–	–
1978	–	–	–	–	–	–	–	–
1979	–	–	3.10	3.10	3.10	3.10	3.10	3.10
1980	9.00	7.70	6.90	6.50	5.00	4.40	4.00	3.90
1981	11.90	8.90	7.00	5.70	5.00	4.50	4.40	4.00
1982	8.50	8.20	6.40	5.60	5.50	5.40	4.50	4.30
1983	10.80	9.90	8.80	6.00	4.60	4.30	3.90	3.90
1984	9.80	8.50	8.40	7.00	5.80	5.40	5.00	4.70
1985	5.30	5.30	5.20	5.00	4.90	4.70	4.25	4.30
1986	10.20	9.30	7.20	5.30	5.20	5.00	4.75	4.70
1987	9.00	7.20	6.90	6.40	5.70	4.70	4.15	4.00
1988	8.30	7.70	7.20	7.00	6.20	5.00	4.55	4.00
1989	10.80	9.50	8.50	6.80	5.20	4.80	4.25	3.90
1990	12.00	11.00	10.30	6.50	4.70	4.00	3.55	3.50

Table 5 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, September (data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	8.28	7.20	6.70	5.79	5.32	5.19	4.72	4.34
1958	9.98	7.81	7.50	6.70	5.80	5.80	4.52	4.22
1959	8.52	8.30	7.15	5.80	5.38	4.65	4.20	4.00
1960	6.90	6.58	6.58	6.58	6.55	4.30	4.30	3.90
1961	9.80	8.80	7.84	6.65	4.80	4.15	3.85	3.88
1962	9.17	9.12	8.83	7.23	6.01	5.32	4.45	3.95
1963	10.53	10.48	8.68	6.78	6.25	5.33	4.20	4.19
1964	8.10	7.70	7.70	7.30	7.00	6.30	4.90	4.30
1965	8.60	8.30	8.00	7.80	7.70	7.20	4.50	4.10
1966	6.40	5.50	5.20	4.80	4.70	4.70	4.70	4.50
1967	8.50	8.40	7.90	7.50	6.50	6.30	4.40	4.15
1968	–	–	–	–	–	–	–	–
1969	–	–	–	–	–	–	–	–
1970	9.30	9.30	9.20	9.00	6.90	4.60	3.70	3.20
1971	–	–	–	–	–	–	–	–
1972	6.70	5.70	5.30	4.60	4.30	4.30	4.00	3.70
1973	8.80	7.90	7.90	6.60	5.00	4.80	4.10	4.00
1974	–	–	–	–	–	–	–	–
1975	7.75	7.40	7.20	6.70	6.50	5.90	4.60	3.90
1976	7.40	6.05	6.00	6.00	5.80	4.90	3.55	3.10
1977	9.70	9.30	8.90	8.00	6.60	5.30	3.70	3.30
1978	7.30	7.00	7.00	7.00	6.90	6.90	4.80	4.00
1979	6.60	6.60	6.20	6.00	5.90	5.60	4.00	3.60
1980	10.50	8.60	7.90	7.30	5.60	5.40	4.32	4.02
1981	9.50	8.35	8.10	6.85	5.80	5.45	4.95	4.45
1982	10.00	9.30	8.80	7.80	6.60	6.40	4.65	4.20
1983	12.10	11.20	10.80	8.00	5.20	4.30	3.75	3.70
1984	9.10	9.50	9.50	9.30	7.00	6.20	4.70	4.40
1985	7.00	7.20	6.90	6.20	5.80	5.50	5.20	4.70
1986	11.05	10.25	7.50	5.50	4.70	4.35	4.20	4.15
1987	8.90	8.70	8.70	8.30	7.50	5.50	4.35	4.00
1988	9.20	8.70	8.70	8.50	7.70	5.50	4.50	4.20
1989	11.30	10.70	10.40	7.80	6.70	6.10	4.15	3.80
1990	11.50	10.70	10.60	10.50	9.00	5.00	3.85	3.60

Table 6 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, October
(data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	6.81	6.77	6.78	6.76	6.75	5.54	4.38	4.17
1960	7.40	7.18	7.18	7.15	7.10	6.69	4.85	4.88
1961	7.21	6.81	6.81	6.97	6.76	4.40	4.36	4.34
1962	7.56	7.52	7.50	7.50	7.48	6.23	4.59	4.12
1963	8.29	8.28	8.22	8.07	5.37	5.37	4.82	4.28
1964	6.30	6.00	5.90	5.80	5.70	5.70	5.40	5.00
1965	7.50	7.30	7.30	7.30	7.30	6.60	4.80	4.30
1966	6.80	5.40	5.40	5.30	5.30	5.20	5.00	4.90
1967	7.40	4.40	7.30	7.30	7.20	7.00	5.20	4.50
1968	–	–	–	–	–	–	–	–
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–	–
1972	6.20	5.70	5.60	5.40	4.60	4.00	3.60	3.30
1973	6.70	5.90	5.90	5.80	5.60	5.30	4.00	3.20
1974	–	–	–	–	–	–	–	–
1975	6.60	5.60	5.50	5.50	5.50	5.40	4.90	3.90
1976	5.20	4.00	4.00	4.00	4.00	4.00	4.00	3.90
1977	9.00	8.50	8.20	8.10	7.30	5.00	3.50	3.10
1978	–	–	–	–	–	–	–	–
1979	–	–	4.70	–	–	4.60	4.20	3.60
1980	–	–	–	–	–	–	–	–
1981	7.00	6.20	6.20	6.20	6.20	6.20	5.55	4.80
1982	7.10	7.10	7.10	7.10	7.10	5.50	4.40	4.00
1983	9.00	10.00	9.80	9.70	5.50	4.40	3.80	3.70
1984	9.00	8.80	8.70	8.70	8.70	8.50	6.15	5.20
1985	5.15	6.30	6.30	6.30	6.20	6.00	5.40	5.00
1986	8.60	8.40	8.40	8.00	6.10	4.70	4.15	4.00
1987	7.80	7.50	7.50	7.50	7.50	7.50	4.40	4.00
1988	9.50	9.00	9.00	9.00	7.50	6.00	4.35	4.00
1989	8.50	8.00	8.00	8.00	8.00	7.50	4.25	3.90
1990	8.20	7.50	7.50	7.50	7.50	7.50	3.85	3.50

Table 7 (appendix). Water temperature horizons in Kuril L. in 1957-1990 at the central station, November (data from Ozernovsky observation point of KoTINRO), °C

Year	Horizon, m							
	0	10	20	30	40	50	75	100
1957	–	–	–	–	–	–	–	–
1958	–	–	–	–	–	–	–	–
1959	7.00	6.20	5.50	5.10	4.63	4.37	4.20	4.11
1960	4.28	4.28	4.30	4.30	4.30	4.30	4.30	4.30
1961	4.40	4.40	4.40	4.40	4.40	4.38	4.38	4.38
1962	4.55	4.55	4.55	4.55	4.55	4.55	4.38	4.38
1963	4.71	4.71	4.71	4.71	4.71	4.71	4.71	4.71
1964	–	–	–	–	–	–	–	–
1965	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20
1966	4.60	4.60	4.60	4.60	4.60	4.60	4.50	4.50
1967	4.60	4.60	4.60	4.60	4.60	4.60	4.60	4.50
1968	–	–	–	–	–	–	–	–
1969	–	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–	–
1972	–	–	–	–	–	–	–	–
1973	3.60	2.90	3.00	3.00	3.00	3.00	3.00	3.00
1974	–	–	–	–	–	–	–	–
1975	4.20	3.50	3.50	3.50	3.50	3.50	3.50	3.50
1976	4.00	3.00	3.00	3.00	3.00	3.00	3.00	2.90
1977	–	–	–	–	–	–	–	–
1978	–	–	–	–	–	–	–	–
1979	–	–	–	–	–	–	–	–
1980	3.60	3.30	3.30	3.30	3.30	3.30	3.30	3.20
1981	5.50	5.40	5.40	5.40	5.40	5.40	5.40	5.30
1982	–	–	–	–	–	–	–	–
1983	4.20	4.00	4.00	4.00	4.00	4.00	4.00	4.00
1984	4.20	5.30	5.30	5.30	5.30	5.30	5.30	5.30
1985	4.20	4.90	4.90	4.90	4.90	4.90	4.90	4.90
1986	4.20	4.40	4.40	4.40	4.50	4.50	4.50	4.50
1987	4.80	4.70	4.70	4.70	4.70	4.70	4.70	4.70
1988	5.50	5.10	5.10	5.10	5.10	5.10	5.10	5.10
1989	4.80	4.50	4.50	4.50	4.50	4.50	4.50	4.50
1990	5.50	5.00	5.00	5.00	5.00	5.00	4.85	4.50

Table 8 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No.5, June (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	10.77	8.57	7.73	7.43	7.30	6.83
1982	5.90	5.03	4.40	4.40	4.33	4.07
1983	5.60	4.30	4.15	4.05	3.95	3.80
1984	6.80	4.85	4.40	4.25	4.20	4.15
1985	5.00	4.70	4.60	4.60	4.50	4.50
1986	8.05	6.90	5.85	5.05	4.95	4.35
1987	4.50	4.35	4.00	4.10	4.10	4.00
1988	9.10	6.60	5.15	4.60	4.30	4.10
1989	7.65	5.85	5.25	4.85	4.25	3.85
1990	8.70	6.20	5.63	5.37	5.10	4.60
1991	3.90	3.80	3.80	3.70	3.70	3.10

Table 9 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No.5, July (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	19.17	14.50	10.70	9.50	8.77	8.30
1982	15.07	10.63	7.20	6.07	5.50	4.63
1983	12.83	8.43	6.37	5.40	4.97	4.53
1984	12.97	9.50	5.40	5.00	4.80	4.57
1985	12.17	8.93	7.73	6.10	5.13	4.70
1986	15.37	13.33	8.83	6.57	5.90	4.77
1987	13.80	10.50	8.43	6.10	5.07	4.33
1988	14.07	12.83	9.33	6.23	4.57	4.23
1989	16.07	14.67	10.83	7.90	6.23	4.67
1990	16.23	15.33	10.67	7.90	6.93	5.47
1991	8.73	7.83	7.33	6.63	6.10	4.77

Table 10 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No.5, August (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	16.63	14.60	12.23	11.37	10.67	9.60
1982	14.53	13.63	10.03	6.77	6.20	5.37
1983	16.70	13.97	10.40	7.57	6.50	5.57
1984	15.13	14.63	6.70	5.80	5.60	5.23
1985	15.70	13.87	10.33	7.97	6.37	5.23
1986	17.77	13.83	9.37	6.97	5.97	5.30
1987	13.83	13.30	11.23	6.97	5.00	4.27
1988	14.60	14.60	12.33	8.97	5.53	4.37
1989	16.80	15.83	11.63	7.37	6.10	4.87
1990	14.73	14.03	12.87	10.27	7.60	6.10
1991	16.40	15.17	12.00	9.93	8.30	5.63

Table 11 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No. 5, September (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	12.33	11.70	11.10	10.47	9.93	9.17
1982	11.67	11.47	10.97	8.93	7.33	6.43
1983	12.53	12.50	11.93	10.30	8.27	6.87
1984	11.07	11.03	9.07	8.10	7.47	6.33
1985	11.17	12.60	11.30	8.03	6.83	5.23
1986	14.70	13.23	9.87	7.33	6.20	5.23
1987	11.43	11.27	10.97	7.63	6.67	5.60
1988	11.40	11.33	11.17	10.57	6.77	5.13
1989	13.73	13.53	11.16	8.77	5.60	4.67
1990	11.60	11.57	11.27	9.97	8.20	7.53
1991	12.87	12.20	11.40	9.63	7.07	5.20

Table 12 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No. 5, October (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	8.23	8.03	7.80	7.53	7.40	7.30
1982	7.80	8.00	7.90	7.80	7.40	7.00
1983	8.20	8.20	8.20	8.27	7.87	7.20
1984	7.90	7.90	7.83	7.63	7.23	6.60
1985	7.30	7.60	7.67	7.13	6.47	4.57
1986	10.17	10.30	8.87	7.43	6.60	5.07
1987	7.17	7.27	7.53	7.40	7.10	6.87
1988	8.90	8.80	8.83	8.77	8.10	5.60
1989	7.90	7.50	7.80	7.30	5.00	4.20
1990	7.07	7.03	7.03	7.07	7.07	7.13
1991	7.83	7.80	7.77	7.60	7.50	5.60

Table 13 (appendix). Water temperature horizons in Azabach L. in 1981-1991 at station No. 5, November (data from Azabachinsky observation point of KoTINRO), °C

Year	Horizon, m					
	0	5	10	15	20	30
1981	4.50	4.47	4.40	4.37	4.33	4.33
1982	2.85	2.95	2.95	3.00	3.10	3.15
1983	4.85	4.85	4.85	5.05	5.15	5.15
1984	4.80	4.75	4.80	4.75	4.70	4.55
1985	4.15	4.20	4.15	4.15	4.60	3.75
1986	4.90	4.95	4.90	4.90	4.70	4.10
1987	4.25	4.25	4.35	4.35	4.50	4.50
1988	4.40	4.45	4.45	4.50	4.50	4.85
1989	3.90	3.90	4.00	4.00	4.10	4.10
1990	3.80	3.90	3.90	4.00	4.00	4.05
1991	3.85	3.88	4.05	4.12	4.10	4.12

Table 14 (appendix). Total number of copepodite stages I to VI *Cyclops scutifer* in May-November 1957-1989 in Kuril L. at the central station (L. V. Milovskaya, KoTINRO archives; Bugaev et al., 1989, 1995), specimens/m³

Year	May	June	July	August	September	October	November
1957	4500	2900	5300	5100	4900	8000	6200
1958	1400	1600	1700	2900	4000	6100	5250
1959	1100	1000	3600	5400	5900	2500	4100
1960	1750	1900	1700	6100	3000	4100	4100
1961	–	–	–	–	–	–	–
1962	–	–	–	–	–	–	–
1963	–	–	–	–	–	–	–
1964	2043	4470	6897	7740	2635	5025	4273
1965	680	1230	1610	2875	10370	10860	2460
1966	3663	5496	5158	7096	6768	4293	7339
1967	2688	5439	5903	9103	10144	7966	5694
1968	3924	4036	6668	9965	–	–	–
1969	–	–	–	–	–	–	–
1970	–	–	–	–	–	–	–
1971	–	–	–	–	–	–	–
1972	–	994	4562	8130	14370	14880	15520
1973	4754	6010	15050	14380	12800	9285	5090
1974	2440	3120	7310	–	–	11650	16740
1975	4480	4870	5460	15670	21275	13780	13670
1976	6240	8930	11960	18630	13020	14280	8470
1977	5965	6370	8150	11000	15460	11700	–
1978	3395	3480	7180	7700	6565	5430	3560
1979	890	1220	1960	7560	23480	18150	19690
1980	1980	3950	3570	5380	–	–	7990
1981	1080	2560	8720	8070	8915	9760	7040
1982	4800	4170	3040	8460	10410	6440	5395
1983	–	4950	7800	13210	11900	10590	11840
1984	4710	4710	3670	9715	9974	11945	11057
1985	6510	7212	10698	18319	14400	26867	15070
1986	6028	7486	11548	20370	21284	14480	16551
1987	3891	2757	6949	17931	17153	12269	10200
1988	4090	4253	7104	12433	12707	18306	10497
1989	928	666	1281	5127	5315	2432	1923

Table 15 (appendix). Abundance of *Daphnia longiremis* in May-November 1973-1989 in Kuril L. at the central station (L. V. Milovskaya, KoTINRO archives; Bugaev et al., 1995), specimens /m³

Year	May	June	July	August	September	October	November
1973	–	–	–	87	326	935	1217
1974	174	326	217	–	–	413	978
1975	200	–	200	500	1261	1326	1370
1976	320	380	420	620	–	–	–
1977	–	40	60	90	320	1280	–
1978	–	30	50	40	–	430	440
1979	100	60	40	60	180	240	300
1980	60	50	30	40	–	–	90
1981	30	40	143	90	–	1510	1350
1982	151	120	132	185	470	330	–
1983	–	80	390	130	–	880	500
1984	66	58	50	116	617	1145	1145
1985	90	33	51	67	54	260	307
1986	201	128	139	230	665	955	623
1987	89	38	22	55	200	686	1614
1988	100	41	52	108	541	1256	665
1989	118	58	82	186	430	1236	879

Table 16 (appendix). Total number of copepodite stages I to VI *Cyclops scutifer* in June-November 1970-1990 in Azabach at station No. 5 (L. A. Bazarkina, KoTINRO archives; Bugaev et al., 1993) specimens/m³

Year	June	July	August	September	October	November
1979	—	—	—	—	72290	—
1980	—	—	—	—	118000	—
1981	131540	85400	45677	109385	105460	44370
1982	25300	19950	8937	29850	75535	57500
1983	16200	9803	3427	11297	40000	32070
1984	8510	5157	1270	5450	23753	26200
1985	3480	1390	547	3747	14150	5290
1986	2397	2383	1310	9730	26770	21850
1987	9860	9070	6453	33403	84733	49520
1988	26465	15773	63145	222750	229475	200950
1989	68700	28465	6915	66847	118770	90040
1990	28500	14100	25500	59150	66567	52050

Table 17 (appendix). Abundance of *Daphnia galeata* in June-November 1981-1990 in Azabach L. at station No.5 (L. A. Bazarkina, KoTINRO archives; Bugaev et al., 1993), specimens/m³

Year	June	July	August	September	October	November
1981	80	2520	15400	4240	310	70
1982	30	330	1030	2740	870	110
1983	0	130	850	1490	470	80
1984	0	130	380	410	320	60
1985	0	100	240	410	170	50
1986	0	130	420	1050	2350	480
1987	0	0	350	630	790	280
1988	0	2960	12100	19350	7080	1150
1989	0	230	1190	3580	220	130
1990	150	980	2060	870	400	70

Table 18 (appendix). The feeding spectrum of anadromous threespine stickleback *Gasterosteus aculeatus* (morph *trashurus*) underyearlings in Azabach L. in 1989 at pelagic station No. 2 (T. N. Travina, T. L. Vvedenskaya, L. A. Bazarkina, V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	1.09.89r.				25.09.89 r.			
	<i>Trachurus</i> , age 0+				<i>Trachurus</i> , age 0+			
	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i>	8	0.1	0.2	3.6	92	35.2	3.1	14.4
N	—	—	—	—	92	29.2	1.7	7.7
I	—	—	—	—	56	6.0	1.3	6.3
II	—	—	—	—	4	+	0.1	0.4
<i>Ergacilus</i> sp.	—	—	—	—	28	1.0	1.0	4.0
<i>Daphnia galeata</i>	84	3.8	5.6	84.6	28	1.5	0.5	2.0
Rotatoria	48	—	+	0.6	—	—	—	—
<i>Chidorus sphaericus</i>	20	1.5	1.0	11.2	—	—	—	—
Detritus	—	—	—	—	76	—	18.2	79.6
Total consumption index, ‰	—	—	6.8	—	—	—	22.8	—
Empty stomachs, %	—	—	12.0	—	—	—	3.8	—
Average body length, mm	—	—	27.0	—	—	—	31.0	—
Number of fish	—	—	25	—	—	—	25	—

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, o/ooo; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 19 (appendix). The feeding spectrum of adult anadromous threespine sticklebacks (*morph trashurus*) in Azabach L. in 1990 at pelagic station No. 2 (T. N. Travina, V. F. Bugaev and S. A. Travin – KOTINRO archives)

Feeding components, collection data	Trachurus, age 3+				Trachurus, age 4+			
	1	2	3	4	1	2	3	4
14.06.90								
<i>Cyclops scutiger</i>	100	8256.0	346.3	78.9	100	7607.0	266.2	84.7
Chironomidae pupae	–	–	–	–	60	27.0	27.4	8.2
Chironomidae imago	20	1.0	1.1	0.3	80	23.6	21.5	7.1
Sockete age 0+	20	0.8	101.3	20.8	–	–	–	–
Remains of plants, algae	20	–	0.3	+	–	–	–	–
Total consumption index, ‰	–	–	449.0	–	–	–	315.1	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–
Average body length, mm	–	–	90.8	–	–	–	97.8	–
Number of fish	–	–	5	–	–	–	5	–
15.07.90								
<i>Cyclops scutiger</i>	–	–	–	–	33	5.0	0.4	0.5
Chironomidae pupae	–	–	–	–	33	0.6	0.9	1.0
Chironomidae imago	40	0.6	1.0	1.0	33	3.6	4.8	5.7
<i>Gammarus lacustris</i>	20	0.2	18.7	19.3	66	1.3	45.4	57.3
<i>Chydorus sphaericus</i>	–	–	–	–	33	1.0	+	+
Insecta larvae	–	–	–	–	33	0.3	18.7	26.1
Insecta imago	60	10.6	15.7	17.0	33	4.0	5.3	6.3
Stickleback eggs	80	20.8	64.1	62.6	66	1.0	2.8	3.1
Remains of plants, algae	20	–	–	0.1	–	–	–	–
Total consumption index, ‰	–	–	99.5	–	–	–	78.3	–
Empty stomachs, %	–	–	0.0	–	–	–	0.0	–
Average body length, mm	–	–	88.5	–	–	–	95.3	–
Number of fish	–	–	5	–	–	–	4	–

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 20 (appendix). The feeding spectrum of the freshwater form of threespine stickleback *Gasterosteus aculeatus* (morph *leiurus*) underyearlings in Azabach L. in 1989 at pelagic station No. 2 (T. N. Travina, V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	01.09.89				08.10.89			
	<i>Leiurus</i> , age 0+				<i>Leiurus</i> , age 0+			
	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i>	-	-	-	-	100	2826.2	666.7	96.3
N	-	-	-	-	100	547.7	27.5	3.9
I	-	-	-	-	100	1518.3	304.3	43.8
II	-	-	-	-	100	666.4	272.3	39.8
III	-	-	-	-	100	93.8	62.6	8.8
<i>Daphnia galeata</i> , mm	72	4.0	7.6	94.1	58	36.2	23.0	3.7
0.40	-	-	-	-	6	0.4	0.1	+
0.45	-	-	-	-	6	5.7	1.6	0.3
0.55	-	-	-	-	6	1.9	0.7	0.1
0.60	-	-	-	-	6	3.8	1.9	0.3
0.65	-	-	-	-	12	15.0	7.9	1.5
0.80	-	-	-	-	23	9.4	10.8	1.5
<i>Chydorus sphaericus</i>	12	0.7	0.9	5.6	-	-	-	-
Rotatoria	20	-	+	0.3	18	1.9	+	+
Total consumption index, ‰	-	-	8.5	-	-	-	689.7	-
Empty stomachs, %	-	-	24.0	-	-	-	0.0	-
Average body length, mm	-	-	23.0	-	-	-	31.0	-
Number of fish	-	-	25	-	-	-	17	-

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, o/ooo; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 21 (appendix). The feeding spectrum of the freshwater form of threespine sticklebacks (morph *leiurus*) in Azabach L. in 1989 at pelagic station No. 2 (T. N. Travina, T. L. Vvedenskaya, L. A. Bazar'kina, V. F. Bugaev and S. A. Travin – KOTINRO archives)

Feeding components, collection data	<i>Leiurus</i> , age 1+				<i>Leiurus</i> , age 2+				<i>Leiurus</i> , age 3+			
	1	2	3	4	1	2	3	4	1	2	3	4
17.06.89												
<i>Cyclops scutifer</i> (IV)	—	—	—	—	100	4270.5	456.1	99.5	100	3836.6	319.6	100.0
(V)	—	—	—	—	100	1400.0	122.2	26.0	100	1253.3	82.0	25.9
(males VI)	—	—	—	—	100	2358.9	273.2	60.4	100	2100.0	192.4	59.8
Plecoptera larvae	—	—	—	—	100	511.6	60.7	13.1	100	483.3	45.2	14.3
Trichoptera larvae	—	—	—	—	5	0.1	0.2	+	—	—	—	—
<i>Gammarus lacustris</i>	—	—	—	—	5	0.1	0.4	0.1	—	—	—	—
Insecta imago	—	—	—	—	5	0.1	1.3	0.3	—	—	—	—
	—	—	—	—	10	0.1	0.3	0.1	—	—	—	—
Total consumption index, ‰	—	—	—	—	—	—	458.3	—	—	—	319.6	—
Empty stomachs, %	—	—	—	—	—	—	10.5	—	—	—	16.0	—
Average body length, mm	—	—	—	—	—	—	69.0	—	—	—	77.0	—
Number of fish	—	—	—	—	—	—	19	—	—	—	6	—
11.07.89												
<i>Cyclops scutifer</i> (V)	100	862.7	550.2	99.6	100	3126.8	529.4	98.8	—	—	—	—
(VI)	6	85.3	49.0	7.6	—	—	—	—	—	—	—	—
<i>Daphnia galeata</i> , mm	83	777.4	501.2	92.0	100	3126.8	529.4	98.8	—	—	—	—
0.55	6	2.7	0.8	0.2	4	5.3	0.6	0.2	—	—	—	—
0.60	—	—	—	—	4	—	—	—	—	—	—	—
0.70	6	0.9	0.2	0.1	4	2.7	0.3	0.1	—	—	—	—
0.75	6	1.8	0.6	0.1	4	1.3	0.1	+	—	—	—	—
0.90	—	—	—	—	4	—	—	—	—	—	—	—
Chironomidae pupae	6	0.1	2.0	0.1	21	1.3	0.2	0.1	—	—	—	—
Insects imago	6	0.1	1.0	0.1	8	0.7	1.9	0.8	—	—	—	—
Total consumption index, ‰	—	—	554.0	—	—	—	532.4	—	—	—	—	—
Empty stomachs, %	—	—	16.6	—	—	—	0.0	—	—	—	—	—
Average body length, mm	—	—	44.0	—	—	—	67.0	—	—	—	—	—
Number of fish	—	—	18	—	—	—	24	—	—	—	—	—

Continued, Table 21 (appendix)

Feeding components, collection data	Letiurus, age 1+				Letiurus, age 2+				Letiurus, age 3+			
	1	2	3	4	1	2	3	4	1	2	3	4
22.07.89												
<i>Cyclops scutifer</i>	56	146.4	198.8	99.0	81	102.8	174.9	95.8	75	673.3	75.7	94.4
<i>Cyclops scutifer</i> (I)	-	-	-	-	5	0.1	+	+	-	-	-	-
<i>Cyclops scutifer</i> (самки VI)	56	146.4	198.8	99.0	81	102.7	174.9	95.8	75	673.33	75.7	94.4
<i>Daphnia galeata</i>	-	-	-	-	14	4.6	0.5	0.2	-	-	-	-
<i>Chidorus sphaericus</i>	-	-	-	-	5	0.1	+	+	-	-	-	-
<i>Leptodora kindti</i>	4	+	0.1	+	-	-	-	-	-	-	-	-
Chironomidae larvae	-	-	-	-	5	0.2	1.3	0.6	-	-	-	-
Chironomidae pupae	-	-	-	-	19	0.2	0.5	0.3	50	0.5	1.1	1.1
Chironomidae imago	-	-	-	-	10	0.1	0.2	0.1	-	-	-	-
Insecta imago	4	+	0.6	0.5	28	0.5	1.0	0.6	25	0.3	0.5	0.6
Stickleback eggs	-	-	-	-	14	0.5	4.5	2.4	25	0.5	3.3	3.9
Detritus	8	-	1.3	0.5	-	-	-	-	-	-	-	-
Total consumption index, ‰ ₀₀₀	-	-	200.8	-	-	-	182.9	-	-	-	80.6	-
Empty stomachs, %	-	-	32.0	-	-	-	14.0	-	-	-	0.0	-
Average body length, mm	-	-	38.0	-	-	-	73.0	-	-	-	82.0	-
Number of fish	-	-	25	-	-	-	21	-	-	-	4	-
21.08.89												
<i>Cyclops scutifer</i> (самки VI)	18	1.8	1.6	3.3	30	11.3	1.9	9.7	-	-	-	-
<i>Daphnia galeata</i> , mm	9	0.4	0.1	0.3	20	5.5	0.3	1.5	-	-	-	-
0.60	-	-	-	-	20	2.6	0.1	0.5	-	-	-	-
0.70	9	0.1	+	0.1	20	2.1	0.1	0.6	-	-	-	-
0.75	9	0.2	0.1	0.1	-	-	-	-	-	-	-	-
0.80	9	0.1	+	0.1	10	0.8	0.1	0.4	-	-	-	-
<i>Chidorus sphaericus</i>	-	-	-	-	18	0.7	+	+	-	-	-	-
<i>Leptodora kindti</i>	-	-	-	-	20	1.7	0.4	1.9	-	-	-	-
Chironomidae pupae	-	-	-	-	10	1.9	7.5	27.1	-	-	-	-
Chironomidae imago	45	2.5	25.4	74.5	70	3.6	10.2	51.3	-	-	-	-
Insecta imago	45	0.7	8.7	21.9	30	0.6	1.7	8.5	-	-	-	-
Hydracarina	-	-	-	-	9	0.7	+	+	-	-	-	-
Total consumption index, ‰ ₀₀₀	-	-	35.9	-	-	-	22.0	-	-	-	-	-
Empty stomachs, %	-	-	45.0	-	-	-	30.0	-	-	-	-	-
Average body length, mm	-	-	48.0	-	-	-	72.0	-	-	-	-	-
Number of fish	-	-	11	-	-	-	10	-	-	-	-	-

Note. At table heading: 1 – frequency of occurrence, %, 2 – number of organisms per stomach; 3 – consumption index, ‰₀₀₀; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 22 (appendix). The feeding spectrum of the freshwater form of threespine sticklebacks (morph *leiurus*) in Azabach L. in 1990 at pelagic station No. 2 (T. N. Travina, V. F. Bugaev and S. A. Travin – KOTINRO archives)

Feeding components, collection data	Leiurus, age 1+					Leiurus, age 2+					Leiurus, age 3+				
	1	2	3	4		1	2	3	4		1	2	3	4	
14.06.90	100	354.0	415.6	97.5		100	6893.0	1438.6	100.0		100	10458.0	920.6	99.8	
<i>Cyclops scutifer</i> (II–V)*	50	10.0	6.1	1.6		–	–	–	–		8	27.0	1.3	0.1	
<i>Daphnia galeata</i>	10	–	0.1	+		–	–	–	–		–	–	–	–	
Rotatoria	10	0.5	0.5	0.1		–	–	–	–		4	0.3	+	+	
Chironomidae larvae	10	0.1	2.6	0.8		–	–	–	–		12	–	–	–	
Chironomidae pupae	–	–	–	–		10	0.1	0.4	+		4	0.1	0.3	+	
Chironomidae imago	–	–	–	–		–	–	–	–		4	0.1	0.5	0.1	
Nematoda	–	–	–	–		–	–	–	–		4	0.6	+	+	
Simuliidae	–	–	–	–		–	–	1439.0	–		–	–	922.7	–	
Total consumption index, ‰	–	–	424.9	–		–	–	–	–		–	–	0.0	–	
Empty stomachs, %	–	–	0.0	–		–	–	0.0	–		–	–	0.0	–	
Average body length, mm	–	–	33.1	–		–	–	56.2	–		–	–	75.5	–	
Number of fish	–	–	10	–		–	–	10	–		–	–	25	–	
25.06.90	100	468.0	259.2	99.0		79	483.0	65.1	24.4		33	472.0	27.3	7.5	
<i>Cyclops scutifer</i> (II–IV)*	5	1.5	2.3	0.8		42	637.0	119.0	74.8		89	2353.0	239.9	86.0	
(V–VI)	15	0.7	0.5	0.2		4	+	+	+		33	3.0	0.1	0.1	
<i>Daphnia galeata</i>	–	–	–	–		4	+	0.4	0.1		–	–	–	–	
Chironomidae pupae	–	–	–	–		16	0.2	1.8	0.7		33	1.0	2.7	0.9	
Chironomidae imago	–	–	–	–		–	–	–	–		11	0.1	10.5	5.5	
<i>Gammarus lacustris</i>	–	–	262.0	–		–	–	186.3	–		–	–	280.5	–	
Total consumption index, ‰	–	–	0.0	–		–	–	0.0	–		–	–	0.0	–	
Empty stomachs, %	–	–	33.4	–		–	–	54.7	–		–	–	73.4	–	
Average body length, mm	–	–	20	–		–	–	24	–		–	–	9	–	
Number of fish	–	–	–	–		–	–	–	–		–	–	–	–	

Continued, Table 22 (appendix)

Feeding components, collection data	Leiurus, age 1+				Leiurus, age 2+				Leiurus, age 3+			
	1	2	3	4	1	2	3	4	1	2	3	4
04.07.90												
<i>Cyclops scutifer</i> (II-IV)* (V-VI)	40	47.0	19.4	10.9	-	-	-	-	-	-	-	-
<i>Daphnia galeata</i>	60	147.0	128.9	77.4	52	291.0	72.9	62.0	75	942.0	83.1	47.7
Rotatoria	30	2.5	1.1	0.7	5	0.1	+	+	15	5.0	1.3	0.1
Chironomidae pupae	60	200.0	1.8	0.9	-	-	-	-	-	-	-	-
Chironomidae imago	5	0.1	1.8	0.7	-	-	-	-	-	-	-	-
Insecta larvae	15	0.3	4.9	3.6	94	6.0	42.3	33.0	100	38.0	87.1	51.1
Insecta imago	5	0.8	6.2	5.7	5	0.7	2.3	2.1	-	-	-	-
Stickleback eggs	-	-	-	-	5	0.5	3.5	2.9	5	0.3	1.3	1.1
Algae	5	-	-	0.1	-	-	-	-	-	-	-	-
Total consumption index, ‰	-	-	164.2	-	-	-	121.0	-	-	-	172.8	-
Empty stomachs, %	-	-	0.0	-	-	-	0.0	-	-	-	0.0	-
Average body length, mm	-	-	37.2	-	-	-	54.5	-	-	-	77.3	-
Number of fish	-	-	20	-	-	-	19	-	-	-	20	-
15.07.90												
<i>Cyclops scutifer</i> (I) (II-IV)* (V-VI)	5	0.3	+	0.1	-	-	-	-	-	-	-	-
<i>Daphnia galeata</i>	5	6.5	4.1	17.8	-	-	-	-	-	-	-	-
<i>Bosmina</i> sp.	10	7.0	8.0	53.5	78	184.0	36.2	93.5	88	1166.0	132.8	95.3
Rotatoria	20	1.0	0.8	4.2	72	15.0	1.7	4.3	70	57.0	3.6	2.0
Chironomidae pupae	35	2.0	0.5	2.8	-	-	-	-	-	-	-	-
Chironomidae imago	75	-	3.1	16.6	-	-	-	-	-	-	-	-
Insecta larvae	-	-	-	-	-	-	-	-	6	0.7	2.8	1.3
Stickleback eggs	-	-	-	-	11	0.2	0.8	2.2	12	0.4	1.0	0.7
Total consumption index, ‰	5	0.1	0.9	5.0	-	-	-	-	6	0.3	0.9	0.7
Empty stomachs, %	-	-	-	-	-	-	-	-	-	-	-	-
Average body length, mm	-	-	17.4	-	-	-	38.7	-	-	-	141.1	-
Number of fish	-	-	0.0	-	-	-	5.8	-	-	-	16.7	-
	-	-	32.6	-	-	-	59.5	-	-	-	76.8	-
	-	-	20	-	-	-	17	-	-	-	18	-

Continued, Table 22 (appendix)

Feeding components, collection data	Leiturus, age 1+				Leiturus, age 2+				Leiturus, age 3+			
	1	2	3	4	1	2	3	4	1	2	3	4
	100	68.0	68.0	36.6	40	9.0	2.2	1.9	50	216.0	25.9	18.3
100	136.0	117.6	63.4	100	865.0	117.2	84.7	50	9.0	0.6	0.4	
Rotatoria	-	-	-	-	-	-	-	25	-	+	+	
Chironomidae pupae	-	-	-	-	20	4.2	4.2	50	2.0	6.8	4.8	
Chironomidae imago	-	-	-	-	80	9.1	6.4	75	4.0	13.2	9.1	
Insecta imago	-	-	-	-	40	1.0	2.8	100	18.0	55.6	38.0	
Threespine stickleback	-	-	-	-	-	-	-	25	0.2	41.7	29.4	
Total consumption index, ‰	-	-	185.6	-	-	136.5	-	-	-	143.8	-	
Empty stomachs, %	-	-	0.0	-	-	20.0	-	-	-	25	-	
Average body length, mm	-	-	40.0	-	-	60.8	-	-	-	70.2	-	
Number of fish	-	-	1	-	-	5	-	-	-	5	-	

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, o/ooo; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1. *II–III stages mostly.

Table 23 (appendix). The feeding spectrum of ninespine sticklebacks in Azabach L. in 1989-1990 at pelagic station No. 2 (T. N. Travina, T. L. Vvedenskaya, L. A. Bazarkina, V. F. Bugaev and S. A. Travin – KoTINRO archives)

Feeding components	12.09.89, age 1+				25.09.90, age 1+				21.08.89, age 2+			
	1	2	3	4	1	2	3	4	1	2	3	4
	17	1.0	0.7	0.6	-	-	-	-	-	-	-	-
33	1.0	0.3	0.3	-	-	-	-	-	-	-	-	-
Bosmina sp.	-	-	-	30	6.4	1.5	2.1	-	-	-	-	-
Chidorus shaeiricus	-	-	-	10	1.1	0.4	0.4	-	-	-	-	-
Rotatoria	-	-	-	10	-	0.1	0.1	-	-	-	-	-
Chironomidae larvae	50	1.3	2.9	10	0.1	0.8	3.9	60	8.0	298.8	90.2	
Chironomidae pupae	50	6.2	73.8	94.8	-	-	-	60	2.2	12.9	3.7	
Chironomidae imago	-	-	-	-	-	-	-	40	0.6	6.1	1.0	
Ostracoda	17	0.2	+	+	20	0.3	1.1	20	0.4	+	+	
Pisidium casertanum	-	-	-	-	-	-	-	20	0.4	2.8	0.7	
Gammarus lacustris	-	-	-	-	10	0.1	92.4	20	0.4	13.9	3.4	
Nematoda	-	-	-	-	-	-	-	20	0.8	0.1	+	
Detritus	-	-	-	-	-	-	-	20	-	4.1	1.0	
Total consumption index, ‰	-	-	77.7	-	-	21.2	-	-	-	338.7	-	
Empty stomachs, %	-	-	15.0	-	-	40.0	-	-	-	0.0	-	
Average body length, mm	-	-	51.0	-	-	34.8	-	-	-	60.0	-	
Number of fish	-	-	6	-	-	10	-	-	-	5	-	

Note. At table heading: 1 – frequency of occurrence, %; 2 – number of organisms per stomach; 3 – consumption index, o/ooo; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 24 (appendix). The feeding spectrum of pond smelt in Azabach L. in 1989 at pelagic station No. 2 (T. N. Travina, T. L. Vvedenskaya, L. A. Bazarikina, V. F. Bugaev and S. A. Travin – KOTINRO archives)

Feeding components	13.08.89, age 0+				22.07.89, age 2+				21.08.89, age 2+			
	1	2	3	4	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i> (female VI)	100	770.6	528.7	97.6	14	104.6	5.0	55.0	100	2221.5	138.5	91.7
<i>Daphnia galeata</i> , mm	71	31.7	12.2	2.2	-	-	-	-	-	-	-	-
0.50	7	0.6	0.1	+	-	-	-	-	-	-	-	-
0.65	7	1.7	0.5	0.1	-	-	-	-	-	-	-	-
0.70	21	4.6	1.5	0.2	-	-	-	-	-	-	-	-
0.75	43	12.6	4.7	0.9	-	-	-	-	-	-	-	-
0.80	36	7.7	2.7	0.5	-	-	-	-	-	-	-	-
0.85	21	2.9	1.7	0.3	-	-	-	-	-	-	-	-
0.90	14	1.7	1.0	0.2	-	-	-	-	-	-	-	-
<i>Leptodora kindtii</i>	7	1.1	1.4	0.2	-	-	-	-	-	-	-	-
Chironomidae pupae	-	-	-	-	43	0.6	0.8	8.2	-	-	-	-
Chironomidae imago	-	-	-	-	71	2.1	3.0	30.7	83	10.2	10.6	7.0
Insects imago	-	-	-	-	29	0.4	0.6	6.1	66	1.8	1.8	1.3
Total consumption index, ‰	-	-	542.3	-	-	-	9.4	-	-	-	150.9	-
Empty stomachs, %	-	-	0.0	-	-	-	0.0	-	-	-	0.0	-
Average body length, mm	-	-	43.0	-	-	-	97.0	-	-	-	102.0	-
Number of fish	-	-	14	-	-	-	7	-	-	-	6	-

Note. At table heading: 1 – frequency of occurrence, %, 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1.

Table 25 (appendix). The feeding spectrum of pond smelt in Azabach L. in 1990 at pelagic station No. 2 (T. N. Travina, V. F. Bugaev and S. A. Travin – KOTINRO archives)

Feeding components	15.07.90, age 2+				17.08.90, age 1+ – 2+				25.09.90, age 1+ – 2+			
	1	2	3	4	1	2	3	4	1	2	3	4
<i>Cyclops scutifer</i> (N)	-	-	-	-	-	-	-	-	-	-	-	-
(I-IV)*	50	30.0	0.8	2.3	-	-	-	-	66	248.0	0.6	4.4
(V-VI)	-	-	-	-	-	-	-	-	33	246.0	5.0	37.5
<i>Daphnia galeata</i>	50	10.0	0.3	1.0	94	4041.0	345.2	96.5	17	1.7	0.1	1.0
Chironomidae pupae	50	4.0	6.7	19.4	72	273.5	12.9	3.5	83	182.5	7.2	57.1
Chironomidae imago	50	16.0	26.7	77.3	-	-	-	-	-	-	-	-
Total consumption index, ‰	-	-	34.5	-	-	-	358.1	-	-	-	12.9	-
Empty stomachs, %	-	-	33.3	-	-	-	11.1	-	-	-	33.3	-
Average body length, mm	-	-	93.0	-	-	-	80.6	-	-	-	84.1	-
Number of fish	-	-	3	-	-	-	18	-	-	-	6	-

Note. At table heading: 1 – frequency of occurrence, %, 2 – number of organisms per stomach; 3 – consumption index, ‰; 4 – weight of organisms per stomach, %. The sign “+” signifies less than 0.1. *I-III stages mostly.

Table 26 (appendix). Average age adult Asian sockeye specimens, years

Watershed	Year	Freshwater period		Marine period		Number of fish
		Range	Average	Range	Average	
Male						
Okhota R.	1983	–	1.32	–	2.91	34
Kukhtuy R.	1983	–	1.23	–	2.86	44
Palana R.	1983,1990	1.90–2.01	1.95	2.95–3.00	2.97	173
Tigil R.	1981	–	0.88	–	3.06	17
Khairyuzova R.	1984,1986	0.98–1.00	0.99	3.00–3.03	3.01	162
Icha R.	1986,1989	1.04–1.05	1.05	3.04–3.14	3.09	68
Vorovskaya R.	1965,1989	1.14–1.59	1.37	3.00–3.02	3.01	77
Kikhchik R.	1989	–	0.86	–	3.19	36
Bolshaya R.*	1987,1989	0.91–1.18	1.05	2.93–3.07	3.00	279
Ozernaya R.	1978–1989	1.96–2.29	2.12	2.15–2.77	2.56	–
Dalneye L.*	–	1.30–1.39	1.35	2.30–2.52	2.41	–
Avacha R.	1988–1989	2.01–2.06	2.03	2.46–2.71	2.59	255
Listvenichnaya R.	1980,1984	1.94–2.60	2.27	2.47–2.72	2.59	38
Kamchatka R.*	1978–1989	0.99–1.49	1.24	2.69–3.08	2.92	1965
Stolbovaya R.	1984	–	1.17	–	3.00	53
Malamvayam R.	1983	–	1.41	–	2.89	44
Khailyulya R.	1977–1989	0.86–1.05	0.97	2.96–3.71	3.17	573
Ivashka R.	1966	–	0.69	–	3.05	42
Karaga R.	1988–1989	1.03–1.07	1.05	2.92–3.02	2.97	231
Tymlat R.	1973	–	0.91	–	3.13	45
Kichiga R.	1983,1982,1989	0.90–1.07	0.99	3.00–3.10	3.05	106
Avyavayam R.	1985,1986,1989	0.98–1.30	1.11	2.27–3.03	2.68	264
Kultushnaya R.	1983–	–	1.96	–	2.87	23
Apuka R.	1985,1989	1.08–1.25	1.17	3.00–3.07	3.03	126
Ananapylgen R.	1980	–	2.88	–	2.50	68
Ukalayat R.	1989	–	1.00	–	3.23	80
Tumanskaya R.	1928	–	1.84	–	2.98	63
Achchen R.	1975	–	2.29	–	3.07	14
Sarannaya R.	1990–1991	2.55–2.90	2.73	2.17–2.45	2.31	173
Sopchnaya R.	1990	–	1.00	–	3.06	31
Urumpet R.	1990	–	2.49	–	2.57	49
Female						
Okhota R.	1983	–	1.15	–	2.83	65
Kukhtuy R.	1983	–	1.30	–	2.86	56
Palana R.	1983, 1990	1.89–2.00	1.95	2.99–3.02	3.02	174
Tigil R.	1981	–	1.10	–	3.00	21
Khairyuzova R.	1984,1986	1.00–1.06	1.03	2.98–2.99	3.00	232
Icha R.	1986,1989	0.89–1.07	0.98	3.00–3.06	3.03	74
Vorovskaya R.	1965,1989	0.96–1.58	1.27	3.03–3.08	3.05	85
Kikhchik R.	1989	–	0.93	–	3.34	41
Bolshaya R.*	1987,1989	0.82–1.16	0.99	3.11–3.15	3.13	358
Ozernaya R.	1978–1989	1.96–2.45	2.15	2.47–2.85	2.73	–
Dalneye L.*	–	1.45–1.49	1.47	2.26–2.44	2.35	–
Avacha R.	1988–1989	2.05–2.14	2.09	2.37–2.65	2.51	202
Listvenichnaya R.	1980,1984	1.94–2.55	2.25	2.91–3.03	2.97	42
Kamchatka R.*	1978–1989	0.93–1.53	1.22	2.86–3.25	3.05	1701
Stolbovaya R.	1984	–	1.15	–	3.11	62
Malamvayam R.	1983	–	1.48	–	3.00	42
Khailyulya R.	1977–1989	0.82–1.08	0.93	3.00–3.45	3.18	504
Ivashka R.	1966	–	0.51	–	3.14	49
Karaga R.	1988–1989	1.03–1.05	1.04	2.79–2.97	2.88	262
Tymlat R.	1973	–	0.95	–	3.03	40
Kichiga R.	1983,1982,1989	0.84–1.04	0.96	3.04–3.07	3.05	97
Avyavayam R.	1985, 1986, 1989	0.97–1.33	1.10	3.00–3.18	3.06	278
Kultushnaya R.	1983	–	1.96	–	2.96	27
Apuka R.	1985,1989	1.06–1.15	1.11	3.08–3.13	3.11	113
Ananapylgen R.	1980	–	3.52	–	2.61	75
Ukalayat R.	1989	–	1.02	–	3.09	82
Tumanskaya R.	1928	–	1.87	–	2.94	112
Achchen R.	1975	–	2.24	–	3.04	25
Sarannaya R.	1990–1991	2.50–2.82	2.66	2.61–2.87	2.74	135
Sopchnaya R.	1990	–	1.00	–	2.96	25
Urumpet R.	1990	–	2.63	–	2.35	51

*Combined data on early and late seasonal runs (rases) of sockeye.

Table 27 (appendix). Average age adult Asian sockeye specimens by seasonal runs (rises), years

Watershed, season race	Year	Male				Female			
		Freshwater period		Marine period		Freshwater period		Marine period	
		Range	Average	Range	Average	Range	Average	Range	Average
Bolshaya R. (early run)	1987,1989	0.86-1.26	1.06	2.94-3.06	3.00	0.72-1.23	0.97	3.14-3.20	3.17
Bolshaya R. (late run)	1987,1989	0.96-1.10	1.03	2.91-3.07	2.99	0.92-1.09	1.01	3.09-3.11	3.10
Dalneye L.* (early run)	-	-	1.30	-	2.52	-	1.45	-	2.44
Dalneye L.* (late run)	-	-	1.39	-	2.30	-	1.49	-	2.26
Kamchatka R.(early run)	1978-1979	0.95-1.46	1.20	2.68-3.12	2.94	0.93-1.55	1.20	2.96-3.37	3.08
Kamchatka R. (late run)	1978-1979	1.04-1.53	1.28	2.71-3.04	2.90	0.92-1.52	1.24	2.76-3.13	3.03

*Calculations based on data from F. V. Krogius et al., 1987.

Table 28 (appendix). Average age adult specimens from local second order stocks and their groups of the Kamchatka R. sockeye from marine trap net catches in 1998-1989 (data for early and late sockeye runs are combined), years

Stock, group of stocks	Male				Female			
	Freshwater period		Marine period		Freshwater period		Marine period	
	Range	Average	Range	Average	Range	Average	Range	Average
"S"	0.00-0.00	0.0	2.92-3.53	3.17 ± 0.06	0.00-0.00	0.0	3.00-3.61	3.27 ± 0.05
"V"	1.00-1.05	1.01 ± 0.01	2.65-3.14	2.90 ± 0.04	1.00-1.05	1.01 ± 0.01	2.83-3.06	2.94 ± 0.03
"E"	1.00-1.13	1.05 ± 0.02	2.87-3.20	2.96 ± 0.04	1.00-1.27	1.06 ± 0.02	2.98-3.19	3.09 ± 0.03
"A"	1.71-2.00	1.87 ± 0.03	2.56-3.18	2.88 ± 0.06	1.68-2.03	1.94 ± 0.04	2.90-3.31	3.05 ± 0.03
"D"	1.87-2.00	1.98 ± 0.01	2.20-3.00	2.67 ± 0.09	1.79-2.05	1.97 ± 0.02	2.36-3.00	2.77 ± 0.07
								Number of years
								12
								11
								12
								12
								10

Table 29 (appendix). Abundance and age composition of the adult portion of sockeye stock in the Ozernaya R. (M. M. Selifonov, KoTINRO archives; data from Soviet-Japanese Fisheries Commission), thou. of specimens

Year	1.1		1.2		1.3		2.1		2.2		2.3		2.4		3.1		3.2		3.3		3.4		Total, thousands, of specimens
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
1970	-	-	-	-	-	-	31	687	774	204	167	-	2	+	171	209	24	32	-	-	-	-	2301
1971	-	-	-	-	-	-	104	454	680	402	419	7	4	+	94	106	33	49	-	-	-	-	2352
1972	-	-	-	-	-	-	18	456	439	441	333	6	4	-	122	69	38	25	-	-	-	-	1951
1973	-	-	-	-	-	-	59	281	305	242	307	3	3	-	104	123	63	49	-	-	-	-	1539
1974	-	-	-	-	-	-	94	209	200	390	584	2	4	-	56	85	25	38	-	-	-	-	1687
1975	-	-	-	-	-	-	79	851	604	235	279	3	1	+	104	76	82	30	-	-	-	-	2344
1976	-	-	-	-	-	-	12	457	467	275	299	7	6	+	84	87	32	27	-	-	-	-	1753
1977	-	-	-	-	-	-	34	229	234	329	358	5	4	5	69	70	58	49	-	-	-	-	1440
1978	2	3	-	3	76	316	323	323	574	626	1	-	25	95	98	149	125	-	-	-	-	-	2420
1979	+	3	32	73	133	564	576	576	358	391	5	3	3	2	58	59	72	61	-	-	-	-	2415
1980	-	6	+	-	24	524	534	534	637	695	3	3	3	-	138	141	33	27	-	-	-	-	2773
1981	-	-	5	6	36	321	283	283	692	726	1	6	1	-	62	60	160	182	-	-	-	-	2540
1982	-	-	-	-	47	362	349	349	326	343	8	6	8	23	58	54	111	106	-	-	-	-	1794
1983	-	-	-	-	9	413	151	151	877	962	7	-	7	6	130	93	48	49	-	-	-	-	2752
1984	-	-	-	-	15	411	189	189	1160	950	36	-	14	14	167	100	400	717	-	-	-	-	4161
1985	-	-	7	8	63	541	382	382	1538	1258	7	76	-	85	208	777	911	20	-	-	-	-	5881
1986	16	23	44	9	38	905	740	740	689	1159	57	67	2	2	37	45	133	273	-	-	-	-	4320
1987	-	7	97	85	169	526	441	441	1797	1936	86	38	-	-	40	65	161	165	-	-	-	-	5680
1988	-	-	112	138	27	796	526	526	839	1052	10	-	-	5	16	7	58	91	-	-	-	-	3700
1989	-	-	-	-	44	1160	605	605	1134	1459	55	102	-	5	152	196	22	38	-	-	-	-	4972
1990	20	-	-	53	114	1538	1095	1095	3121	3214	141	155	-	-	176	73	264	545	-	-	-	-	10583
1991	-	3	12	8	216	1113	796	796	1328	1846	93	63	-	5	146	205	317	487	-	-	-	-	6679

Note. Sign "+" less than one thou. specimens.

Table 30 (appendix). Age composition of adult Kamchatka R. sockeye from marine trap net catches in 1978-1989, %

Year	0.2	1.1	0.3	1.2	2.1	0.4	1.3	2.2	1.4	2.3	3.2	1.5	2.4	3.3	2.5	3.4	4.3	Number of fish
Early run																		
1978	-	-	3.5	2.5	0.5	0.5	60.3	2.5	-	29.7	-	-	-	0.5	-	-	-	199
1979	0.5	-	14.3	3.1	1.0	4.0	48.0	10.1	5.7	12.3	-	-	1.0	-	-	-	-	227
1980	-	-	3.5	4.7	-	3.7	64.2	5.4	1.6	16.5	-	-	0.2	0.2	-	-	-	430
1981	-	-	6.7	3.4	0.3	2.9	49.3	2.3	5.2	29.0	-	0.3	0.6	-	-	-	-	345
1982	0.3	-	6.6	13.9	0.3	3.7	52.3	9.3	2.0	10.7	-	-	0.9	-	-	-	-	346
1983	0.7	-	11.3	4.7	-	1.3	50.7	3.3	2.7	25.3	-	-	-	-	-	-	-	150
1984	-	-	6.4	1.4	-	2.0	42.4	1.4	3.1	41.0	-	-	2.0	0.3	-	-	-	295
1985	-	-	3.1	-	-	1.0	39.0	1.0	9.2	42.1	-	-	4.1	0.5	-	-	-	195
1986	-	-	10.9	3.1	-	1.1	30.7	8.9	2.1	37.5	-	-	4.7	0.5	0.5	0.5	-	192
1987	-	-	15.5	-	-	1.6	49.8	2.7	0.8	28.4	-	-	0.8	0.4	-	-	-	257
1988	-	-	6.2	1.0	-	15.5	33.0	1.0	6.2	32.0	-	-	4.1	1.0	-	-	-	97
1989	-	-	17.2	1.0	-	3.0	32.3	-	3.0	38.4	-	-	4.1	-	-	-	-	99
Late run																		
1978	-	0.4	11.7	10.1	-	1.2	64.5	4.0	0.4	6.9	-	-	0.4	0.4	-	-	-	248
1979	-	-	14.5	4.4	1.2	2.4	54.5	6.5	3.2	12.5	-	-	-	0.8	-	-	-	248
1980	-	-	7.1	2.7	-	6.0	65.6	2.2	1.6	14.8	-	-	-	-	-	-	-	183
1981	-	-	14.4	1.2	-	2.4	56.9	1.8	1.8	21.5	-	-	-	-	-	-	-	167
1982	-	-	4.6	10.3	-	6.9	39.1	6.9	2.3	29.3	-	-	0.6	-	-	-	-	174
1983	0.7	-	10.2	1.4	-	1.4	58.9	0.7	1.4	24.6	-	-	0.7	-	-	-	-	146
1984	0.3	-	1.7	4.1	0.7	2.0	35.5	9.9	3.1	37.9	0.3	-	3.1	1.4	-	-	-	293
1985	-	-	2.6	2.6	-	-	44.3	7.7	3.1	31.4	0.5	-	5.7	2.1	-	-	0.5	194
1986	-	-	3.8	0.5	-	0.5	46.8	1.6	-	43.1	-	-	2.7	-	-	-	-	186
1987	-	-	9.9	1.7	-	1.4	36.3	7.7	2.5	38.4	-	-	1.8	0.3	-	-	-	284
1988	1.0	-	7.1	11.1	-	5.1	41.4	3.0	2.0	23.2	-	-	6.1	-	-	-	-	99
1989	-	-	11.8	1.6	-	0.8	43.9	5.7	6.9	21.2	0.4	-	7.3	0.4	-	-	-	246

Table 31 (appendix). Age composition of adult Kamchatka R. sockeye from river gill net catches in 1978-1989, %

Year	0.2	1.1	1.2	2.1	0.4	1.3	2.2	1.4	2.3	3.2	1.5	2.4	3.3	2.5	3.4	4.3	Number of fish
Early run																	
1978	-	-	3.2	0.2	0.9	75.1	1.6	1.3	16.1	-	-	-	-	-	-	-	446
1979	-	-	16.8	0.3	3.9	48.0	2.9	4.8	19.1	-	-	2.6	0.6	-	-	-	309
1980	-	-	5.1	-	4.3	53.5	2.1	2.1	30.0	-	-	1.3	0.3	-	-	-	374
1981	-	-	9.5	-	2.0	55.8	1.8	5.9	22.6	-	0.3	1.5	0.3	-	0.3	-	389
1982	-	-	4.6	-	1.0	59.0	4.3	2.3	21.9	-	-	0.5	-	-	-	-	393
1983	-	-	12.7	-	1.4	53.2	1.8	0.9	26.8	-	-	1.4	-	-	-	-	220
1984	-	-	3.7	-	1.2	49.4	0.8	8.9	33.6	-	-	1.6	-	-	-	-	247
1985	-	-	5.1	-	1.7	34.2	2.4	14.1	34.9	-	0.3	5.0	0.3	-	0.3	-	298
1986	-	-	8.3	-	1.0	26.2	5.5	2.1	49.3	-	-	5.9	1.0	-	-	-	290
1987	-	-	11.7	-	2.0	35.9	1.6	2.0	43.7	-	-	2.8	0.3	-	-	-	359
1988	-	-	5.3	-	6.7	30.8	0.9	10.2	33.7	-	-	9.7	1.5	0.3	0.3	-	341
1989	-	-	13.1	-	2.3	36.0	-	9.3	29.9	-	-	8.4	0.5	-	-	-	214
Late run																	
1978	-	-	14.6	-	3.7	53.7	2.6	1.1	20.6	-	-	1.1	0.6	-	-	-	350
1979	-	-	16.3	0.4	4.1	55.6	4.5	3.2	12.7	-	-	0.9	-	-	-	-	221
1980	-	-	-	-	-	82.2	2.2	-	15.6	-	-	-	-	-	-	-	45
1981	1.0	-	10.0	-	-	54.0	-	9.0	25.0	-	-	1.0	-	-	-	-	100
1982	-	-	4.7	-	3.4	53.4	3.4	6.1	23.0	-	-	2.0	-	-	-	-	148
1983	-	-	7.1	-	-	62.6	1.4	1.8	23.1	-	-	1.8	-	-	-	-	281
1984	-	-	3.4	-	4.7	24.1	16.1	5.4	36.9	-	-	5.4	2.0	-	-	-	149
1985	-	-	0.3	-	1.4	28.8	14.9	4.1	36.9	-	-	8.8	1.4	0.3	-	-	295
1986	-	-	6.6	-	-	38.6	5.1	0.5	46.2	-	-	2.0	-	-	-	-	197
1987	-	-	4.3	-	1.7	36.8	3.1	3.9	48.1	-	-	1.7	-	-	-	-	231
1988	0.5	-	4.6	-	4.1	38.7	0.5	10.8	25.3	0.4	-	11.3	1.1	-	0.5	-	194
1989	-	-	6.1	-	2.5	43.0	4.1	10.7	25.4	-	-	7.8	0.4	-	-	-	244

Table 32 (appendix). Average body length of adult sockeye from the Ozernaya R. (of the most abundant age groups) during the spawning run in 1988-1990 (M. M. Selifonov, KoTINRO archives), cm

Year	Age	Sex	Sampling dates					Mean value
			10.07-12.07	21.07-27.07	3.08-7.08	17.08-21.08	1.09	
1988	2.2	Male	54.8	54.2	54.6	57.9	54.6	55.1 54.5 62.3 59.6
	2.2	Female	51.6	54.5	54.1	54.9	55.2	
	2.3	Male	59.2	62.6	63.3	64.0	63.5	
	2.3	Female	57.4	60.4	60.1	60.8	61.5	
1989	2.2	Male	51.5	52.6	54.1	54.0	53.6	53.2 52.8 62.9 59.6
	2.2	Female	50.6	51.6	52.9	53.9	55.3	
	2.3	Male	59.5	61.5	62.7	65.0	66.6	
	2.3	Female	56.7	58.6	60.1	60.1	63.7	
1990	2.2	Male	54.0	56.0	57.1	60.8	55.7	55.6 54.3 63.8 60.8
	2.2	Female	52.2	54.6	54.9	56.1	57.7	
	2.3	Male	60.9	62.4	64.1	64.6	65.4	
	2.3	Female	58.0	59.6	60.7	60.8	63.1	

Table 33 (appendix). Average body weight of adult sockeye from the Ozernaya R. (of the most abundant age groups) during the spawning run in 1988-1990 (M. M. Selifonov, KoTINRO archives), kg

Year	Age	Sex	Sampling dates					Mean value
			10.07-12.07	21.07-27.07	3.08-7.08	17.08-21.08	1.09	
1988	2.2	Male	2.28	2.10	2.21	2.66	2.23	2.67 2.21 3.37 2.91
	2.2	Female	1.85	2.18	2.17	2.33	2.24	
	2.3	Male	2.90	3.38	3.49	3.76	3.48	
	2.3	Female	2.56	3.01	3.01	3.14	3.10	
1989	2.2	Male	1.71	1.99	2.24	2.12	2.04	2.03 1.92 3.34 2.85
	2.2	Female	1.63	1.81	2.00	2.06	2.11	
	2.3	Male	2.64	3.26	3.51	3.61	3.76	
	2.3	Female	2.31	2.76	3.02	2.94	3.37	
1990	2.2	Male	1.94	2.37	2.69	3.10	2.21	2.30 2.15 3.58 3.02
	2.2	Female	1.85	2.19	2.34	2.43	2.48	
	2.3	Male	2.73	3.39	3.81	3.71	3.75	
	2.3	Female	2.49	2.84	3.08	3.10	3.30	

Table 34 (appendix). Body length of adult Kamchatka *R. sockeye* from marine trap net catches in 1978-1989, cm

Year	Male						Female					
	Early run			Late run			Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
1978	30.5-67.5	58.38 ± 0.47	113	34.0-70.0	58.59 ± 0.70	108	48.0-60.0	54.40 ± 0.24	88	46.5-65.6	57.54 ± 0.27	136
1979	34.0-67.0	56.47 ± 0.70	117	33.5-72.0	60.38 ± 0.74	89	48.0-67.5	56.16 ± 0.26	108	35.5-67.5	57.19 ± 0.47	87
1980	41.5-67.5	57.25 ± 0.62	134	54.0-69.0	62.11 ± 0.52	35	52.0-59.5	56.15 ± 0.17	85	54.0-62.5	57.76 ± 0.32	33
1981	34.0-69.0	59.17 ± 0.53	146	-	-	-	46.0-63.0	56.52 ± 0.26	102	-	-	-
1982	35.0-66.0	55.31 ± 0.66	130	48.0-65.0	58.83 ± 1.27	21	45.5-63.0	55.71 ± 0.26	117	49.0-61.0	55.19 ± 0.71	29
1983	41.0-62.0	56.05 ± 1.10	21	56.0-79.0	65.31 ± 0.40	60	47.0-66.0	53.38 ± 0.72	26	57.0-64.5	60.57 ± 0.30	37
1984	45.5-66.0	60.35 ± 0.37	78	47.0-68.0	58.83 ± 0.85	53	50.0-63.5	56.21 ± 0.32	70	48.0-65.0	57.68 ± 0.35	93
1985	49.0-73.0	64.00 ± 0.42	103	51.0-69.5	63.90 ± 1.06	26	51.0-66.0	59.97 ± 0.28	92	57.0-67.0	62.05 ± 0.51	22
1986	40.0-71.0	59.85 ± 0.50	134	55.0-69.0	63.96 ± 0.57	46	43.0-69.0	56.31 ± 0.57	60	52.0-65.0	59.39 ± 0.47	33
1987	52.5-73.0	63.90 ± 0.30	148	47.0-77.0	67.36 ± 0.50	109	53.0-66.0	59.49 ± 0.24	98	52.0-69.0	63.25 ± 0.27	126
1988	45.0-72.0	62.05 ± 0.90	48	47.0-73.0	61.02 ± 0.83	72	49.0-67.5	59.88 ± 0.50	47	51.0-69.0	60.08 ± 0.50	75
1989	43.0-68.0	59.48 ± 0.70	54	46.5-68.5	61.56 ± 0.42	99	50.0-66.5	55.81 ± 0.42	49	48.0-66.0	57.46 ± 0.33	101
Average 1978-1989	55.3-64.1	59.36 ± 0.84	12*	58.6-67.4	61.99 ± 0.87	11*	53.4-60.0	56.67 ± 0.60	12*	55.2-63.3	58.92 ± 0.72	11*

*Data signifies the number of observations years.

Table 35 (appendix). Body weight of adult Kamchatka *R. sockeye* from marine trap net catches in 1978-1989, kg

Year	Male						Female					
	Early run			Late run			Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
1978	0.57-4.26	2.665 ± 0.053	113	0.48-4.92	2.734 ± 0.094	108	1.25-2.91	2.107 ± 0.032	88	0.97-4.00	2.516 ± 0.040	136
1979	0.48-3.90	2.331 ± 0.079	117	0.43-4.24	2.874 ± 0.087	89	1.20-3.13	2.148 ± 0.034	108	1.00-4.05	2.373 ± 0.054	87
1980	0.81-4.15	2.483 ± 0.073	134	2.00-4.75	3.139 ± 0.093	35	1.61-2.90	2.214 ± 0.027	85	1.85-3.00	2.369 ± 0.045	33
1981	0.47-4.10	2.653 ± 0.062	146	-	-	-	1.00-3.28	2.261 ± 0.036	102	-	-	-
1982	0.51-4.20	2.308 ± 0.084	130	1.20-3.73	2.784 ± 0.180	21	1.14-3.46	2.245 ± 0.036	117	1.44-2.97	2.173 ± 0.086	29
1983	1.00-3.14	2.357 ± 0.142	21	2.01-4.00	3.019 ± 0.050	60	1.20-3.76	2.108 ± 0.091	26	1.91-3.22	2.454 ± 0.049	37
1984	1.11-4.22	2.794 ± 0.067	78	1.15-4.48	2.704 ± 0.120	53	1.59-3.17	2.167 ± 0.043	70	1.19-3.23	2.438 ± 0.049	93
1985	1.30-4.75	2.946 ± 0.058	103	1.40-3.75	2.877 ± 0.137	26	1.44-4.50	2.451 ± 0.047	92	2.00-3.61	2.707 ± 0.093	22
1986	0.82-4.93	2.846 ± 0.068	134	2.08-4.34	3.466 ± 0.091	46	1.20-3.98	2.193 ± 0.061	60	1.91-3.20	2.643 ± 0.061	33
1987	1.26-4.40	2.832 ± 0.046	148	1.00-4.55	3.185 ± 0.076	109	1.50-3.03	2.257 ± 0.033	98	1.30-5.20	2.530 ± 0.041	126
1988	0.91-3.92	2.475 ± 0.104	48	1.05-4.20	2.457 ± 0.097	72	1.20-3.15	2.184 ± 0.061	47	1.30-3.55	2.256 ± 0.059	75
1989	0.96-4.51	2.784 ± 0.087	54	1.02-4.51	3.078 ± 0.070	99	1.73-3.00	2.268 ± 0.047	49	1.30-3.55	2.405 ± 0.046	101
Average 1978-1989	2.31-2.95	2.623 ± 0.065	12*	2.46-3.47	2.938 ± 0.083	11*	2.11-2.46	2.217 ± 0.027	12*	2.17-2.71	2.442 ± 0.047	11*

*Data signifies the number of observations years.

Table 36 (appendix). Average body length adult specimens from local second order stocks and their groups of the Kamchatka R. sockeye from marine trap nets in 1978-1989 (data for early and late sockeye runs are combined), cm

Stock, group of stocks	Male						Female					
	Early run			Late run			Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
"S"	43.0-72.0	61.70 ± 0.38	139	49.0-73.0	63.99 ± 0.54	66	50.0-67.0	57.70 ± 0.35	106	50.0-69.0	59.72 ± 0.43	89
"V"	43.0-67.5	60.53 ± 0.59	73	42.0-72.5	60.07 ± 0.55	162	49.5-66.0	56.62 ± 0.46	58	47.0-68.0	58.10 ± 0.32	168
"E"	36.5-73.0	59.61 ± 0.26	562	34.0-77.0	62.44 ± 0.44	200	46.0-69.0	56.85 ± 0.15	439	35.5-69.0	58.99 ± 0.26	229
"N"	55.0-67.0	60.95 ± 0.54	32	43.5-71.0	61.11 ± 0.98	27	47.0-63.5	57.59 ± 0.61	35	49.5-65.0	57.82 ± 0.59	34
"A"	30.5-73.0	57.95 ± 0.45	327	34.5-79.0	63.35 ± 0.46	203	45.5-66.5	56.40 ± 0.22	219	47.0-68.5	59.83 ± 0.29	196
"D"	44.0-68.0	59.80 ± 0.50	94	50.0-71.0	61.14 ± 0.58	56	43.0-61.0	56.36 ± 0.38	82	50.5-67.0	57.44 ± 0.62	50

Table 37 (appendix). Average body weight adult specimens from local second order stocks and their groups of the Kamchatka R. sockeye from marine trap nets in 1978-1989 (data for early and late sockeye runs are combined), kg

Stock, group of stocks	Male						Female					
	Early run			Late run			Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
"S"	0.87-4.22	2.907 ± 0.045	139	1.40-4.92	3.243 ± 0.084	66	1.57-3.76	2.334 ± 0.037	106	1.45-4.05	2.598 ± 0.054	89
"V"	0.89-4.26	2.823 ± 0.082	73	0.80-4.32	2.674 ± 0.071	162	1.41-3.88	2.238 ± 0.050	58	1.19-3.47	2.328 ± 0.035	168
"E"	0.50-4.93	2.700 ± 0.031	562	0.48-4.55	2.997 ± 0.054	200	1.14-4.50	2.271 ± 0.018	439	0.97-3.61	2.475 ± 0.028	229
"N"	2.22-3.70	2.817 ± 0.062	32	1.08-4.00	3.023 ± 0.133	27	1.34-3.08	2.307 ± 0.060	35	1.44-3.17	2.405 ± 0.075	34
"A"	0.47-4.50	2.429 ± 0.050	327	0.43-4.51	3.079 ± 0.054	203	1.15-3.17	2.120 ± 0.023	219	1.00-5.20	2.513 ± 0.034	196
"D"	1.01-3.98	2.391 ± 0.060	94	1.51-4.01	2.594 ± 0.088	56	1.20-3.98	2.104 ± 0.041	82	1.30-3.13	2.116 ± 0.067	50

Table 38 (appendix). Length and body weight of early run adult *Bolshaya R. sockeye* in 1973-1990

Year	Male						Female					
	Length, cm		Weight, kg		Number of fish	Number of fish	Length, cm		Weight, kg		Number of fish	
	Range	Average	Range	Average			Range	Average	Range	Average		
1973	—	62.0	—	2.65	—	—	58.5	—	2.21	—	—	
1974	—	53.5	—	1.80	—	—	58.1	—	1.90	—	—	
1975	—	60.5	—	2.37	—	—	56.6	—	2.10	—	—	
1976	—	56.1	—	2.81	—	—	52.3	—	2.28	—	—	
1977	—	—	—	—	—	—	—	—	—	—	—	
1978	—	55.6	—	2.32	—	—	53.5	—	2.06	—	—	
1979	—	58.3	—	2.60	—	—	56.1	—	2.27	—	—	
1980	—	53.3	—	2.08	—	—	56.0	—	2.36	—	—	
1981	—	55.7	—	2.15	—	—	56.3	—	2.13	—	—	
1982	—	—	—	—	—	—	—	—	—	—	—	
1983	—	50.6	—	1.44	—	—	56.0	—	1.87	—	—	
1984	—	—	—	—	—	—	—	—	—	—	—	
1985	—	53.3	—	1.98	—	—	55.0	—	2.04	—	—	
1986	43.0–68.0	58.54 ± 0.71	0.82–3.56	2.346 ± 0.075	100	51.0–63.0	57.26 ± 0.19	1.53–5.80	2.165 ± 0.037	129	—	
1987	45.0–69.0	59.94 ± 0.60	0.99–4.80	2.461 ± 0.066	110	52.0–64.0	57.15 ± 0.22	1.41–2.74	2.070 ± 0.025	117	—	
1988	—	—	—	—	—	—	—	—	—	—	—	
1989	52.0–71.0	62.61 ± 0.31	1.55–4.35	2.778 ± 0.042	132	50.0–69.0	58.71 ± 0.22	1.34–3.89	2.277 ± 0.026	211	—	
1990	43.0–67.5	60.83 ± 1.40	1.00–3.86	2.975 ± 0.175	21	50.5–61.5	55.91 ± 0.49	1.67–3.03	2.231 ± 0.060	33	—	
Average 1973–1990	50.6–2.61	57.20 ± 1.00	1.440–2.975	2.340 ± 0.113	14*	52.30–8.71	56.25 ± 0.48	1.870–2.360	2.140 ± 0.039	14*	—	

*Data signifies the number of observations years. 1973–1985 – data from T. V. Yegorova (KotINRO archives).

Table 39 (appendix). Length and body weight of late run adult *Bolshaya R. sockeye* in 1973-1990

Year	Male				Female				
	Length, cm		Weight, kg		Number of fish	Length, cm		Weight, kg	
	Range	Average	Range	Average		Range	Average	Range	Average
1973	-	66.0	-	3.53	-	61.5	-	3.13	-
1974	-	65.6	-	3.77	-	63.6	-	2.88	-
1975	-	62.0	-	2.93	-	58.4	-	2.80	-
1976	-	62.9	-	3.42	-	59.3	-	2.92	-
1977	-	64.3	-	3.50	-	60.5	-	2.78	-
1978	-	63.1	-	3.43	-	58.7	-	2.85	-
1979	-	62.6	-	3.25	-	61.8	-	2.91	-
1980	-	59.2	-	2.68	-	57.6	-	2.45	-
1981	-	59.3	-	2.80	-	60.1	-	2.80	-
1982	-	65.8	-	3.53	-	62.8	-	2.84	-
1983	-	62.6	-	2.67	-	59.5	-	2.57	-
1984	-	-	-	-	-	-	-	-	-
1985	-	60.8	-	3.37	93	58.6	-	2.83	-
1986	50.0-76.0	68.54 ± 0.56	1.33-5.71	3.802 ± 0.084	142	64.63 ± 0.28	55.0-76.0	3.172 ± 0.042	95
1987	40.0-75.0	64.49 ± 0.61	0.59-5.11	3.231 ± 0.082	44	63.44 ± 0.24	48.0-71.0	2.960 ± 0.037	168
1988	51.0-72.0	66.59 ± 0.61	1.48-4.70	3.524 ± 0.112	28	63.33 ± 0.34	59.0-67.0	2.976 ± 0.062	45
1989	56.0-75.0	67.14 ± 0.83	1.87-4.80	3.537 ± 0.135	85	62.82 ± 0.28	59.0-66.0	2.933 ± 0.064	38
1990	52.0-73.0	67.95 ± 0.44	1.60-5.09	3.902 ± 0.072	-	63.87 ± 0.28	55.0-74.0	3.121 ± 0.045	115
Average 1973-1990	62.00-68.54	64.05 ± 0.69	2.670-3.902	3.346 ± 0.091	17*	61.21 ± 0.55	57.60-4.63	2.878 ± 0.044	17*

*Data signifies the number of observations years. 1973-1985 - data from T. V. Yegorova (KoTINRO archives).

Table 40 (appendix). Length and body weight of adult *Khailiyuba R. sockeye* in 1977-1991

Year	Male						Female					
	Length, cm		Weight, kg		Number of fish		Length, cm		Weight, kg		Number of fish	
	Range	Average	Range	Average			Range	Average	Range	Average		
1977	59.5-70.5	66.27 ± 0.56	2.80-4.50	3.976 ± 0.106	22		57.0-65.0	60.96 ± 0.36	2.38-3.73	3.029 ± 0.072	27	
1978	—	—	—	—	—		—	—	—	—	—	
1979	49.5-73.5	65.81 ± 0.52	1.45-5.49	3.672 ± 0.082	85		51.0-68.5	61.61 ± 0.25	1.49-4.13	3.042 ± 0.042	96	
1980	46.5-72.5	64.78 ± 0.69	1.09-5.34	3.661 ± 0.109	60		51.5-66.0	60.24 ± 0.37	1.84-4.09	2.920 ± 0.061	44	
1981	57.0-72.5	65.90 ± 0.36	2.10-5.00	3.650 ± 0.071	51		55.0-63.5	59.96 ± 0.32	1.80-3.40	2.772 ± 0.054	36	
1982	41.0-71.0	62.97 ± 1.32	0.85-4.91	3.545 ± 0.196	29		56.0-67.5	61.33 ± 0.37	2.24-3.62	3.076 ± 0.044	38	
1983	46.0-68.0	60.52 ± 0.88	1.30-4.27	2.973 ± 0.117	47		51.0-62.5	58.21 ± 0.33	1.08-3.26	2.579 ± 0.059	50	
1984	—	—	—	—	—		—	—	—	—	—	
1985	—	—	—	—	—		—	—	—	—	—	
1986	36.0-73.5	65.01 ± 0.73	0.52-4.94	3.724 ± 0.103	80		53.0-68.0	61.97 ± 0.38	1.67-4.41	3.074 ± 0.068	50	
1987	40.0-72.0	63.84 ± 0.66	0.78-6.80	3.662 ± 0.098	80		53.5-65.0	60.18 ± 0.32	1.95-3.88	2.948 ± 0.051	63	
1988	46.0-73.5	62.96 ± 0.76	1.35-5.44	3.674 ± 0.123	77		53.0-65.0	59.82 ± 0.33	2.04-4.06	3.056 ± 0.058	56	
1989	45.0-71.0	59.41 ± 1.22	1.30-5.07	2.955 ± 0.169	48		46.0-64.0	58.85 ± 0.45	1.29-3.62	2.758 ± 0.062	51	
1990	41.0-73.5	61.30 ± 2.36	0.86-5.67	3.486 ± 0.372	15		54.0-68.0	60.97 ± 0.95	2.16-4.95	3.390 ± 0.168	19	
1991	52.0-67.5	63.25 ± 0.73	1.90-4.41	3.660 ± 0.132	22		54.0-65.0	59.53 ± 0.49	2.20-3.86	2.983 ± 0.070	31	
Average 1977-1991	59.41-5.81	63.50 ± 0.64	2.955-3.976	3.554 ± 0.086	12*		58.21-61.97	60.30 ± 0.32	2.579-3.390	2.969 ± 0.059	12*	

*Data signifies the number of observations years.

Table 41 (appendix). Average body length adult Kamchatka R. sockeye from marine trap net catches in 1978-1989 (most abundant age groups), cm

Year	0.3		0.4		1.2		2.1		1.3		2.2		1.4		2.3		2.4		Average	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Early run																				
1978	59.07	55.21	59.00	45.37	48.00	30.50	59.50	54.45	43.00	49.00	—	59.11	54.47	—	58.38	54.40				
1979	60.39	55.89	61.00	45.57	51.00	36.25	60.20	56.25	46.92	53.0	63.87	56.93	66.00	56.47	56.16					
1980	61.00	56.75	64.25	43.62	—	—	60.46	56.27	45.95	—	63.33	60.38	—	57.25	56.15					
1981	60.07	56.00	65.25	45.68	46.00	34.00	61.00	56.54	46.84	—	63.00	60.98	65.50	59.17	56.52					
1982	62.08	55.79	59.00	46.65	50.00	35.00	59.76	55.71	49.07	50.37	62.25	59.43	66.00	55.31	55.71					
1983	—	53.00	66.00	48.67	50.50	—	58.33	53.50	50.00	50.00	—	—	58.00	56.05	53.38					
1984	59.83	56.70	65.50	55.00	—	—	60.74	56.24	—	52.25	59.50	57.13	—	56.05	56.21					
1985	64.00	58.00	63.00	—	—	—	63.41	60.26	52.75	—	68.28	62.61	71.30	64.10	59.97					
1986	60.69	57.00	64.50	44.63	53.33	—	61.76	57.97	50.61	49.00	62.33	60.90	65.90	59.85	56.31					
1987	64.13	59.23	68.75	—	—	—	64.43	60.28	55.67	54.00	—	63.41	58.20	63.90	59.49					
1988	65.20	59.00	69.60	46.00	—	—	62.37	57.50	45.00	—	72.00	64.40	66.00	62.05	59.88					
1989	59.95	55.67	58.67	44.50	—	—	60.37	54.78	45.00	—	66.00	60.86	65.00	59.48	55.81					
Average 1978–1989	61.49	56.52	63.43	46.57	49.81	33.94	61.03	56.65	48.26	51.09	64.51	60.46	66.19	58.67	59.36	56.67				
Late run																				
1978	63.15	58.63	70.00	46.90	52.61	—	61.09	57.48	51.19	55.00	65.00	62.17	59.00	65.50	58.59	57.54				
1979	61.89	56.59	67.00	44.17	48.00	34.33	62.02	57.74	55.20	52.70	68.87	61.59	58.35	—	60.38	57.19				
1980	64.50	57.50	65.00	—	—	—	62.36	57.63	54.50	—	—	60.30	57.50	—	62.11	57.76				
1981	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
1982	61.00	—	—	51.58	51.17	—	60.94	55.68	—	51.00	—	63.30	57.32	—	58.83	55.19				
1983	64.80	59.00	64.00	56.00	—	—	64.94	60.50	—	—	—	66.97	60.18	62.00	63.31	60.57				
1984	—	57.50	68.00	48.75	49.87	—	60.40	58.60	51.75	53.56	—	62.56	57.81	58.00	58.83	57.68				
1985	67.00	60.50	—	56.00	—	—	65.50	60.87	53.50	—	67.50	65.17	62.60	—	63.90	62.05				
1986	67.50	—	—	—	—	—	63.78	59.21	56.00	—	—	64.24	59.47	62.25	63.96	59.39				
1987	68.56	63.32	72.50	48.50	52.00	—	68.77	63.09	57.00	57.40	77.00	67.47	63.97	73.25	67.36	63.25				
1988	60.00	59.58	72.00	49.06	53.33	—	61.98	58.85	53.83	—	69.75	63.69	59.67	64.71	61.02	60.08				
1989	59.77	58.41	—	47.25	49.50	—	61.68	57.14	56.63	52.56	65.70	62.78	57.29	60.70	61.56	57.46				
Average 1978–1989	63.82	59.00	69.08	49.80	50.93	34.33	63.04	58.80	54.40	53.70	68.97	63.66	59.38	67.06	61.99	58.92				

Table 42 (appendix). Average body weight adult Kamchatka R. sockeye from marine trap net catches in 1978-1989 (most abundant age groups), kg

Year	0.3		0.4		1.2		2.1		1.3		2.2		1.4		2.3		2.4		Average		
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Early run																					
1978	2.780	2.289	—	2.650	1.133	1.250	0.570	2.793	2.125	0.945	1.400	—	—	—	2.649	2.061	—	—	2.665	2.107	
1979	2.739	2.069	2.857	2.293	1.200	1.800	0.525	2.729	2.165	1.260	1.653	3.390	2.434	2.309	2.081	3.400	2.570	2.331	2.148		
1980	2.895	2.395	3.635	2.450	0.986	—	—	2.861	2.238	1.444	—	3.267	—	2.730	2.031	—	1.850	2.483	2.214		
1981	2.696	2.157	3.450	2.560	1.237	1.000	0.470	2.867	2.260	1.227	—	3.253	2.830	2.780	2.131	3.700	—	2.653	2.261		
1982	3.138	2.350	2.787	3.037	1.260	1.610	0.510	2.877	2.234	1.413	1.577	3.110	2.653	2.713	2.194	4.170	2.580	2.308	2.245		
1983	—	2.106	2.300	3.760	1.253	2.020	—	2.675	2.105	1.200	1.700	—	2.680	—	1.580	—	—	2.357	2.108		
1984	2.782	2.146	3.935	—	1.490	—	—	2.881	2.275	—	1.780	2.930	2.243	2.602	2.066	2.560	2.100	2.794	2.167		
1985	2.954	2.270	—	2.825	—	—	—	2.926	2.513	1.565	—	3.624	2.777	2.783	2.284	3.868	2.487	2.946	2.451		
1986	2.920	2.353	3.500	—	1.121	1.650	—	3.152	2.391	1.626	1.634	3.808	2.025	2.879	2.154	3.655	2.403	2.846	2.193		
1987	2.926	2.235	3.500	2.620	—	—	—	2.908	2.357	1.860	1.570	—	2.885	2.682	2.101	3.895	—	2.832	2.257		
1988	2.964	2.000	3.484	2.545	1.000	—	—	2.537	1.961	0.910	—	3.720	2.764	2.109	1.931	2.800	2.403	2.475	2.184		
1989	2.836	2.259	—	2.540	1.150	—	—	2.874	2.236	0.970	—	4.510	2.255	2.911	2.269	3.100	2.217	2.784	2.268		
Average 1978-1989	2.875	2.219	3.272	2.728	1.183	1.555	0.519	2.840	2.238	1.284	1.616	3.512	2.555	2.650	2.074	3.461	2.326	2.623	2.217		
Late run																					
1978	3.461	2.805	4.920	3.850	1.255	1.822	—	3.002	2.482	1.671	2.100	3.630	—	3.220	2.690	—	—	2.734	2.516		
1979	3.028	2.391	4.240	3.120	1.010	1.815	0.447	3.068	2.390	2.112	1.746	3.907	3.035	2.907	2.296	—	—	2.874	2.373		
1980	3.485	2.250	3.875	2.825	—	—	—	3.096	2.327	2.150	—	—	2.350	3.120	2.430	—	—	3.139	2.369		
1981	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
1982	3.050	—	—	—	1.745	1.700	—	3.104	2.281	—	1.653	—	—	—	2.385	—	—	2.784	2.173		
1983	2.976	2.100	—	2.970	2.010	—	—	2.979	2.469	—	—	—	3.000	3.193	2.382	—	—	3.019	2.454		
1984	—	2.310	4.480	2.800	1.323	1.395	—	2.833	2.526	1.861	1.853	—	2.993	3.257	2.480	1.980	2.750	2.704	2.438		
1985	3.220	2.400	—	—	1.885	—	—	3.129	2.601	1.705	—	3.385	3.167	2.898	2.656	—	—	2.877	2.707		
1986	4.210	—	—	—	—	—	—	3.519	2.589	2.135	—	—	—	3.457	2.653	—	3.260	3.466	2.643		
1987	3.251	2.561	3.800	2.527	1.107	1.300	—	3.383	2.517	1.570	1.756	4.550	2.642	3.206	2.610	—	—	3.185	2.530		
1988	2.525	2.068	3.520	3.088	1.153	1.527	—	2.496	2.152	2.543	—	3.450	2.400	2.687	2.150	4.000	2.826	2.457	2.256		
1989	2.784	2.472	—	2.340	1.060	1.450	—	3.124	2.389	2.093	1.727	3.844	2.997	3.198	2.328	3.830	2.830	3.078	2.405		
Average 1978-1989	3.199	2.373	4.139	2.940	1.394	1.573	0.447	3.067	2.429	1.982	1.806	3.794	2.823	3.141	2.460	3.391	2.968	2.938	2.442		

Table 43 (appendix). Average body length of adult Kamchatka *R. sockeye* aged 1.3 and 2.3 years from marine trap net catches in 1978-1989 (principal age groups), cm

Year	Male				Female			
	1.3	Number of fish	2.3	Number of fish	1.3	Number of fish	2.3	Number of fish
	Average		Average		Average		Average	
Early run								
1978	59.50 ± 0.29	86	59.11 ± 0.63	13	54.45 ± 0.27	60	54.47 ± 0.42	12
1979	60.20 ± 0.44	49	56.93 ± 1.65	14	56.25 ± 0.28	60	55.61 ± 0.59	14
1980	60.46 ± 0.32	78	60.38 ± 0.82	21	56.27 ± 0.17	62	55.20 ± 0.46	15
1981	61.00 ± 0.42	61	60.98 ± 0.42	47	56.54 ± 0.30	47	55.70 ± 0.35	37
1982	59.76 ± 0.57	57	59.43 ± 1.05	14	55.71 ± 0.21	78	55.65 ± 0.47	13
1983	58.33 ± 0.71	15	–	–	53.50 ± 0.33	13	50.85 ± 2.68	3
1984	60.74 ± 0.38	41	59.50 ± 0.90	23	56.24 ± 0.47	31	56.26 ± 0.52	27
1985	63.41 ± 0.62	38	63.56 ± 0.51	44	60.26 ± 0.33	38	58.78 ± 0.43	38
1986	61.76 ± 0.46	42	60.90 ± 0.58	46	57.97 ± 0.87	17	56.44 ± 0.64	25
1987	64.43 ± 0.37	74	63.41 ± 0.56	38	60.28 ± 0.25	44	58.20 ± 0.42	35
1988	62.37 ± 1.08	15	60.00 ± 1.12	19	57.50 ± 0.81	15	58.54 ± 0.41	12
1989	60.37 ± 0.74	15	60.86 ± 0.60	22	54.79 ± 0.51	19	56.34 ± 0.99	16
Average 1978–1989	61.03 ± 0.49	12*	60.46 ± 0.57	11*	56.65 ± 0.60	12*	56.00 ± 0.61	12*
Late run								
1978	61.09 ± 0.56	60	62.17 ± 0.44	9	57.48 ± 0.26	99	59.00 ± 0.79	7
1979	62.02 ± 0.47	48	61.59 ± 0.73	16	57.74 ± 0.40	45	58.35 ± 1.21	10
1980	62.36 ± 0.45	25	60.30 ± 1.70	5	57.63 ± 0.39	23	57.50 ± 0.45	5
1981	–	–	–	–	–	–	–	–
1982	60.94 ± 1.45	9	60.30 ± 0.92	5	55.68 ± 1.12	11	57.32 ± 0.84	11
1983	64.94 ± 0.40	33	66.97 ± 0.91	16	60.50 ± 0.32	19	60.18 ± 0.55	14
1984	60.40 ± 0.95	20	62.56 ± 0.77	18	58.60 ± 0.37	41	57.81 ± 0.59	27
1985	65.50 ± 1.17	12	65.17 ± 1.70	6	60.87 ± 0.53	12	62.60 ± 0.83	5
1986	63.78 ± 1.06	16	64.24 ± 0.60	25	59.21 ± 0.85	14	59.47 ± 0.52	16
1987	68.77 ± 0.45	40	67.47 ± 0.52	50	63.09 ± 0.36	51	63.97 ± 0.35	47
1988	61.98 ± 0.98	30	63.69 ± 0.95	24	58.85 ± 0.66	31	59.67 ± 0.83	18
1989	61.68 ± 0.48	51	62.78 ± 0.68	23	57.14 ± 0.40	38	57.29 ± 0.46	21
Average 1978–1989	63.04 ± 0.76	11*	63.66 ± 0.66	11*	58.80 ± 0.62	11*	59.38 ± 0.66	11*

*Data signifies the number of observations years.

Table 44 (appendix). Average body weight of adult Kamchatka *R. sockeye* aged 1.3 and 2.3 years from marine trap net catches in 1978-1989 (principal age groups), kg

Year	Male				Female			
	1.3	Number of fish	2.3	Number of fish	1.3	Number of fish	2.3	Number of fish
	Average		Average		Average		Average	
Early run								
1978	2.793 ±0.040	86	2.649 ±0.110	12	2.125 ±0.034	60	2.061 ±0.071	16
1479	2.729 ±0.082	49	2.309 ±0.192	14	2.165 ±0.045	60	2.081 ±0.077	14
1980	2.861 ±0.046	78	2.730 ±0.124	21	2.238 ±0.026	62	2.031 ±0.083	15
1981	2.867 ±0.064	61	2.780 ±0.059	47	2.260 ±0.039	47	2.131 ±0.051	37
1982	2.877 ±0.088	57	2.713 ±0.164	14	2.234 ±0.034	78	2.194 ±0.066	13
1983	2.675 ±0.093	15	–	–	2.105 ±0.058	13	1.580 ±0.265	3
1984	2.881 ±0.079	41	2.602 ±0.136	23	2.275 ±0.062	31	2.066 ±0.064	27
1985	2.926 ±0.088	38	2.783 ±0.065	44	2.513 ±0.080	38	2.284 ±0.058	38
1986	3.152 ±0.086	42	2.879 ±0.093	46	2.391 ±0.095	17	2.154 ±0.096	25
1987	2.908 ±0.059	74	2.682 ±0.085	38	2.357 ±0.044	44	2.101 ±0.048	35
1988	2.537 ±0.126	15	2.109 ±0.115	19	1.961 ±0.080	15	1.931 ±0.062	12
1989	2.874 ±0.121	15	2.911 ±0.082	22	2.236 ±0.077	19	2.269 ±0.090	16
Average 1978–1989	2.840 ±0.043	12*	2.650 ±0.073	11*	2.238 ±0.041	12*	2.074 ±0.053	12*
Late run								
1978	3.002 ±0.091	60	3.220 ±0.102	9	2.482 ±0.039	99	2.690 ±0.122	7
1479	3.068 ±0.073	48	2.907 ±0.120	16	2.390 ±0.052	45	2.296 ±0.192	10
1980	3.096 ±0.090	25	3.120 ±0.245	5	2.327 ±0.050	23	2.430 ±0.112	5
1981	–	–	–	–	–	–	–	–
1982	3.104 ±0.194	9	3.402 ±0.131	5	2.281 ±0.144	11	2.385 ±0.101	11
1983	2.979 ±0.058	33	3.193 ±0.095	16	2.469 ±0.056	19	2.382 ±0.087	14
1984	2.833 ±0.138	20	3.257 ±0.124	18	2.526 ±0.051	41	2.480 ±0.085	27
1985	3.129 ±0.177	12	2.898 ±0.175	6	2.601 ±0.139	12	2.656 ±0.103	5
1986	3.519 ±0.154	16	3.457 ±0.104	25	2.589 ±0.093	14	2.653 ±0.085	16
1987	3.383 ±0.080	40	3.206 ±0.103	50	2.517 ±0.046	51	2.610 ±0.075	47
1988	2.496 ±0.119	30	2.687 ±0.102	24	2.152 ±0.069	31	2.150 ±0.109	18
1989	3.124 ±0.078	51	3.198 ±0.126	23	2.389 ±0.051	38	2.328 ±0.078	21
Average 1978–1989	3.067 ±0.080	11*	3.141 ±0.069	11*	2.429 ±0.041	11*	2.460 ±0.053	11*

*Data signifies the number of observations years.

Table 45 (appendix). Average body length of adults from some of Asian sockeye (most common age groups), cm

Watershed	Year	Male				Female			
		1.3		2.3		1.3		2.3	
		Average	Number of fish	Average	Number of fish	Average	Number of fish	Average	Number of fish
Okhota R. Kykhtuy R. Palana R. -- Tigil R. Khairyuzova R. -- Icha R. -- -- Vorovskaya R. -- -- Kikhcik R. Bolshaya R. (early run)	1983	60.28 ± 0.75	22	59.19 ± 1.34	8	57.27 ± 0.30	43	55.06 ± 1.05	8
	1981	59.18 ± 0.57	33	58.93 ± 0.98	6	57.49 ± 0.45	35	56.63 ± 0.76	9
	1983	--	--	65.10 ± 0.31	130	--	--	62.35 ± 0.20	146
	1990	--	--	67.85 ± 0.60	24	--	--	61.96 ± 0.63	14
	1981	63.83 ± 1.46	12	--	--	59.83 ± 0.94	18	--	--
	1984	64.24 ± 0.24	113	--	--	59.92 ± 0.15	158	59.60 ± 1.33	5
	1986	64.63 ± 0.51	30	--	--	61.21 ± 0.29	53	61.00 ± 0.86	6
	1989	64.67 ± 0.41	27	--	--	59.39 ± 0.41	21	--	--
	1986	70.26 ± 0.33	23	--	--	66.20 ± 0.39	25	--	--
	1989	67.93 ± 0.35	29	68.67 ± 1.09	6	65.57 ± 0.44	35	--	--
	1965	69.95 ± 0.55	38	68.70 ± 2.40	5	64.71 ± 0.35	39	--	--
	1989	61.90 ± 1.15	10	60.75 ± 0.98	12	57.29 ± 0.41	12	58.68 ± 0.64	17
	1990	62.66 ± 0.38	47	62.14 ± 0.67	31	57.54 ± 0.32	79	58.81 ± 0.54	21
	1989	68.75 ± 0.54	24	--	--	63.30 ± 0.59	20	--	--
1987–1989	60.37 ± 1.31	6*	--	--	56.51 ± 0.94	6*	--	--	
Bolshaya R. (late run)	1986–1990	67.95 ± 0.67	8*	--	--	63.59 ± 0.26	8*	--	--
Ozernaya R. Kamchatka R. (early run)	1970–1991	62.47 ± 1.32	9*	63.22 ± 0.21	22*	59.85 ± 0.77	10*	60.22 ± 0.23	22*
	1978–1989	61.03 ± 0.49	12*	60.46 ± 0.57	11*	56.65 ± 0.60	12*	56.00 ± 0.61	12*
Kamchatka R. (late run)	1978–1989	63.04 ± 0.76	11*	66.66 ± 0.66	11*	58.62 ± 0.69	11*	59.38 ± 0.66	11*
Avacha R. -- --	1988	66.83 ± 0.83	6	63.24 ± 0.55	29	59.57 ± 1.56	7	60.56 ± 0.68	18
	1989	59.40 ± 4.08	5	63.79 ± 0.32	109	60.71 ± 1.11	7	60.17 ± 0.32	71
	1990	--	--	59.61 ± 0.39	75	64.83 ± 0.87	6	57.14 ± 0.41	73
Stolbovaya R.	1984	66.65 ± 0.48	34	68.10 ± 1.00	10	62.40 ± 0.41	42	61.17 ± 1.01	6
Malamvayam R.	1983	62.82 ± 1.07	22	63.69 ± 0.94	16	58.63 ± 0.75	15	57.38 ± 0.41	21
Khailulya R.	1977–1991	64.49 ± 0.38	12*	--	--	60.07 ± 0.32	12*	--	--
Ivashka R.	1966	68.37 ± 1.46	19	--	--	62.82 ± 0.59	22	--	--
Karaga R. --	1988	60.67 ± 0.43	75	60.05 ± 0.54	11	56.84 ± 0.38	63	57.83 ± 0.87	9
	1989	64.27 ± 0.23	110	--	--	59.91 ± 0.18	141	59.70 ± 0.83	5

Continued, Table 45 (appendix)

Watershed	Year	Male				Female			
		1.3		2.3		1.3		2.3	
		Average	Number of fish	Average	Number of fish	Average	Number of fish	Average	Number of fish
Tymlat R.	1973	67.91 ± 0.65	32	–	–	63.35 ± 0.49	33	–	–
Kichiga R. –“– –“– –“–	1981	66.76 ± 0.42	45	–	–	60.58 ± 0.32	38	–	–
	1982	63.74 ± 0.54	19	–	–	58.53 ± 0.51	17	–	–
	1989	69.94 ± 0.90	16	–	–	63.67 ± 0.56	24	–	–
	1990	71.05 ± 0.45	31	70.20 ± 0.98	5	64.66 ± 0.48	37	–	–
Avyayayam R. –“– –“–	1985	65.07 ± 0.69	48	–	–	62.12 ± 0.52	33	–	–
	1986	65.92 ± 0.53	90	–	–	61.70 ± 0.16	183	–	–
	1989	67.73 ± 1.25	26	71.29 ± 0.36	29	64.54 ± 0.61	27	66.56 ± 0.61	16
Kultushmaya R.	1983	–	–	63.31 ± 0.72	13	–	–	59.39 ± 0.79	23
Apuka R. –“– –“– –“–	1980	69.17 ± 1.01	20	–	–	62.27 ± 0.55	20	–	–
	1985	66.74 ± 0.56	36	–	–	61.27 ± 0.32	43	–	–
	1989	68.64 ± 0.45	42	69.47 ± 0.71	19	62.40 ± 0.34	41	63.29 ± 1.36	7
	1990	68.11 ± 1.09	23	–	–	63.47 ± 0.33	48	63.64 ± 0.99	7
Ananapylgen R.	1980	–	–	62.88 ± 1.00	17	–	–	59.40 ± 0.62	15
Ukalayat R.	1989	67.41 ± 0.29	53	65.71 ± 0.79	7	61.11 ± 0.22	65	61.17 ± 1.35	6
Tumanskaya R.	1928	64.46 ± 1.27	12	67.58 ± 0.41	43	59.90 ± 0.76	10	60.88 ± 0.30	81
Sarannaya R. –“–	1990	–	–	56.75 ± 1.03	4	–	–	53.08 ± 0.74	12
	1991	–	–	57.97 ± 0.65	30	–	–	54.29 ± 0.56	28
Urumpet R.	1990	–	–	67.05 ± 0.79	19	–	–	62.92 ± 0.83	13

*Data signifies the number of observations years.

Table 46 (appendix). Average body weight of adults from some of Asian sockeye (most common age groups), kg

Watershed	Year	Male				Female			
		1.3		Number of fish	1.3		Number of fish	2.3	
		Average	Number of fish		Average	Number of fish			
Okhota R. Kukhtuy R. Palana R. -- Tigl R. Khairyuzova R. -- -- Icha R. -- Vorovskaya R. -- -- Kikhchik R. Bolshaya R. (early run)	1983	3.829 ± 0.112	22	2.679 ± 0.210	8	2.386 ± 0.045	43	2.233 ± 0.138	8
	1981	2.292 ± 0.070	33	2.515 ± 0.107	6	2.335 ± 0.057	35	2.247 ± 0.099	9
	1983	--	--	2.941 ± 0.042	130	--	--	2.552 ± 0.025	146
	1990	--	--	3.194 ± 0.097	24	--	--	2.471 ± 0.071	14
	1981	2.896 ± 0.207	12	--	--	2.253 ± 0.115	18	--	--
	1984	3.477 ± 0.036	113	--	--	2.780 ± 0.023	158	2.736 ± 0.142	5
	1986	3.619 ± 0.083	30	--	--	3.010 ± 0.047	53	3.157 ± 0.157	6
	1989	3.543 ± 0.080	27	--	--	3.753 ± 0.047	21	--	--
	1986	3.661 ± 0.073	23	--	--	3.265 ± 0.047	25	--	--
	1989	3.858 ± 0.123	29	3.845 ± 0.157	6	3.470 ± 0.045	35	--	--
1965	3.549 ± 0.084	38	3.500 ± 0.477	5	2.944 ± 0.053	39	--	--	
1989	3.046 ± 0.188	10	2.900 ± 0.140	12	2.491 ± 0.062	12	2.565 ± 0.098	17	
1990	3.213 ± 0.060	47	3.230 ± 0.088	31	2.436 ± 0.035	79	2.551 ± 0.065	21	
1989	3.983 ± 0.121	24	--	--	3.033 ± 0.060	20	--	--	
1987–1989	2.490 ± 0.139	6*	--	--	2.139 ± 0.036	6*	--	--	
Bolshaya R. (late run)	1986–1990	3.726 ± 0.097	8*	--	--	3.030 ± 0.050	8*	--	--
Ozemaya R. Kamchatka R. (early run)	1970–1991	3.233 ± 0.208	9*	3.337 ± 0.033	22*	2.790 ± 0.119	10*	2.851 ± 0.027	22*
	1978–1989	2.840 ± 0.043	12*	2.650 ± 0.073	11*	2.238 ± 0.041	12*	2.073 ± 0.053	12*
Kamchatka R. (late run)	1978–1989	3.067 ± 0.080	11*	3.141 ± 0.069	11*	2.403 ± 0.040	11*	2.506 ± 0.060	11*
Avacha R. -- --	1988	3.820 ± 0.140	6	2.810 ± 0.077	29	2.776 ± 0.147	7	2.363 ± 0.082	18
	1989	2.334 ± 0.390	5	2.690 ± 0.040	109	2.691 ± 0.134	7	2.221 ± 0.037	71
	1990	--	--	2.308 ± 0.056	75	3.230 ± 0.172	6	1.971 ± 0.052	73

*Data signifies the number of observations years.

Continued, Table 46 (appendix)

Watershed	Year	Male				Female			
		1.3		Number of fish	1.3		Number of fish	2.3	
		Average			Average			Average	
Stolbovaya R.	1984	3.505 ± 0.072	34	3.853 ± 0.203	10	2.940 ± 0.063	42	2.683 ± 0.139	6
Malamvayam	1983	2.670 ± 0.130	22	2.713 ± 0.142	16	2.238 ± 0.097	15	1.997 ± 0.036	21
Khailyulya R.	1977–1991	3.663 ± 0.071	12*	–	–	2.939 ± 0.052	12*	–	–
Ivashka R.	1966	4.242 ± 0.229	19	–	–	3.271 ± 0.087	22	–	–
Karaga R.	1988	2.996 ± 0.082	75	3.010 ± 0.089	11	2.436 ± 0.055	63	2.542 ± 0.110	9
–“–	1989	3.323 ± 0.037	110	–	–	2.665 ± 0.026	141	2.490 ± 0.108	5
Tymlat R.	1973	3.550 ± 0.094	32	–	–	3.000 ± 0.051	33	–	–
Kichiga R.	1981	3.864 ± 0.070	45	–	–	2.911 ± 0.053	38	–	–
–“–	1982	3.657 ± 0.105	19	–	–	2.766 ± 0.086	17	–	–
–“–	1989	3.901 ± 0.168	16	–	–	2.882 ± 0.075	24	–	–
–“–	1990	4.452 ± 0.079	31	4.166 ± 0.257	5	3.201 ± 0.065	37	–	–
Avyavayam R.	1985	3.309 ± 0.116	48	–	–	2.825 ± 0.072	33	–	–
–“–	1986	3.716 ± 0.086	90	–	–	2.951 ± 0.022	183	–	–
–“–	1989	3.792 ± 0.164	26	4.183 ± 0.091	29	3.166 ± 0.099	27	3.325 ± 0.127	16
Kultushnaya R.	1983	–	–	2.754 ± 0.134	13	–	–	2.272 ± 0.100	23
Apuka R.	1980	3.810 ± 0.158	20	–	–	3.219 ± 0.058	20	–	–
–“–	1985	3.628 ± 0.087	36	–	–	2.813 ± 0.046	43	–	–
–“–	1989	3.994 ± 0.099	42	4.060 ± 0.133	19	3.091 ± 0.059	41	2.971 ± 0.157	7
–“–	1990	3.883 ± 0.185	23	–	–	2.965 ± 0.059	48	2.917 ± 0.177	7
Ananapylgen R.	1980	–	–	2.574 ± 0.128	17	–	–	2.161 ± 0.083	15
Ukalayay R.	1989	4.065 ± 0.064	53	3.543 ± 0.120	7	3.083 ± 0.037	65	3.047 ± 0.202	6
Tumanskaya R.	1928	3.183 ± 0.204	12	3.678 ± 0.077	43	2.490 ± 0.073	10	2.730 ± 0.048	81
Sarannaya R.	1990	–	–	2.637 ± 0.146	4	–	–	2.129 ± 0.078	12
–“–	1991	–	–	2.893 ± 0.095	30	–	–	2.352 ± 0.071	28
Urumpet R.	1990	–	–	3.244 ± 0.108	19	–	–	2.665 ± 0.101	13

*Data signifies the number of observations years.

Table 47 (appendix). Average length and body weight of adult Bolshaya R. sockeye, 1.3 years of age (principal age group) in 1986-1990

Year	Early run				Late run			
	May		June		July		August	
	Male	Female	Male	Female	Male	Female	Male	Female
	Body length, cm							
1986	61.16	57.27	61.14	56.89	68.51	64.61	71.12	64.42
1987	-	-	61.41	56.64	66.43	63.64	65.93	63.64
1988	-	-	-	-	66.26	63.09	-	-
1989	60.81	58.06	63.53	58.20	67.74	62.21	-	-
1990	54.15	52.00	-	-	67.38	63.57	70.21	63.50
Average 1986-1990*	58.71	55.78	62.03	57.24	67.26	63.42	69.09	63.85
	Body weight, kg							
1986	2.682	2.195	2.527	2.110	3.912	3.324	3.992	3.024
1987	-	-	2.553	2.034	3.526	3.007	3.383	2.980
1988	-	-	-	-	3.414	2.931	-	-
1989	2.588	2.255	2.770	2.189	3.637	2.869	-	-
1990	1.820	2.048	-	-	3.848	3.137	4.099	2.969
Average 1986-1990*	2.363	2.166	2.617	2.111	3.667	3.054	3.825	2.991

* Average yearly values.

Table 48 (appendix). Average length and body weight of adult *Khailiyulya R. sockeye*, 1.3 years of age (principal age group) in 1977-1991

Year	Body length, cm				Body weight, kg			
	Male	Number of fish	Female	Number of fish	Male	Number of fish	Female	Number of fish
1977	66.33 ± 0.54	15	60.98 ± 0.40	24	4.029 ± 0.116	15	3.048 ± 0.075	24
1978	—	—	—	—	—	—	—	—
1979	65.49 ± 0.42	40	61.35 ± 0.25	63	3.535 ± 0.067	40	3.020 ± 0.041	63
1980	64.63 ± 0.79	24	59.08 ± 0.47	24	3.589 ± 0.127	24	2.695 ± 0.065	24
1981	64.92 ± 0.44	13	59.71 ± 0.33	19	3.535 ± 0.080	13	2.815 ± 0.051	19
1982	63.75 ± 0.86	12	61.12 ± 0.44	21	3.498 ± 0.153	12	3.083 ± 0.046	21
1983	62.45 ± 0.67	21	58.65 ± 0.35	30	3.231 ± 0.093	21	2.622 ± 0.063	30
1984	—	—	—	—	—	—	—	—
1985	—	—	—	—	—	—	—	—
1986	66.73 ± 0.29	60	62.04 ± 0.35	35	3.962 ± 0.062	60	3.084 ± 0.067	35
1987	65.19 ± 0.28	60	60.22 ± 0.36	50	3.789 ± 0.060	60	2.961 ± 0.057	50
1988	63.19 ± 0.69	43	58.97 ± 0.41	29	2.652 ± 0.118	43	2.934 ± 0.066	29
1989	63.08 ± 1.10	26	59.17 ± 0.42	39	3.398 ± 0.174	26	2.780 ± 0.058	39
1990	64.33 ± 1.45	3	60.40 ± 0.40	5	3.983 ± 0.228	3	3.242 ± 0.370	5
1991	63.83 ± 0.49	15	59.13 ± 0.46	28	3.757 ± 0.102	15	2.990 ± 0.064	28
Average 1977-1991	64.49 ± 0.38	12*	60.07 ± 0.32	12*	3.663 ± 0.071	12*	2.939 ± 0.052	12*

*Data signifies the number of observations years.

Table 49 (appendix). Range and average body length of adult *Asian sockeye* of some stocks homing an extended freshwater period 0+, distinguished by the duration of their marine period, cm

Watershed	Sex	Year	0.3		0.4	
			Range	Average	Range	Average
Bolshaya R. (early run)	Male	1986-1990	59.0-68.0	62.96 ± 0.42	—	—
	Female	1986-1990	50.0-67.0	57.60 ± 0.34	54.0-57.0	55.50 ± 1.50
Bolshaya R. (late run)	Male	1986-1990	64.0-76.0	68.70 ± 1.10	71.0-72.0	71.50 ± 0.50
	Female	1986-1990	59.0-66.0	62.79 ± 0.56	65.0-66.0	65.60 ± 0.50
Kamchatka R. (early run)	Male	1978-1989	52.5-68.5	61.67 ± 0.30	55.0-72.0	64.07 ± 0.87
	Female	1978-1989	50.0-67.5	56.42 ± 0.34	55.0-67.0	60.81 ± 0.56
Kamchatka R. (late run)	Male	1978-1989	49.0-73.0	64.46 ± 0.54	61.0-72.5	68.50 ± 1.46
	Female	1978-1989	50.0-68.5	58.93 ± 0.44	55.0-69.0	62.43 ± 0.89
Khailiyulya R.	Male	1977-1991	53.5-68.5	63.98 ± 0.41	62.5-73.5	68.50 ± 0.83
	Female	1977-1991	54.0-65.5	59.28 ± 0.36	58.0-66.0	± 0.51

Table 50 (appendix). Range and average body length of adult Asian sockeye of some stocks homing an extended freshwater period 1+, distinguished by the duration of their marine period, cm

Watershed	Sex	Year	1.2			1.3			1.4		
			Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
Khaiyuzova R. --“	Male	1984-1989	-	-	-	55.0-71.0	64.38 ± 0.19	170	-	-	-
	Female	1984-1989	-	-	-	54.0-67.0	60.16 ± 0.13	233	64.0-66.0	65.00 ± 1.00	2
Vorovskaya R. --“	Male	1965-1990	-	-	-	55.5-77.5	65.49 ± 0.49	95	61.5-75.0	67.37 ± 1.68	8
	Female	1965-1990	-	-	-	50.0-69.5	59.65 ± 0.36	131	55.0-67.0	61.61 ± 1.36	9
Bolshaya R. (early run) --“	Male	1986-1990	43.0-52.0	46.19 ± 0.30	32	46.0-69.0	61.52 ± 0.25	210	53.0-71.0	64.87 ± 0.75	35
	Female	1986-1990	-	-	-	50.0-67.0	57.19 ± 0.15	290	54.0-68.0	60.58 ± 0.33	76
Bolshaya R. (late run) --“	Male	1986-1990	45.0-57.0	50.95 ± 0.62	22	47.0-76.0	67.64 ± 0.25	291	64.0-75.0	70.11 ± 0.45	28
	Female	1986-1990	48.0-56.0	52.00 ± 2.31	3	54.0-74.0	63.68 ± 0.14	352	60.0-76.0	65.92 ± 0.40	52
Avacha R. --“	Male	1988-1990	45.0-53.0	49.63 ± 1.10	8	48.0-70.0	61.92 ± 2.08	13	-	-	-
	Female	1988-1990	-	-	-	51.0-68.0	61.55 ± 0.85	20	-	-	-
Kamchatka R. (early run) --“	Male	1978-1989	36.5-55.5	45.74 ± 0.42	82	46.5-72.5	61.09 ± 0.15	572	49.0-73.0	64.68 ± 0.82	33
	Female	1978-1989	46.0-56.0	50.00 ± 0.92	12	48.0-67.0	56.62 ± 0.13	484	53.5-67.5	60.21 ± 0.47	47
Kamchatka R. (late run) --“	Male	1978-1989	42.0-60.0	48.67 ± 0.60	45	47.5-73.0	62.98 ± 0.24	344	64.0-77.0	68.03 ± 0.93	15
	Female	1978-1989	45.5-59.0	51.13 ± 0.84	26	46.5-69.0	58.73 ± 0.17	384	57.0-69.0	62.37 ± 0.55	30
Khaiyulya R. --“	Male	1977-1991	42.0-60.0	49.28 ± 0.53	46	49.0-71.0	64.78 ± 0.19	332	57.0-73.6	67.63 ± 0.32	132
	Female	1977-1991	46.0-53.0	49.50 ± 3.50	2	51.5-67.5	60.17 ± 0.13	367	56.0-68.5	62.35 ± 0.25	90
Kichiga R. --“	Male	1981-1990	57.0-57.5	57.25 ± 0.25	2	55.0-79.5	64.98 ± 0.30	228	64.0-79.0	70.31 ± 0.99	16
	Female	1981-1990	-	-	-	55.0-71.0	62.22 ± 0.31	117	64.0-73.5	68.37 ± 0.94	8
Apuka R. --“	Male	1980-1990	47.5-52.0	49.95 ± 0.52	10	54.5-78.0	68.06 ± 0.35	41	61.0-78.0	69.64 ± 0.74	29
	Female	1980-1990	-	-	-	56.5-70.0	62.40 ± 0.19	153	60.0-67.0	63.48 ± 0.36	24

Table 51 (appendix). Range and average body length of adult Asian sockeye of some stocks homing an extended freshwater period 2+, distinguished by the duration of their marine period, cm

Watershed	Sex	Year	2.1			2.2		
			Range	Average	Number of fish	Range	Average	Number of fish
Vorovskaya R. --	Male	1965–1990	–	–	–	58.5–63.0	60.75 ± 2.25	2
	Female	1965–1990	–	–	–	–	–	–
Bolshaya R. (early run)	Male	1986–1990	–	–	–	43.0–47.0	45.33 ± 1.20	3
	Female	1986–1990	–	–	–	–	–	–
Bolshaya R. (late run)	Male	1986–1990	–	–	–	–	–	–
	Female	1986–1990	–	–	–	–	–	–
Avacha R. --	Male	1988–1990	–	–	–	54.0–61.0	57.80 ± 0.17	80
	Female	1988–1990	–	–	–	50.0–60.0	54.75 ± 0.23	84
Kamchatka R. (early run)	Male	1978–1989	30.5–38.5	34.40 ± 1.29	5	40.0–58.5	48.50 ± 0.53	78
	Female	1978–1989	–	–	–	43.0–58.5	50.67 ± 0.82	18
Kamchatka R. (late run)	Male	1978–1989	33.5–35.0	34.33 ± 0.44	3	44.0–63.0	53.76 ± 0.82	37
	Female	1978–1989	–	–	–	47.0–59.0	53.50 ± 0.51	31
Khailyulya R. --	Male	1977–1991	36.0–41.0	39.25 ± 1.11	4	47.0–56.5	51.80 ± 1.60	5
	Female	1977–1991	–	–	–	51.0–55.5	53.10 ± 0.95	5
Sarannaya R. --	Male	1991	32.0–37.0	34.00 ± 0.50	9	43.0–54.0	48.05 ± 0.72	20
	Female	1991	–	–	–	45.0–51.0	47.23 ± 0.61	13
Urumpet R. --	Male	1991	–	–	–	62.0–64.0	62.50 ± 0.34	6
	Female	1991	–	–	–	57.0–60.5	58.58 ± 0.61	6

Continued, Table 51 (appendix)

Watershed	Sex	Year	2.3			2.4		
			Range	Average	Number of fish	Range	Average	Number of fish
Vorovskaya R. --	Male	1965–1990	49.0–74.0	62.48 ± 0.63	48	–	–	–
	Female	1965–1990	54.0–64.5	58.89 ± 0.41	40	–	–	–
Bolshaya R. (early run)	Male	1986–1990	52.0–69.0	61.82 ± 0.48	45	58.0–69.0	64.43 ± 1.66	7
	Female	1986–1990	52.0–63.0	56.75 ± 0.29	51	57.0–69.0	59.78 ± 1.24	9
Bolshaya R. (late run)	Male	1986–1990	47.0–72.0	65.55 ± 1.08	31	72.0–73.0	72.50 ± 0.50	2
	Female	1986–1990	55.0–66.0	62.19 ± 0.42	32	65.0–67.0	65.67 ± 0.67	3
Avacha R. --	Male	1988–1990	51.0–70.0	62.24 ± 0.26	52	–	–	–
	Female	1988–1990	52.0–67.0	58.82 ± 0.27	163	–	–	–
Kamchatka R. (early run)	Male	1978–1989	46.5–71.5	61.05 ± 0.24	302	56.5–73.0	67.08 ± 0.97	19
	Female	1978–1989	47.0–66.5	56.65 ± 0.18	251	52.0–69.0	59.24 ± 1.04	17
Kamchatka R. (late run)	Male	1978–1989	53.0–79.0	64.48 ± 0.29	197	58.0–75.0	67.64 ± 2.09	7
	Female	1978–1989	48.0–68.0	60.03 ± 0.27	181	54.0–68.0	62.78 ± 0.60	25
Khailyulya R. --	Male	1977–1991	49.5–68.5	60.92 ± 1.15	24	65.5–71.0	69.00 ± 1.04	5
	Female	1977–1991	54.5–65.0	59.08 ± 0.59	18	59.0–65.0	61.25 ± 0.70	8
Sarannaya R. --	Male	1991	46.0–63.0	57.97 ± 0.65	30	–	–	–
	Female	1991	16.0–59.0	54.29 ± 0.56	28	–	–	–
Urumpet R. --	Male	1990	61.0–71.0	67.05 ± 0.79	19	–	–	–
	Female	1990	57.0–66.0	62.92 ± 0.83	13	–	–	–

Table 52 (appendix). Range and average body length of adult Asian sockeye of some stocks homing an extended freshwater period 3+, distinguished by the duration of their marine period, cm

Watershed	Sex	Year	3.1			3.2			3.3		
			Range	Average	Number of fish	Range	Average	Number of fish	Range	Average	Number of fish
Avacha R. —“—	Male	1988–	–	–	–	54.0–61.0	58.13 ± 0.53	15	56.0–67.0	61.67 ± 0.75	21
	Female	1990	–	–	–	51.0–58.0	55.15 ± 0.31	26	52.0–62.0	56.74 ± 0.75	19
Sarannaya R. —“—	Male	1991	34.0–39.0	36.35±0.35	20	47.0–55.0	50.18 ± 0.85	11	55.0–63.0	59.78 ± 0.58	18
	Female	1991	–	–		45.0–56.0	48.22 ± 0.71	18	47.0–59.0	54.35 ± 0.74	20
Urumpet R. —“—	Male	1990	–	–	–	59.0–66.0	62.77 ± 0.42	15	61.0–71.0	64.78 ± 1.18	9
	Female	1990	–	–	–	57.0–64.0	59.93 ± 0.34	27	58.0–65.0	60.80 ± 1.20	5

Table 53 (appendix). Absolute fecundity in females of typical age groups of Asian sockeye stocks, number of eggs

Watershed	Year	1.3			2.3		
		Range	Average	Number of fish	Range	Average	Number of fish
Uega R. (Okhota R.)	1968	–	2869	25	–	3533	18
Tigil R.	1981	2025–6318	3534 ± 273	18	–	–	–
Vorovskaya R.	1965,1989,1990	1148–6647	3190 ± 111	129	1428–6390	2823 ± 156	37
Kikhchik R.	1989	4095–7722	5489 ± 285	13	–	–	–
Bolshaya R. (early run)	1987,1989	1476–7078	3775 ± 60	173	2482–5159	3333 ± 107	34
Bolshaya R. (late run)	1986–1990	1362–9980	5022 ± 68	243	2751–6137	4198 ± 169	25
Ozernaya R.**	1970–1991	3451–4227	3805	6	3760–4440	4033	22
Avacha R.	1988–1990	2568–6419	4255 ± 270	16	–	–	–
Kamchatka R. (early run)	1978–1989	1287–6710	3622 ± 45	331	1227–6363	3311 ± 64	205
Kamchatka R. (late run)	1978–1989	1209–9024	4619 ± 76	338	1334–7920	4269 ± 113	145
Stolbovaya R.	1984	1512–9716	3371 ± 195	42	2475–5019	3558 ± 559	5
Malamvayam R.	1983	2328–5412	3384 ± 262	14	1263–3629	2462 ± 121	22
Khailyulya R.	1977–1988	2700–8711	5010 ± 71	175	2909–4536	3646 ± 357	5
Karaga R.	1988–1989	902–5376	2971 ± 159	45	–	–	–
Tymlat R.	1973	3629–9710	5309 ± 639	9	–	–	–
Kichiga R.	1981,1989–1990	2977–7743	4878 ± 106	81	–	–	–
Avyavayam R.	1985	2910–6885	5184 ± 180	31	–	–	–
Apuka R.	1980–1990	2407–8964	4883 ± 115	144	2135–7320	4249 ± 345	18
Ukalayat R.	1989	4590–7253	6042 ± 76	65	5329–6333	5763 ± 137	6
Seutakan R.***	1976	3214–5300	4789	28	–	–	–
Urumpet R.	1990	–	–	–	2871–4832	3960 ± 142	13

*Nikulin, 1975; ** M. M. Selifonov (table 83); ***Chereshnev, 1981.

Table 54 (appendix). Absolute fecundity in females of some Asian sockeye stocks (by total age groups), number of eggs

Age	Bolshaya R. (early run), 1987–1990			Bolshaya R. (late run), 1986–1990		
	Range	Average	Number of fish	Range	Average	Number of fish
0.2	–	–	–	–	–	–
0.3	2241–4927	4024 ± 73	53	3145–9990	4928 ± 523	13
1.2	–	–	–	3180–5423	4604 ± 715	3
0.4	–	–	–	–	4865	1
1.3	1476–7078	3775 ± 60	173	1362–9980	5022 ± 68	243
2.2	–	–	–	–	3310	1
1.4	2122–5839	4070 ± 90	59	3232–8440	5394 ± 145	43
2.3	2482–5159	3333 ± 107	34	2751–6137	4198 ± 169	25
3.2	–	–	–	–	–	–
1.5	–	–	–	–	6179	1
2.4	3523–4141	3876 ± 184	3	4001–7448	5725 ± 1723	2
3.3	–	–	–	–	–	–
4.2	–	–	–	–	–	–
2.5	–	–	–	–	5400	1
4.3	–	–	–	–	–	–
5.2	–	–	–	–	–	–
6.2	–	–	–	–	–	–

Continued, Table 54 (appendix)

Age	Khailyulya R., 1977-1988			Ananapylgen R., 1980		
	Range	Average	Number of fish	Range	Average	Number of fish
0.2	–	3960	1	–	–	–
0.3	3000–7827	5330 ± 276	17	–	–	–
1.2	–	–	–	–	–	–
0.4	4814–5684	5262 ± 119	8	–	–	–
1.3	2700–8711	5010 ± 71	175	–	4352	1
2.2	–	3154	1	2000–2453	2232 ± 131	3
1.4	3221–7240	5391 ± 124	48	–	–	–
2.3	2909–4536	3646 ± 357	5	1584–6690	2761 ± 319	15
3.2	–	–	–	2809–3220	3015 ± 205	2
1.5	–	–	–	–	–	–
2.4	–	4365	1	–	–	–
3.3	–	–	–	1889–9840	4172 ± 308	26
4.2	–	–	–	2116–3780	2893 ± 483	3
2.5	–	3381	1	–	–	–
4.3	–	–	–	2460–4820	3640 ± 1180	2
5.2	–	–	–	2737–5138	3599 ± 207	12
6.2	–	–	–	2592–4410	3575 ± 216	9

Table 55 (appendix). Year-to-year variability in absolute fecundity of Kamchatka *R. sockeye* from marine trap net catches in 1978-1989, number of eggs

Year	Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish
1978	1700–5029	3432 ± 96	72	2125–7737	4876 ± 103	124
1979	1620–8190	3656 ± 92	111	1514–7277	3711 ± 98	96
1980	2220–5236	3584 ± 75	84	3202–5625	4372 ± 162	19
1981	1375–6363	3584 ± 100	86	–	–	–
1982	–	–	–	–	–	–
1983	–	–	–	2526–5875	4474 ± 181	24
1984	1452–4992	3156 ± 144	27	1209–9890	4839 ± 167	91
1985	1227–8855	3989 ± 140	74	2850–7200	4295 ± 219	22
1986	1998–6406	3586 ± 111	60	2480–6466	3884 ± 164	33
1987	1250–6305	3191 ± 94	94	1570–9024	4263 ± 162	104
1488	2526–6584	4524 ± 177	42	1334–7080	4160 ± 155	55
1989	2227–6452	± 139	48	2799–9174	5350 ± 158	92
Average 1978–1989	3156–4524	3633 ± 124	10*	3711–5350	4422 ± 155	10*

*Data signifies the number of observations years.

Table 56 (appendix). Absolute fecundity of Kamchatka *R. female sockeye* from all age groups found in marine trap net catches (combine date of 1978-1989), number of eggs

Age	Early run			Late run		
	Range	Average	Number of fish	Range	Average	Number of fish
0.2	–	3817	1	–	6030	1
0.3	2985–8190	3635 ± 135	57	2256–9870	4757 ± 174	62
1.2	1375–3437	2498 ± 286	6	2885–6237	4293 ± 188	19
0.4	3025–6452	4558 ± 191	28	2877–7520	5019 ± 374	17
1.3	1287–6710	3622 ± 45	331	1209–9024	4619 ± 76	338
2.2	1863–4501	2982 ± 254	9	1570–7030	3430 ± 268	29
0.5	–	4180	1	–	–	–
1.4	2330–6780	4276 ± 200	36	2273–7140	4498 ± 231	22
2.3	1227–6363	3311 ± 64	205	1334–7920	4269 ± 113	145
1.5	–	3472	1	–	–	–
2.4	2528–8855	4520 ± 417	16	3270–7909	4835 ± 234	25
3.3	3010–5481	4174 ± 339	6	2925–9174	5216 ± 1987	3
3.4	–	5114	1	–	3960	1
4.3	–	–	–	–	4260	1
Total age groups	1227–8855	3613 ± 37	698	1209–9890	4512 ± 54	663

Table 59 (appendix). Year-to-year variability of average values in the coefficient of maturity of adult Kuril L. sockeye (M. M. Selifonov, KoTINRO archives; data from Soviet-Japanese Fisheries Commission), %

Year	1.1		1.2		1.3		2.1		2.2		2.3		2.4		3.1		3.2		3.3		3.4	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1977	-	-	2.60	-	6.30	3.00	7.50	2.10	6.70	-	9.20	-	2.40	6.60	2.40	6.00	-	-	2.40	6.00	-	-
1978	3.10	-	3.90	-	6.40	2.90	5.90	2.30	5.80	3.40	-	3.30	3.40	5.40	2.10	5.20	-	-	2.10	5.20	-	-
1979	-	-	2.04	8.35	5.80	3.70	9.24	2.15	6.57	2.50	-	2.15	2.00	6.00	1.76	5.82	-	-	1.76	5.82	-	-
1980	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1981	-	-	2.78	7.52	5.83	3.37	8.15	2.60	6.81	1.61	10.95	2.60	2.62	5.90	2.45	7.15	-	-	2.45	7.15	-	-
1982	-	-	-	-	5.82	3.33	7.10	2.40	6.92	3.33	7.10	2.40	2.88	5.87	4.21	5.67	-	-	2.30	5.47	-	-
1983	-	-	-	-	-	3.79	8.50	2.59	7.60	3.58	6.63	2.46	2.57	7.30	2.53	6.40	-	-	2.53	6.40	-	-
1984	-	-	-	-	-	3.58	6.63	2.46	7.55	3.12	6.54	2.49	1.43	5.14	2.77	5.81	-	-	2.41	7.11	-	-
1985	-	-	2.36	5.57	4.25	3.12	6.54	2.43	6.88	3.12	6.78	2.43	2.52	7.45	3.35	6.51	-	-	2.35	6.08	-	7.83
1986	5.74	-	2.55	-	5.26	3.12	6.78	2.40	6.60	3.12	6.78	2.40	2.52	7.45	3.99	12.45	-	-	2.18	5.15	-	5.33
1987	-	-	2.70	7.90	5.80	3.00	8.00	2.40	6.60	3.00	8.00	2.40	2.40	8.90	2.80	6.70	-	-	2.70	10.80	-	-
1988	-	-	2.50	9.50	3.00	3.30	8.00	2.80	8.30	3.30	8.00	2.80	2.00	5.70	-	6.20	-	-	-	6.20	-	-
1989	-	-	-	-	6.20	3.80	8.00	2.60	9.80	3.80	8.00	2.60	2.50	6.60	3.30	8.40	-	-	2.40	9.80	-	-
1990	-	-	-	13.63	5.11	3.66	9.21	2.58	8.80	3.66	9.21	2.58	-	8.44	3.22	8.39	-	-	2.11	7.10	-	-
1991	-	-	7.69	-	6.41	3.36	6.55	2.81	7.56	3.36	6.55	2.81	2.72	6.98	3.72	7.64	-	-	1.96	6.00	-	-
Average 1977-1991	5.74	8.30	3.24	8.75	5.51	3.36	7.58	2.48	7.31	3.36	7.58	2.48	2.34	7.73	3.16	7.03	2.28	6.73	2.28	6.73	2.33	6.58

Table 60 (appendix). Year-to-year variability of average values in the coefficient of maturity of adult Kamchatka R. sockeye from marine trap net catches in 1978-1989 (principal age groups), %

Year	0.3		0.4		1.2		2.1		1.3		2.2		1.4		2.3		2.4		Average		
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Early run																					
1978	2.29	7.51	—	7.92	5.08	8.00	9.64	2.75	8.01	4.76	8.71	—	—	—	—	2.89	7.67	—	—	2.91	7.95
1979	3.79	9.11	3.63	10.83	6.38	8.33	6.63	3.50	8.94	5.39	8.24	2.96	8.60	—	—	4.17	7.85	4.70	10.12	4.14	8.84
1980	2.43	8.31	3.29	7.94	5.20	—	—	2.57	8.14	4.50	—	2.28	—	—	2.46	7.42	—	—	7.56	3.05	7.99
1981	3.69	8.85	2.09	9.89	5.11	5.00	8.51	3.17	7.57	5.16	—	3.04	8.58	—	2.81	7.60	—	1.62	—	3.31	7.90
1982	3.30	8.27	3.87	8.58	4.99	7.50	—	2.89	7.95	5.55	6.09	2.48	9.79	—	2.67	7.65	—	—	7.36	3.79	8.04
1983	—	8.81	2.17	5.32	7.50	11.13	—	3.66	9.49	5.00	8.24	—	9.70	—	—	8.26	—	—	—	4.27	9.14
1984	3.89	8.96	2.89	—	3.36	—	—	2.90	8.34	—	8.86	4.68	8.92	—	—	3.15	9.20	5.37	9.52	3.19	8.78
1985	5.48	8.37	—	8.59	—	—	—	3.16	8.61	7.13	—	3.06	8.40	—	3.39	9.12	—	2.77	10.72	3.42	8.88
1986	2.77	7.49	2.43	—	5.34	8.63	—	2.19	8.39	4.21	7.42	2.19	6.91	—	2.55	8.55	—	2.71	8.70	3.32	8.30
1987	3.37	9.59	1.83	9.47	—	—	—	3.35	8.51	3.59	6.37	—	6.39	—	3.27	7.96	—	3.41	—	3.32	8.41
1988	5.03	9.00	4.14	11.19	8.00	—	—	5.23	10.60	10.99	—	4.03	11.56	—	5.04	10.02	—	6.07	12.10	5.19	10.72
1989	3.80	9.07	—	10.87	5.03	—	—	3.47	9.53	2.06	—	2.88	8.65	—	4.85	8.62	—	2.58	12.35	4.13	9.40
Average 1978-1989	3.62	8.61	2.93	9.06	5.60	8.10	8.26	3.24	8.67	5.30	7.70	3.07	8.75	—	3.39	8.33	—	3.65	9.80	3.62	8.69
Late run																					
1978	3.43	7.97	2.43	5.27	5.97	7.48	—	3.27	8.13	3.73	10.23	2.89	—	—	2.66	7.32	—	—	—	3.73	7.94
1979	3.63	9.43	2.83	8.17	5.63	10.34	5.26	2.95	7.55	4.12	4.96	3.63	9.37	—	2.81	7.55	—	—	—	3.25	7.95
1980	2.38	9.70	2.47	7.64	—	—	—	2.95	8.81	4.41	—	—	11.91	—	2.54	10.92	—	—	—	2.87	9.21
1981	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1982	2.62	—	—	—	4.00	7.39	—	2.57	7.38	—	7.00	—	—	—	3.59	7.88	—	—	—	3.22	7.52
1983	2.97	—	—	11.45	3.48	—	—	2.95	7.65	—	—	—	10.00	—	2.92	7.27	—	—	4.33	2.95	5.57
1984	—	14.29	2.68	8.81	5.52	9.45	—	3.98	9.34	3.87	5.55	3.72	7.70	—	3.72	10.12	—	4.04	9.82	4.04	6.81
1985	2.80	6.67	—	—	4.61	—	—	3.35	7.56	5.23	—	2.59	7.62	—	2.63	7.08	—	—	6.44	3.33	7.37
1986	2.37	—	—	—	—	—	—	2.15	7.37	1.75	—	—	—	—	2.18	6.79	—	—	9.99	2.18	7.22
1987	3.58	9.29	1.32	11.61	3.26	3.08	—	4.11	9.41	1.88	3.25	3.30	7.65	—	2.64	7.35	—	3.43	11.02	3.25	8.33
1988	8.45	8.40	2.84	9.41	6.13	7.22	—	5.24	9.10	3.78	—	5.90	12.28	—	4.29	9.07	—	2.50	8.96	5.01	9.10
1989	4.68	9.44	—	13.73	7.07	12.50	—	4.17	9.75	3.72	10.30	4.34	8.99	—	4.04	10.25	—	4.26	9.55	4.28	9.96
Average 1978-1989	3.69	9.15	2.43	9.51	5.07	8.21	5.26	3.43	8.37	3.61	6.88	3.77	9.44	—	3.09	8.33	—	3.56	8.23	3.46	7.91

Table 61 (appendix). Year-to-year variability of average values in the coefficient of maturity of some stocks of Asian sockeye (total age groups), %

Year	Bolshaya R. (early run)		Bolshaya R. (late run)		Ozernaya R.		Kamchatka R. (early run)		Kamchatka R. (late run)		Khailiyulua R.	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1973	3.90	8.80	3.50	7.91	-	-	-	-	-	-	-	-
1974	3.70	6.20	4.25	6.00	-	-	-	-	-	-	-	-
1975	3.00	6.20	-	-	-	-	-	-	-	-	-	-
1976	2.05	6.78	-	-	-	-	-	-	-	-	-	-
1977	-	-	-	-	2.60	6.90	-	-	-	-	2.33	8.51
1978	2.32	5.73	3.95	8.10	3.00	5.70	2.91	7.95	3.73	7.94	-	-
1979	3.10	6.82	-	-	3.51	8.11	4.14	8.84	3.25	7.95	2.44	8.44
1980	3.91	6.92	3.75	7.84	-	-	3.05	7.99	2.87	9.21	2.69	8.66
1981	4.21	6.46	4.36	8.81	2.84	7.22	3.31	7.80	-	-	2.72	9.17
1982	-	-	4.02	9.41	3.10	6.75	3.79	8.04	3.22	7.52	2.94	9.86
1983	6.21	8.24	2.83	9.26	2.94	7.60	4.27	9.14	2.95	7.57	3.46	9.71
1984	-	-	-	-	2.65	7.21	3.19	8.78	3.99	9.19	-	-
1985	4.72	7.62	3.18	8.32	2.61	6.32	3.42	8.88	3.33	7.37	-	-
1986	3.24	6.87	3.17	9.50	2.94	6.72	2.72	8.30	2.18	7.22	2.97	9.68
1987	3.72	7.64	3.82	9.85	2.80	7.30	3.22	8.41	3.25	8.33	2.86	9.53
1988	-	-	2.95	9.12	3.10	8.10	5.19	10.72	5.01	9.10	2.85	8.75
1989	2.63	7.07	3.18	9.62	3.20	9.30	4.13	9.40	4.25	9.96	3.38	9.21
1990	-	-	2.94	8.84	3.11	8.90	-	-	-	-	-	-
1991	-	-	-	-	3.25	7.17	-	-	-	-	3.48	8.83

Table 62 (appendix). Year-to-year variability of average values in the coefficient of maturity Kamchatka R. sockeye from marine trap net catches in 1978–1989 (total age groups), %

Year	Male						Female					
	Early run		Late run		Number of fish	Number of fish	Early run		Late run		Number of fish	Number of fish
	Range	Average	Range	Average			Range	Average	Range	Average		
1978	1.26–9.64	2.91 ± 0.12	0.29–10.54	3.73 ± 0.19	113	108	3.34–13.22	7.95 ± 0.21	88	2.86–13.92	7.94 ± 0.16	136
1979	1.54–9.82	4.14 ± 0.16	1.39–7.76	3.25 ± 0.14	117	89	4.95–14.73	8.84 ± 0.18	108	1.50–13.69	7.95 ± 0.23	87
1980	1.25–6.70	3.05 ± 0.11	1.39–4.41	2.87 ± 0.14	134	35	1.52–11.85	7.99 ± 0.18	85	5.28–14.00	9.21 ± 0.40	33
1981	0.70–8.51	3.31 ± 0.11	–	–	146	–	2.64–13.30	7.80 ± 0.19	102	–	–	–
1982	1.32–7.84	3.79 ± 0.21	1.23–8.39	3.22 ± 0.37	62	21	3.41–12.50	8.04 ± 0.24	61	4.29–11.67	7.52 ± 0.29	29
1983	0.42–9.38	4.27 ± 0.48	1.17–5.25	2.95 ± 0.11	21	60	3.55–14.69	9.14 ± 0.56	26	4.23–11.45	7.57 ± 0.31	37
1984	0.88–11.01	3.19 ± 0.18	0.70–8.82	3.99 ± 0.27	78	53	3.92–17.05	8.78 ± 0.33	70	3.97–21.48	9.19 ± 0.34	93
1985	1.02–11.54	3.42 ± 0.18	1.07–8.06	3.33 ± 0.31	103	26	3.87–14.74	8.88 ± 0.22	92	3.85–13.33	7.37 ± 0.40	22
1986	0.66–8.09	2.72 ± 0.11	0.69–5.00	2.18 ± 0.11	134	46	4.50–14.59	8.30 ± 0.27	60	2.37–11.30	7.22 ± 0.35	33
1987	1.30–8.55	3.32 ± 0.10	0.87–9.38	3.25 ± 0.17	148	109	4.35–16.67	8.41 ± 0.24	98	2.44–19.08	8.33 ± 0.28	126
1988	2.69–10.99	5.19 ± 0.25	1.71–10.33	5.01 ± 0.30	48	72	6.19–17.48	10.72 ± 0.33	47	3.64–17.78	9.10 ± 0.35	75
1989	0.85–7.33	4.13 ± 0.21	1.43–8.45	4.25 ± 0.16	54	99	4.84–20.05	9.40 ± 0.43	49	3.86–20.00	9.96 ± 0.28	101
Average 1978–1989	2.72–5.19	3.62 ± 0.20	2.18–5.01	3.46 ± 0.23	12*	11*	7.95–10.72	8.69 ± 0.24	12*	7.22–9.96	8.31 ± 0.28	11*

*Data signifies the number of observations years.

Table 63 (appendix). Average values in the coefficient maturity of adult specimens from local second order stocks and their groups of the Kamchatka R. sockeye from marine traps nets in 1978–1989 (data for early and late sockeye runs are combined), %

Stock, group of stocks	Male						Female					
	Early run		Late run		Number of fish	Number of fish	Early run		Late run		Number of fish	Number of fish
	Range	Average	Range	Average			Range	Average	Range	Average		
“S”	1.30–9.29	3.44 ± 0.12	1.32–11.43	3.57 ± 0.22	134	66	3.34–14.00	9.13 ± 0.23	102	4.52–19.03	9.10 ± 0.29	89
“V”	0.42–9.38	3.16 ± 0.21	0.91–11.63	3.75 ± 0.16	67	162	3.60–12.90	7.73 ± 0.32	48	3.08–17.94	8.51 ± 0.20	168
“E”	0.57–11.01	3.26 ± 0.06	0.29–10.54	3.87 ± 0.13	525	200	1.52–17.39	8.57 ± 0.11	406	2.95–17.62	8.59 ± 0.16	229
“N”	1.15–6.45	3.09 ± 0.21	1.06–10.33	4.30 ± 0.47	32	27	4.62–14.23	8.46 ± 0.38	35	4.46–15.77	8.82 ± 0.45	34
“A”	0.66–11.54	3.77 ± 0.11	1.00–9.47	3.37 ± 0.11	309	203	2.64–20.05	8.76 ± 0.17	212	1.50–21.48	8.63 ± 0.21	196
“D”	1.23–9.28	3.39 ± 0.15	0.69–7.88	2.48 ± 0.18	93	56	4.35–11.58	7.65 ± 0.21	80	2.44–15.38	6.32 ± 0.39	50

Table 64 (appendix). Sockeye catches by government commercial fisheries in the Kamchatka Region, 1957-1991 (data from Kamchatka Region canneries), tons

Year	Khairuzovskiy cannery	Krutogorovskiy cannery	Oktiabryskiy cannery	Ozernovskiy cannery	Petropavlovskiy cannery	Ust-Kamchatka cannery	Khailiulianskiy cannery	Ossorskiy cannery	Anapkinskiy cannery	Korfiskiy cannery	Olutorskiy cannery	Total G.P.H.*	Total catches for the Kamchatka Region
1957	2.5	27.3	53.4	2561.0	2.4	559.1	13.0	-	-	0.4	4.7	-	3223.8
1958	7.4	-	19.8	579.0	8.7	402.7	14.4	-	-	0.9	13.2	-	1046.1
1959	1.2	59.6	294.5	2075.0	3.1	1416.5	103.4	7.9	-	-	4.2	-	3965.4
1960	18.5	12.7	95.8	2052.0	1.7	1802.9	20.1	-	-	-	10.7	-	4014.4
1961	-	79.6	388.0	5165.0	1.0	916.2	110.6	-	-	55.6	9.5	-	6725.5
1962	0.4	35.9	110.4	3763.0	1.0	479.4	60.0	-	-	-	8.3	-	4458.4
1963	28.8	-	107.8	2346.0	1.0	893.8	4.1	-	-	-	2.1	-	3383.6
1964	0.3	-	114.5	594.0	-	1904.8	23.0	-	-	-	4.4	-	2641.0
1965	-	-	185.2	1946.0	-	1876.6	7.6	-	-	-	-	-	4015.4
1966	11.5	3.1	62.3	1456.0	0.1	2156.0	6.5	-	-	-	0.3	-	3695.8
1967	-	-	8.8	1070.0	0.7	1938.1	3.2	-	-	-	-	-	3020.8
1968	-	-	12.9	173.0	-	2063.6	-	-	-	-	0.7	-	2250.2
1969	0.7	-	5.2	74.0	-	1559.5	-	-	-	-	-	-	1639.4
1970	0.2	-	65.5	468.0	1.1	3809.6	-	-	-	-	1.6	-	4346.0
1971	-	-	36.1	997.0	1.2	1279.9	-	-	-	0.1	-	-	2314.3
1972	3.0	-	1.0	336.0	-	615.0	-	-	-	-	-	-	955.0
1973	34.0	-	46.0	393.0	-	1293.0	-	-	-	-	-	70.3	1836.3
1974	-	-	20.0	798.0	-	223.0	1.0	-	-	-	-	57.6	1099.6
1975	-	-	22.0	446.0	-	928.0	-	-	-	-	1.0	117.6	1514.6
1976	-	-	47.0	365.0	-	714.0	3.0	-	-	-	4.0	155.9	1288.9
1977	-	-	19.0	181.0	2.0	1603.0	6.0	-	-	-	6.0	76.0	1893.0
1978	4.0	-	44.0	707.0	12.0	2553.0	15.0	-	-	9.0	34.0	192.2	3570.2
1979	3.0	1.0	41.0	497.0	4.0	2158.0	-	-	-	2.0	75.0	248.1	3029.1
1980	2.0	-	35.0	1297.0	6.0	2508.0	2.0	-	-	2.0	26.0	273.4	4151.4
1981	6.0	-	53.0	1646.0	-	2035.0	36.0	-	-	-	51.0	495.4	4222.4
1982	2.0	-	36.0	1241.0	-	1625.0	12.0	-	1.0	-	37.0	336.6	3290.6
1983	4.0	4.0	46.0	1336.0	-	2353.0	270.0	-	2.0	-	209.0	563.0	4792.0
1984	37.0	-	196.0	2687.0	-	3151.0	20.0	-	5.0	-	7.0	563.8	6777.8
1985	19.0	-	348.0	6261.0	1.0	2518.0	162.0	-	1.0	7.0	251.0	767.6	10335.6
1986	56.8	41.0	792.0	4953.0	24.0	2006.0	388.0	1.0	-	16.0	162.0	798.7	9238.5
1987	44.5	34.0	306.0	7989.0	-	2667.0	139.0	1.0	1.0	7.0	202.0	841.3	12231.8
1988	33.0	86.0	1080.0	4637.0	2.0	1706.0	251.0	-	-	4.0	405.0	562.8	8766.8
1989	74.0	34.2	719.8	6751.0	1.0	1341.8	485.0	14.5	10.3	1.7	195.0	825.1	10453.4
1990	38.0	12.0	950.0	14432.0	54.0	214.0	238.0	4.0	-	1.0	194.0	814.6	16951.6
1991	59.0	21.4	1049.0	10809.0	1.0	509.0	26.0	3.0	-	3.0	100.0	867.3	13447.7

Note. See table 65 in detail. *Total G.P.H. - small scale government commercial enterprises ("gospromkhoz").

Table 65 (appendix). Sockeye catches by G.P.H. enterprises in Kamchatka Region, 1973-1991, tons

Year	Tigil'skiy & Lesnovskiy G.P.H.*	Sobolevskiy G.P.H.	Ust-Bolshereztskiy G.P.H.	Petropavlovskiy & Elizovskiy G.P.H.	Ust-Kamchatskiy, Bystrinskiy & Milkovskiy G.P.H.	Karaginskiy G.P.H.	Olutorskiy G.P.H.	Total G.P.H.
1973	5.5	-	4.3	16.5	42.9	-	1.1	70.3
1974	1.0	-	13.7	17.1	25.8	-	-	57.6
1975	15.7	0.2	32.8	2.3	65.8	-	0.8	117.6
1976	20.9	0.4	16.2	43.1	74.9	-	0.4	155.9
1977	-	-	-	-	75.4	-	0.6	76.0
1978	43.8	-	17.4	52.9	63.6	11.2	3.3	192.2
1979	64.1	-	19.7	65.3	88.1	3.4	7.5	248.1
1980	68.8	-	46.0	7.4	138.9	9.0	3.3	273.4
1981	141.2	1.1	67.7	72.1	196.8	10.4	6.1	495.4
1982	89.0	-	37.0	28.6	167.0	5.0	10.0	336.6
1983	167.0	-	33.0	74.0	266.0	5.0	18.0	563.0
1984	96.0	-	84.0	119.0	250.0	-	14.8	563.8
1985	173.0	-	112.2	126.0	343.0	0.4	13.0	767.7
1986	154.8	0.2	113.8	286.6	202.8	9.8	30.7	798.7
1987	185.5	-	149.8	188.4	281.3	13.4	22.9	841.3
1988	94.0	0.5	126.3	229.9	79.3	12.8	20.0	562.8
1989	156.3	1.0	226.8	303.8	118.4	7.6	11.2	825.1
1990	100.7	-	230.4	416.5	26.6	33.7	6.7	814.6
1991	25.0	5.2	683.6	80.9	60.4	2.5	9.7	867.3

* 90 % Palana R.; ** Kamchatka R. In all remaining instances it was impossible assign the origin of catches.

Table 66 (appendix). Total sockeye escapement in Kamchatka Region in 1957-1991 (data based on aerial observations by A. G. Ostroumov, KoTINRO archives), thou. of specimens

Year	N-W (from Lesnaya R. to Satchik R.)	N-W (Palana R.)	W (from Icha R. to Bolshaya R.)	S-W (from Udoshik R. to Kambalnaya R.)	S-W (Ozernaya R.)*	S-E (from Vestnik R. to Avacha R.)	E (from Nalycheva R. to Bystraya R.)	E (Kamchatka R.)	N-E (Karaginsky (from Stolbovaya R. to Anapka R.)	N-E (Olutorsky (from Khai-Anapka R. to Apuka R.)	Total Kamchatka Region
1957	-	-	137.5	30.0	1400.0	80.0	-	800.0	50.0	65.0	2562.5
1958	12.5	3.5	155.0	10.0	500.0	65.0	5.0	600.0	42.5	40.0	1433.5
1959	30.0	600.0	292.5	45.0	2100.0	45.0	17.5	2000.0	130.0	165.0	5425.0
1960	30.0	275.0	297.5	15.0	1550.0	25.5	18.5	1500.0	62.5	50.0	3824.0
1961	52.5	900.0	360.0	25.0	2500.0	30.0	10.0	1500.0	242.5	335.0	5955.0
1962	40.0	550.0	260.0	22.5	800.0	42.5	10.0	1000.0	100.0	95.0	2920.0
1963	65.0	500.0	185.0	15.0	500.0	47.5	5.0	450.0	45.0	40.0	1852.5
1964	22.5	62.5	115.0	10.0	300.0	35.0	2.3	550.0	25.0	67.5	1189.8
1965	37.5	350.0	165.0	15.0	1000.0	60.0	17.5	725.0	102.5	115.0	2587.5
1966	47.5	135.0	165.0	12.5	1000.0	79.5	10.0	475.0	42.5	118.5	2085.5
1967	17.5	75.0	105.0	12.5	700.0	45.5	12.5	350.0	25.0	40.0	1383.0
1968	17.5	200.0	87.5	5.0	650.0	37.5	7.5	800.0	15.0	42.5	1862.5
1969	10.0	45.0	70.0	5.5	370.0	10.0	8.0	575.0	32.5	27.5	1153.5
1970	12.5	81.0	65.0	6.0	380.0	12.5	17.5	1225.0	75.0	80.0	1954.5
1971	21.5	55.0	90.0	8.5	550.0	12.5	13.5	425.0	35.0	80.0	1291.0
1972	13.5	20.5	29.5	9.0	450.0	4.5	8.0	440.0	25.5	48.5	1049.0
1973	11.0	8.0	27.0	4.5	260.0	5.5	7.5	350.0	17.5	40.5	731.5
1974	12.5	25.0	22.5	4.5	460.0	8.5	5.0	130.0	8.5	62.5	739.0
1975	8.0	45.5	47.5	7.5	530.0	7.5	4.0	355.0	17.5	36.0	1058.5
1976	11.0	75.0	38.5	7.5	400.0	4.0	5.5	435.0	21.5	64.5	1062.5
1977	21.5	70.0	64.0	16.5	750.0	2.3	10.5	1060.0	44.0	167.0	2205.8
1978	20.5	65.0	64.5	11.0	1450.0	5.5	15.0	720.0	62.5	122.0	2536.0
1979	42.0	94.5	56.0	11.5	1350.0	11.0	13.5	515.0	80.0	231.5	2405.0
1980	16.5	37.0	49.5	8.0	1500.0	7.0	6.5	560.0	44.0	217.5	2446.0
1981	26.0	125.0	69.0	12.5	1250.0	4.5	15.0	640.0	37.0	229.5	2408.5
1982	17.5	41.0	40.5	11.0	750.0	16.5	25.5	790.0	61.0	162.0	1915.0
1983	27.5	68.0	90.0	15.5	1650.0	25.0	48.0	1265.0	43.0	237.5	3469.5
1984	18.0	127.5	108.5	15.0	2750.0	108.0	34.6	1361.0	53.0	226.0	4801.5
1985	29.0	155.0	154.5	18.0	3420.0	65.0	30.5	741.0	79.0	380.0	5072.0
1986	29.5	76.0	105.0	11.5	2350.0	27.0	21.5	305.0	51.5	271.0	3248.0
1987	45.5	218.5	162.5	27.0	3000.0	130.0	52.5	465.0	111.5	300.0	4512.5
1988	22.8	18.5	146.0	18.9	2050.0	162.0	56.3	293.0	98.3	159.1	3024.9
1989	38.2	113.5	256.9	12.9	2500.0	80.1	50.5	361.0	156.4	315.1	3884.6
1990	25.8	36.0	421.1	17.5	6000.0	77.2	46.0	511.0	144.1	509.3	7788.0
1991	27.6	78.0	174.3	11.7	2500.0	36.7	26.6	398.0	109.2	262.0	3624.1

*Data from Ozernomsky observation point of KoTINRO.

Table 67 (appendix). Ratio of adult group "E" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May												
25–31	65.7	48.0	–	58.1	62.5	–	28.6	–	14.0	–	29.8	21.8
June												
1–5	65.7	48.0	53.8	58.1	57.3	53.3	28.6	39.6	14.3	20.0	29.2	21.8
6–10	55.1	62.5	39.3	42.9	49.4	53.3	28.6	30.0	26.6	26.0	29.2	21.8
11–15	60.0	47.4	47.3	52.0	72.3	50.0	36.0	39.5	12.8	30.0	38.8	19.6
16–20	70.7	40.8	63.2	53.0	64.0	54.0	53.0	42.9	32.7	16.0	32.6	42.6
21–25	70.7	35.4	56.2	57.6	74.0	34.8	75.0	38.0	40.9	36.0	37.5	41.5
26–30	60.6	31.9	57.7	56.0	53.1	28.0	50.0	18.0	39.4	60.0	26.0	39.6
July												
1–5	28.0	42.9	65.1	34.0	51.0	43.5	50.0	24.0	27.8	57.0	27.8	28.0
1–10	42.0	32.7	60.0	22.0	38.7	59.2	35.0	17.0	15.5	54.0	29.8	28.0
11–15	30.0	22.5	–	25.5	38.3	53.4	19.1	10.0	15.5	20.4	30.6	33.7
16–20	20.0	34.5	60.0	25.3	38.0	47.6	19.1	10.0	14.0	20.2	–	16.3
21–25	25.0	30.4	60.0	25.0	16.3	44.0	65.0	12.8	6.8	20.9	–	–
26–31	25.0	44.0	60.0	28.3	16.3	43.2	6.1	14.3	6.8	19.5	–	–

Note. June 11-30 is the main catch period. Rarely occurring specimens from stock "K" are combined with group "E" due to the relative insignificance of their numbers.

Table 68 (appendix). Ratio of adult stock "A" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May												
25–31	25.5	22.0	–	16.3	22.9	–	53.1	–	26.0	–	25.5	17.4
June												
1–5	23.5	22.0	26.7	16.3	26.4	29.3	53.1	37.5	29.6	30.0	29.2	17.4
6–10	12.3	25.0	45.3	32.7	44.6	29.3	53.1	46.0	36.7	26.0	27.1	17.4
11–15	24.0	20.3	43.4	27.0	19.2	42.0	42.0	45.8	46.8	40.0	32.6	13.4
16–20	3.0	18.4	29.5	22.7	18.0	24.0	14.3	26.6	36.7	38.0	24.5	27.6
21–25	3.0	6.3	23.0	16.3	10.0	13.0	18.7	54.0	18.2	30.0	22.9	22.4
26–30	14.2	27.7	23.9	18.0	12.2	12.0	28.0	28.0	17.0	10.0	42.0	22.9
July												
1–5	22.0	16.3	16.3	16.0	26.6	13.1	28.0	48.0	32.0	19.0	35.0	30.0
6–10	26.0	13.2	13.3	24.0	26.6	14.2	35.1	56.0	43.3	28.0	27.7	27.0
11–15	31.0	10.2	–	25.5	26.3	27.4	42.6	64.0	43.3	55.1	34.7	26.5
16–20	18.0	13.8	13.3	20.3	26.0	40.5	42.6	64.0	38.0	53.6	–	26.5
21–25	13.0	13.3	13.3	15.0	36.7	44.0	5.0	48.9	25.0	46.5	–	–
26–31	13.0	17.7	13.3	26.1	36.7	44.5	36.3	36.7	25.0	42.7	–	–

Note. June 11-30 is the main catch period.

Table 69 (appendix). Ratio of adult group "S" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980.	1981	1982	1983	1984	1985.	1986	1987	1988	1989
May												
25-31	2.0	8.0	–	18.6	10.4	–	6.1	–	6.0	–	6.4	17.4
June												
1-5	2.0	8.0	10.9	18.6	8.2	9.3	6.1	18.7	3.1	13.6	8.3	17.4
6-10	8.2	0.0	5.1	10.2	4.0	9.3	6.1	6.0	10.2	12.0	20.8	17.4
11-15	10.0	19.2	3.1	7.0	6.4	6.0	8.0	0.0	12.8	14.0	8.2	18.6
16-20	7.1	26.5	4.1	12.7	4.0	16.0	8.2	12.2	12.3	24.0	22.5	14.9
21-25	7.1	41.6	12.5	16.3	8.0	28.3	0.0	2.0	15.9	12.0	10.5	17.0
26-30	3.0	17.0	13.9	0.0	4.1	16.0	2.0	0.0	9.6	6.0	4.0	15.6
July												
1-5	12.0	10.2	3.1	8.0	2.0	10.1	2.0	0.0	3.1	5.0	7.2	6.0
6-10	4.0	15.3	0.0	14.0	8.2	4.1	6.2	1.0	7.2	4.0	10.6	10.0
11-15	7.0	20.4	–	13.7	11.1	6.8	10.6	2.0	7.2	8.2	8.2	8.2
16-20	28.0	34.5	0.0	24.3	14.0	9.5	10.6	2.0	12.0	10.1	–	14.3
21-25	34.0	21.9	0.0	35.0	32.7	2.0	5.0	6.4	13.6	9.3	–	–
26-31	34.0	17.6	0.0	21.7	32.7	2.3	6.1	24.5	13.6	2.4	–	–

Note. June 11-30 is the main catch period.

Table 70 (appendix). Ratio of adult group "V" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May												
25-31	0.0	12.0	–	0.0	0.0	–	0.0	–	2.0	–	0.0	0.0
June												
1-5	0.0	12.0	0.0	0.0	0.0	0.0	0.0	4.2	2.0	0.0	0.0	0.0
6-10	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
11-15	0.0	1.0	0.0	1.0	0.0	0.0	0.0	2.1	4.2	0.0	4.1	0.0
16-20	6.0	2.0	0.0	2.5	6.0	6.0	14.3	0.0	2.0	4.0	8.2	0.0
21-25	6.0	10.4	2.1	6.2	8.0	23.9	4.2	6.0	9.1	14.1	12.5	5.3
26-30	14.2	14.9	0.0	22.0	26.6	38.0	20.0	46.0	18.1	22.0	16.0	12.5
July												
1-5	30.0	20.4	8.9	34.0	16.3	28.2	20.0	22.0	21.6	16.0	19.6	24.0
6-10	22.0	31.6	17.8	28.0	24.5	18.4	19.6	18.0	10.3	10.0	23.4	21.0
11-15	17.0	42.9	–	25.5	16.3	9.2	19.1	14.0	10.3	12.3	16.3	19.4
16-20	22.0	6.9	17.8	22.7	8.0	0.0	19.1	14.0	4.0	12.1	–	22.5
21-25	10.0	13.5	17.8	20.0	10.2	2.0	5.0	19.1	18.2	14.0	–	–
26-31	10.0	5.9	17.8	17.3	10.2	2.3	9.1	16.3	18.2	17.1	–	–

Note. June 11-30 is the main catch period.

Table 71 (appendix). Ratio of adult stock "D" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May												
25-31	4.8	10.0	–	7.0	0.0	–	12.2	–	50.0	–	36.2	39.1
June												
1-5	4.8	10.0	6.4	7.0	5.0	5.3	12.2	0.0	44.9	34.6	27.1	39.1
6-10	12.2	12.5	7.2	12.2	2.0	5.3	12.2	12.0	20.4	30.0	18.7	39.1
11-15	4.0	7.1	3.1	8.0	2.1	2.0	8.0	6.3	21.3	14.0	4.1	44.3
16-20	2.0	8.2	0.0	4.5	4.0	0.0	8.2	6.1	6.1	12.0	6.1	8.5
21-25	2.0	6.3	2.1	1.5	0.0	0.1	0.0	0.0	15.9	6.0	8.3	8.5
26-30	0.0	2.1	2.4	0.0	2.0	2.0	0.0	4.0	13.8	2.0	4.0	6.3
July												
1-5	2.0	4.1	0.0	6.0	4.1	1.0	0.0	2.0	9.3	3.0	5.2	4.0
6-10	4.0	3.1	0.0	6.0	0.0	0.0	4.1	3.0	13.4	4.0	6.4	4.0
11-15	3.0	2.0	–	5.9	4.0	1.2	8.6	4.0	13.4	2.0	0.0	5.1
16-20	2.0	0.0	0.0	2.9	8.0	2.4	8.6	4.0	20.0	3.0	–	14.3
21-25	9.0	11.2	0.0	0.0	4.1	6.0	15.0	6.4	22.8	8.1	–	–
26-31	9.0	17.6	0.0	4.4	4.1	4.2	42.4	8.2	22.8	15.9	–	–

Note. June 11-30 is the main catch period.

Table 72 (appendix). Ratio of adult group "N" Kamchatka *R. sockeye* from river gill net catches (every five days), %

Data	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
May												
25-31	4.0	0.0	–	0.0	4.2	–	0.0	–	2.0	–	2.1	4.3
June												
1-5	4.0	0.0	2.2	0.0	3.1	2.8	0.0	0.0	6.1	1.8	6.2	4.3
6-10	10.2	0.0	3.1	2.0	0.0	2.8	0.0	6.0	4.1	6.0	4.2	4.3
11-15	2.0	5.0	3.1	5.0	0.0	0.0	6.0	6.3	2.1	2.0	12.2	4.1
16-20	11.2	4.1	3.2	4.6	4.0	0.0	2.0	12.2	10.2	6.0	6.1	6.4
21-25	11.2	0.0	4.1	2.1	0.0	0.0	2.1	0.0	0.0	2.0	8.3	5.3
26-30	8.0	6.4	2.1	4.0	2.0	4.0	0.0	4.0	2.1	0.0	8.0	3.1
July												
1-5	6.0	6.1	6.6	2.0	0.0	4.1	0.0	4.0	6.2	0.0	5.2	8.0
6-10	2.0	4.1	8.9	6.0	2.0	4.1	0.0	5.0	10.3	0.0	2.1	10.0
11-15	12.0	2.0	–	3.9	4.0	2.0	0.0	6.0	10.3	2.0	10.2	7.1
16-20	10.0	10.3	8.9	4.5	6.0	0.0	0.0	6.0	12.0	1.0	–	6.1
21-25	9.0	6.9	8.9	5.0	0.0	2.0	5.0	6.4	13.6	1.2	–	–
26-31	9.0	0.0	8.9	2.2	0.0	3.5	0.0	0.0	13.6	2.4	–	–

Note. June 11-30 is the main catch period.

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(1-376 in Russian, 377-612 in English)

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Notes

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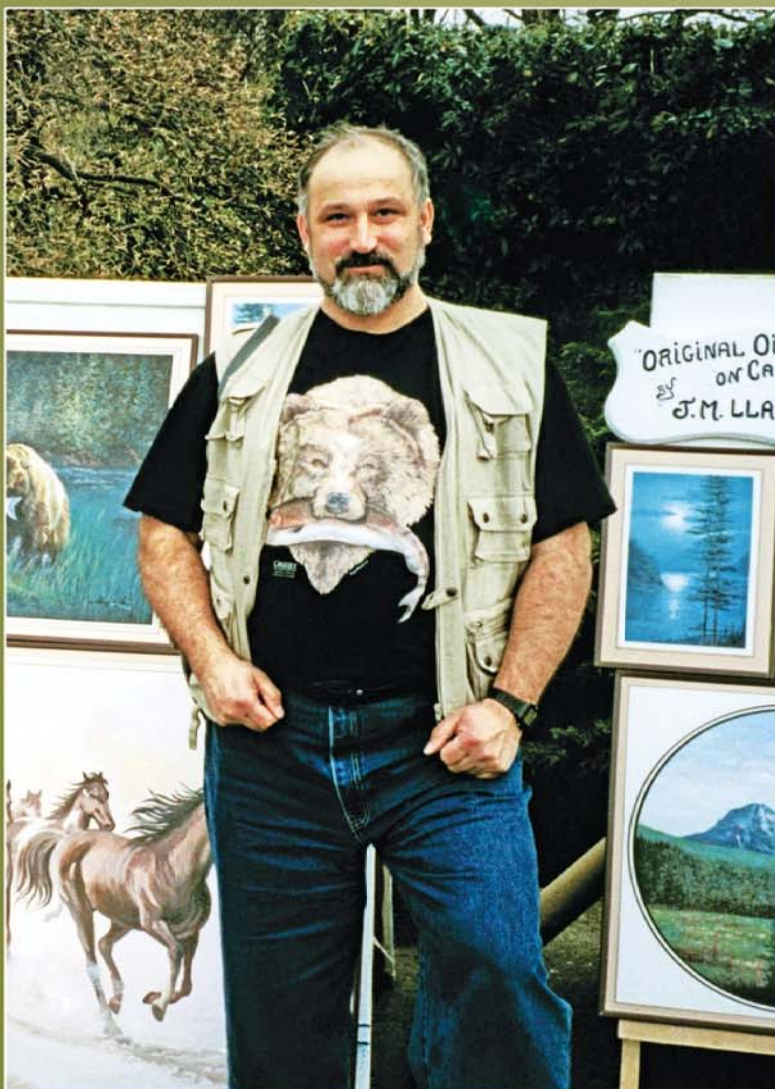
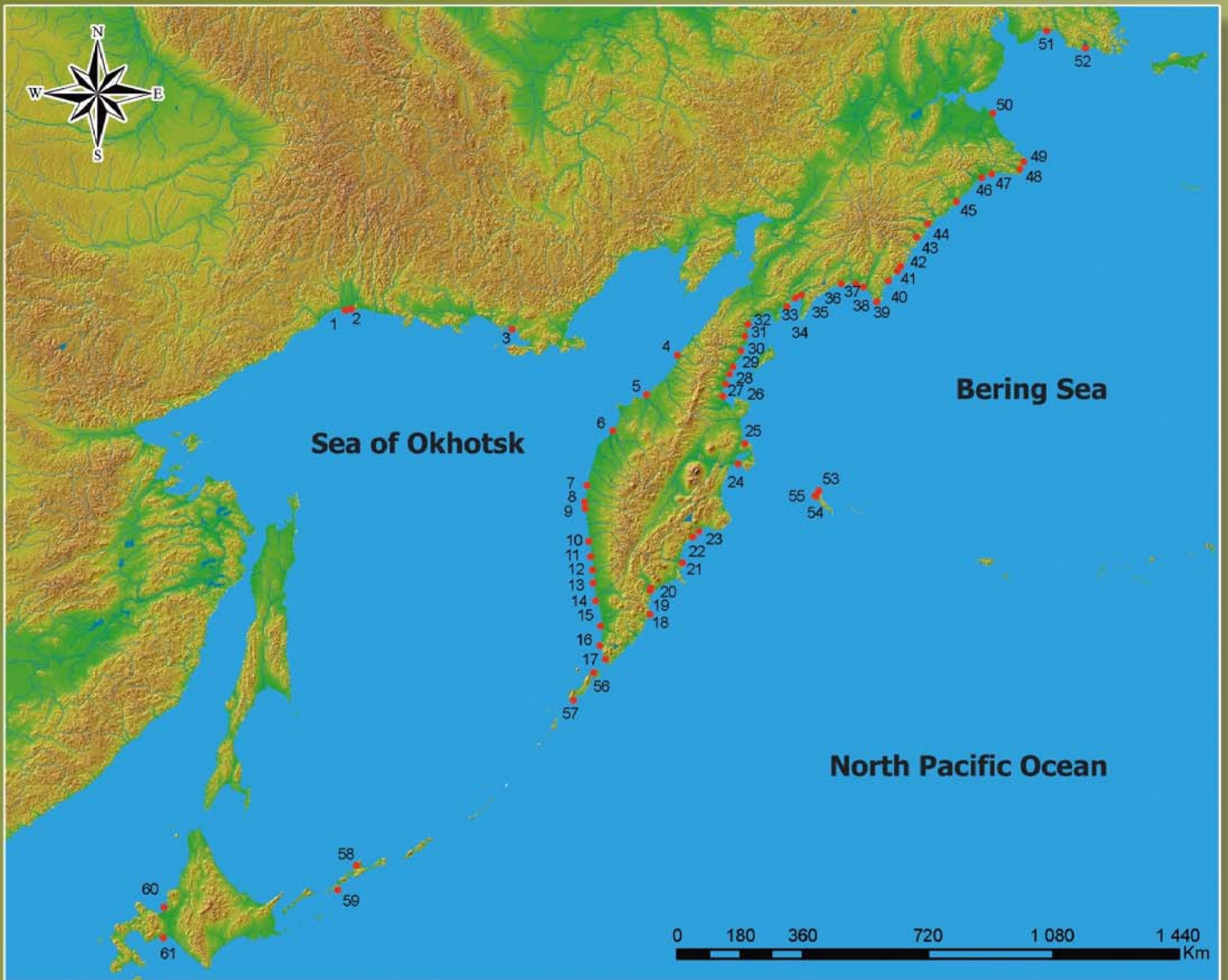
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