Calanoid copepod resting eggs – a safeguard against adverse environmental conditions in the German Bight and the Kara Sea?

Dauereier calanoider Copepoden – eine Anpassung an ungünstige Umweltbedingungen auch in der Deutschen Bucht und der Karasee?

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CONTENTS

ZUSAMMENFASSUNG

Die als Anpassung an eine ausgeprägte Variabilität der Umwelt geltenden Dormanz- oder Dauereier sind das bei calanoiden Copepoden am weitesten verbreitete Ruhestadium. In Zeiten ungünstiger Bedingungen kommt die Embryonalentwicklung dieser Eier vorübergehend zum Erliegen. Sie sinken auf den Gewässergrund ab und verbringen Monate oder sogar Jahre im Sediment, ohne Schaden zu nehmen. Indem sie erst dann schlüpfen, wenn sich eine Verbesserung der Umweltbedingungen abzeichnet, passen Dauereier den Lebenszyklus einer Art zeitlich an die Schwankungen bestimmter abiotischer und/oder biotischer Faktoren an. Dadurch haben sie auch Auswirkungen auf die Populationsdynamik und können als integraler Bestandteil im Lebenszyklus dominanter Copepodenarten sogar einen Einfluss auf die Dynamik ganzer Zooplanktongesellschaften ausüben.
Trotz ihrer Bedeutung für die Planktonökologie ist bisher wenig über Dauereier mariner, calanoider Copepoden bekannt. Darüber hinaus lassen die häufig beobachteten inter- und intraspezifischen Unterschiede verallgemeinernde Aussagen über nicht untersuchte Gebiete oder Arten anhand der bisher vorliegenden Erkenntnisse kaum zu.

Die Zielsetzung der vorliegenden Arbeit ist es daher, grundlegende Fragen zum Vorkommen, zum Schlupf und zur Bedeutung von Dauereiern calanoider Copepoden in der Deutschen Bucht und der Karasee zu beantworten, da zurzeit für beide Gebiete noch jegliche Informationen zu diesem Thema fehlen.
Laborversuche sollen Aufschluss über die Artenzusammensetzung sowie die Verbreitung von Dauereiern in der Deutschen Bucht geben. Ferner gilt es, den Einfluss verschiedener abiotischer Faktoren auf die Beendigung der Ruhephase zu ermitteln. Einen weiteren Schwerpunkt bilden saisonale Aspekte des Schlüpfens. Außerdem ist vorgesehen, die Abhängigkeit des Schlupfes von der Versuchsdauer zu bestimmen. Freilanduntersuchungen sollen die Verhältnisse unter *in-situ* Bedingungen aufzeigen und Hinweise über die Aussagekraft der im Labor erzielten Ergebnisse liefern.
Bedingt durch den zeitlichen Rahmen, der für die Probennahme in der Karasee zur Verfügung steht, konzentrieren sich die Arbeiten in diesem Gebiet auf die Artenzusammensetzung sowie die räumliche Verteilung von Dauereiern.

An 5 Stationen in der Deutschen Bucht wurden zwischen März 2002 und Februar 2003 insgesamt 34 Sedimentkerne gezogen. Die obersten 5-7 cm eines jeden Kerns wurden zusammen mit gefiltertem Seewasser über einen Zeitraum von 1,5 bis 12 Monaten inkubiert und wöchentlich auf frisch geschlüpfte Nauplien hin untersucht. Andere Proben wurden abrupten Änderungen der Inkubationstemperatur, der Photoperiode oder der Sauerstoffkonzentration ausgesetzt. Darüber hinaus wurden spezielle Fallen entwickelt und eingesetzt, um den Schlupf von Dauereiern im Freiland zu untersuchen.

Die Probennahme in der Karasee erfolgte im Rahmen einer Expedition im Herbst 2001. Hierbei wurden in der Regel 3 Sedimentkerne an jeder der 32 Stationen gezogen. Ein Satz unbehandelter Proben wurde für 3-6 Monate inkubiert und der Schlupferfolg alle 3-7 Tage ermittelt. Aus anderen Proben wurden Ei-ähnliche Objekte extrahiert und ohne Sediment inkubiert.

Die Ergebnisse zeigen, dass in der Deutschen Bucht mindestens drei calanoide Copepodenarten Dauereier produzieren, nämlich *Temora longicornis*, *Centropages hamatus* und *Acartia* sp.. Aus den 34 Proben, die zwischen März 2002 und Februar 2003 gesammelt wurden, schlüpften insgesamt 13 559 Nauplien. Der Schlupf erwies sich als abhängig von Probenahmeort und -zeitpunkt. Maximalwerte wurden im Frühjahr und Herbst registriert. Die höchsten gefunden Dichten entsprachen 1 269 996 Nauplien pro Quadratmeter Meeresboden. Obwohl Unterschiede zwischen *T. longicornis* und *C. hamatus* in den Langzeitversuchen deutlich wurden, wurden selbst nach einer Laufzeit von 12 Monaten noch Nauplien beider Arten bei den Kontrollen gefunden. Die Experimente deuten des Weiteren darauf hin, dass alle drei getesteten Umweltparameter Auswirkungen auf die Beendigung der Ruhephase haben. Der Abfall der Temperatur auf für den Winter übliche Werte löste einen Anstieg und eine Synchronisation des Schlupfes aus, während völlige Dunkelheit einen hemmenden Einfluss hatte. Erhöhte Konzentrationen gelösten Sauerstoffs hatten ebenfalls eine fördernde Wirkung.
Es ist anzunehmen, dass die in der Deutschen Bucht ganzjährig vorkommende Art *T. longicornis* durch die Produktion von Dauereiern einem erhöhten Prädationsdruck im Sommer ausweicht und gleichzeitig die Nutzung der Frühjahrsblüte im Phytoplankton optimiert. Im Gegensatz dazu könnte die besondere Bedeutung der Dauereier für *C. hamatus* darin liegen, dass sie das Überleben der Population während des Winters sicherstellen, wenn die Art im Plankton fehlt.

Die Versuchsergebnisse für die Karasee deuten auf eine gänzlich andere Situation im zweiten Untersuchungsgebiet der vorliegenden Arbeit hin. Nur 10 Nauplien calanoider Copepoden wurden insgesamt gefunden, und selbst diese stammen wahrscheinlich nicht aus Dauereiern. Neun der 10 Nauplien sind vermutlich Vertreter der Gattung *Pareuchaeta*.
Offensichtlich wird die Produktion von Dauereiern in der Karasee durch andere Anpassungen an eine extrem variable Umwelt ersetzt. Manche Copepodenarten durchlaufen zum Beispiel eine Ruhephase während der postembryonalen Entwicklung. Andere akkumulieren besondere Speicherfette, um Zeiten des Nahrungsmangels zu überstehen, oder erschließen sich neue Futterquellen (z.B. Eisalgen). Dies könnte auch für die Copepoden angrenzender Schelfgebiete gelten.

Zusammenfassend lässt sich sagen, dass Dauereier in der Deutschen Bucht weit verbreitet sind und zumindest für einige Arten calanoider Copepoden einen wichtigen Schutzmechanismus zum Überstehen widriger Umweltbedingungen darstellen. Im Gegensatz dazu scheinen sie in der Karasee zu fehlen und durch andere Anpassungen an extreme Umweltbedingungen ersetzt worden zu sein.

SUMMARY

Numerous species of calanoid copepods produce eggs that are able to undergo a period of developmental arrest in times when conditions in the water column are unfavourable for planktonic stages. These eggs are referred to as dormant or resting eggs. They accumulate in the sediment, are often characterised by an increased resistance to environmental harshness and can remain viable for many months or even years. As dormancy synchronizes an organism's life-cycle to its environment, resting eggs ultimately affect population dynamics. Wherever they occur in the life-cycle of dominant copepod species they may even influence entire zooplankton communities. But despite their importance to plankton ecology the information available on resting eggs in marine and brackish water calanoid copepods is still fragmentary. Moreover, inter- and intra-specific differences have repeatedly been observed, so that it is difficult to draw conclusions from results obtained from a related species or a far-away location.

The present study therefore focuses on two regions for which resting eggs of calanoid copepods have not previously been reported.
In the German Bight the aim is to determine species composition and abundance of viable eggs in the seabed by means of hatching experiments, to elucidate the stimuli that induce the termination of dormancy, to study the seasonal variability of nauplii emergence and to identify inter-specific differences in hatching. Long-term emergence patterns are to be analysed, too. In addition, field tests shall be conducted in order to investigate in-situ hatching of resting eggs.
The objectives for the Kara Sea are to analyse species composition and abundance of resting eggs as well as their spatial distribution in sea bottom sediments.

Between March 2002 and February 2003 a total of 34 sediment cores were collected at 5 stations in the inner German Bight. The top 5-7 cm of each core were incubated with filtered seawater for up to one year and bottles checked weekly for freshly hatched nauplii. Additional samples, collected in June and October 2003, were subjected to abrupt changes in temperature, photoperiod or the concentration of dissolved oxygen during the incubation period. In order to follow hatching of resting eggs in-situ, diver-operated emergence traps were designed and constructed. These were repeatedly deployed near the island of Helgoland for extended periods of time.
In the Kara Sea, usually three sediment cores were collected at each of the 32 stations sampled during a cruise in autumn 2001. One set of unprocessed samples was incubated for 3-6 months and screened approximately weekly. Other samples were used to extract egg-like objects prior to incubation.

The results indicate, that in the German Bight at least three species of calanoid copepods produce resting eggs, i.e. *Temora longicornis, Centropages hamatus*

and *Acartia* sp.. From the 34 samples collected between March 2002 and February 2003, 13 559 specimens emerged in total. Hatching varied among sampling stations and with season. Highest values were recorded in spring and autumn. Maximum densities were equivalent to 1 269 996 nauplii per square meter of seafloor. Emergence continued for up to one year, but significant differences in long-term patterns seem to exist between *T. longicornis* and *C. hamatus*. Laboratory experiments indicated that the three environmental parameters tested all influence the termination of dormancy. A drop to temperatures characteristic for winter enhanced and synchronised hatching, while complete darkness inhibited emergence. Elevated levels of dissolved oxygen also resulted in an increase in hatching.
In the German Bight, the perennial *T. longicornis* is believed to benefit from the production of resting eggs by reducing mortality from predation in times when predators are abundant as well as by an improved utilisation of the spring bloom. *C. hamatus*, in contrast, which is absent from the plankton in winter, appears to rely on resting eggs for cold season population survival.
Results from the Kara Sea were quite different. Only 10 calanoid copepod nauplii were found in total. However, it is unlikely that they originated from resting eggs, as 9 of them were assumed to *Pareuchaeta* spp.. Females of this genus produce egg sacs rather than releasing their eggs into the water column. The almost complete lack of nauplii in the Kara Sea samples suggests that alternative strategies, including dormancy in developmental stages other than the egg stage, the accumulation of storage lipids and the utilisation of ice algae, are used by the calanoids in order to cope with environmental variability in this area. This might also be true for the adjacent shelf seas.

So while resting eggs are common in the German Bight and appear to be an important safeguard against adverse environmental conditions in at least a couple of species, they are obviously absent from the Kara Sea, where calanoid copepods exhibit different adaptations to environmental variability.

INTRODUCTION

CHANGE IS THE ONLY CONSTANT

The environmental conditions in an ecosystem are never constant. Depending on latitude and type of habitat, numerous abiotic and biotic factors vary with time (Schwerdtfeger, 1978; Remmert, 1984). These changes are often cyclic, as much of the variability ultimately results from the planetary movements of the earth around its own axis and around the sun. Levels of incident solar radiation and temperature, for example, will usually follow the day/night cycle in a desert, a lowland forest or a supralittoral rock pool, while they may hardly fluctuate at all in a subterranean cave or the deep sea. Similarly, photoperiod and hence primary productivity are strongly linked to season, particularly beyond the tropics.
Other cyclic changes are caused by the moon orbiting the earth. These predominantly influence aquatic ecosystems. High and low tides occur once or twice (diurnal ↔ semidiurnal) per lunar day (24 h 50 min), depending on latitude. Equally, spring and neap tides occur twice per lunar month (29 d 12 h) (The Oceanography Course Team, 1994). As a result of the emersion-submersion cycle, species living in the intertidal zone are exposed to strong variations of many abiotic and biotic environmental factors (Little and Kitching, 1996), including nutrient availability, humidity and predation pressure.
But continual variability is not always as easily recognisable as it is on the shore. In the abyssal depths of the world's oceans perpetual darkness prevails and temperature changes very little. Nevertheless, availability of food depends on the import of organic material from the photic zone (Auel, 1999) and consequently fluctuates over the course of a year (Tyler, 2003). Though most parameters have a period length of 12 months or less, multi year cycles are also common (Meehl, 1994; White and Tourre, 2003).
The examples given above allude to cyclic and thus predictable changes. Yet acyclic, unpredictable variability of environmental factors is equally widespread, and irregular events like storm surges, droughts, overpopulation, or anthropogenic pollution can become a thread to the biota, too.

RESPONSE TO TEMPORARILY ADVERSE ENVIRONMENTAL CONDITIONS

Irrespective of the variability pattern (cyclic ↔ acyclic), an environmental factor becomes unfavourable/lethal to an organism once it approaches/exceeds the limits of its range of tolerance towards that factor. Thus appropriate response mechanisms are essential to prevent a species from extinction due to temporary adverse conditions in an otherwise suitable habitat. Under non-lethal conditions these may simply enhance a species' viability. Three different approaches can be distinguished:

Migration

Sufficient motility provided, an animal may actively move to a more beneficial location and return only after conditions have improved again.
In the African savannah, for instance, many species of ungulates migrate long distances every year in search of food and water (Tischler, 1993). Likewise, many birds reproduce in high latitudes during the Arctic summer but spend the winter months in the southern hemisphere (Johnson and Herter, 1990). In the ocean, whales may travel thousands of miles every year between their feeding and breeding grounds located in polar and subtropical waters, respectively (Tardent, 1993). Along the same lines, several zooplanktonic species migrate vertically over hundreds of meters every day (Maycas et al., 1999) in order to minimize mortality from predation and also to reduce the metabolic rate in times when they do not feed by moving to deeper, colder water layers.

Polymorphism and polyphenism

Rather than leaving for a more suitable location, organisms may stay put and undergo a change in phenotype (e.g. morphology or colour) in order to improve their viability under adverse conditions.
This ecological strategy is common among insects, cladocerans and rotifers and differs from dormancy (see below) in that it does not involve a suspension of development. Wing colouration in butterflies (Roskam and Brakefield, 1999) and wing length in crickets (Olvido et al., 2003) vary with season. In the Cladocera body shape may be affected by a number of biotic and abiotic factors (Laforsch and Tollrian, 2004). In *Daphnia cucullata* for example, kairomones from a variety of potential invertebrate predators were found to induce polymorphism (Agrawal et al., 1999). Similarly, filtrates from copepod and cladoceran cultures can induce spine development in rotifers like *Keratella tropica* (Marinone and Zagarese, 1991).

Dormancy

Species may remain on site and enter dormancy, a phase of metabolic and/or developmental arrest, which is usually characterised by an increased resistance to adverse conditions (Siewering, 1980).
It has evolved in numerous bacterial, fungal, protist, plant and animal species (Caceres, 1997). Like migration and polymorphism, dormancy enables an organism to cope with both acyclic and cyclic variability. The mechanisms, however, clearly differ. According to Hand (1991), two main subtypes can be distinguished, quiescence and diapause:

Quiescence is usually a response to acyclic variability. It is a reversible state of suppressed metabolism and/or development imposed by critical values of parameters like temperature, moisture or nutrition. Generally the disadvantageous factor itself is the cue that induces quiescence, a short-term, irregular phenomenon controlled by the central nervous system. Quiescence

can be induced repeatedly in a certain ontogenetic stage and does not insure long-term survival.
Diapause is a neurohormonally mediated, dynamic state of low metabolic activity, an adaptation to cyclic environmental change. It occurs during a genetically determined stage of the ontogenetic development (Tauber et al., 1986). However this stage can vary between species. Unlike quiescence, diapause is not brought about by harsh conditions, but rather by token stimuli that presage a change in the environment (e.g. decreasing photoperiod heralds the coming of winter and thus adverse temperatures). These do not have a negative impact themselves. Perception of token stimuli and expression of diapause can be rather close in time, or widely separated. In the aphid *Megoura* the grandparental generation is the sensitive stage. Diapause begins before the unfavourable conditions arise and metabolic activity is suppressed even if they remain favourable for development. Token stimuli are also involved in breaking diapause, but will only be effective, if the refractory phase has been completed.
Copepods rely predominantly on quiescence and diapause as a response to seasonally deteriorating environmental conditions. Though migration has been occasionally observed, too, it is usually linked to dormancy. Polymorphism and polyphenism as a response to adverse conditions appear to be unknown in the Copepoda.

DORMANCY IN THE COPEPODA

Dormancy has been reported for the free-living representatives of three copepod taxa: the Cyclopoida, the Harpacticoida, and the Calanoida (see Williams-Howze, 1997 for a review). It has been found in marine and freshwater species, especially from temperate and higher latitudes, and is expressed in various ontogenetic stages (Dahms, 1995 for a review).
Cyclopoids are particularly common in all types of freshwater habitats, from temporary ponds and roadside ditches to large permanent lakes and rivers. But they also occur in the sea. However, dormancy in this group appears to be restricted to freshwater species and is most commonly expressed in the copepodite stages 4 and 5. In permanent bodies of water cyclopoid dormancy is frequently induced by temperature and/or photoperiod and found in summer or winter.
A dormant stage has been recognised in only comparatively few harpacticoid species, from marine and freshwater habitats alike. These usually outlive unfavourably high temperatures or low levels of dissolved oxygen in summer as encysted adults.
In the Calanoida two taxa can be distinguished. Species belonging to the exclusively marine Megacalanoidea overwinter as dormant copepodids, mainly C4 or C5, in deep water. Being herbivores, they live in the photic zone when active. Thus migration is strongly associated with dormancy in representatives from this group. Substantial reserves of lipids (wax esters; triacylglycerols) are equally characteristic of dormant copepodids from the Megacalanoidea.
In contrast, members of the Centropagoidea produce dormant eggs (= resting eggs) in fresh- and seawater. These sink to the bottom and accumulate in the

sediment, from where a new generation may emerge into the plankton once dormancy is terminated.

CALANOID COPEPOD RESTING EGGS IN MARINE AND BRACKISH WATER ENVIRONMENTS

To date resting eggs have been reported for 49 species of marine and estuarine calanoid copepods (Table 1), almost exclusively from locations in the northern hemisphere (Figure 1). They can remain viable in the sediment for many months or even years (Viitasalo, 1992; Katajisto, 1996).

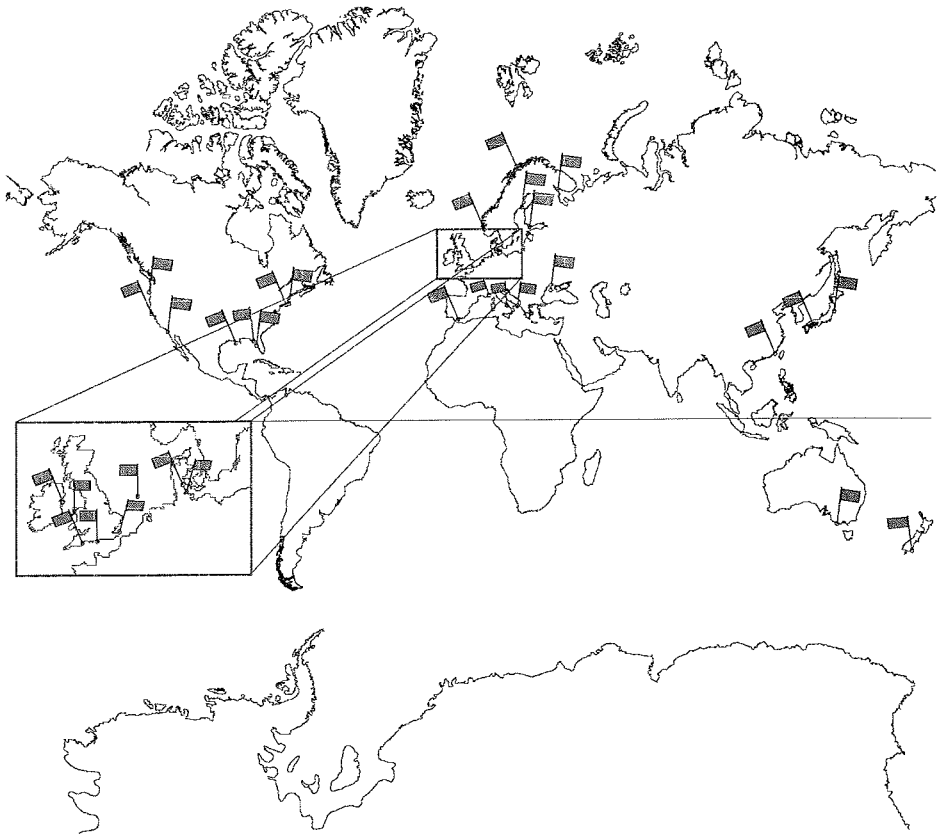

Figure 1: The global distribution of calanoid copepod resting eggs. Flags indicate sites where these eggs have been found in the sediment in marine and brackish water environments (solid horizontal line = equator)

Table 1: Calanoid copepod species, from marine and brackish waters, known to produce resting eggs

Species	Location	Reference
Acartia adriatica	Porto Cesareo, Ionic Sea, Italy	Belmonte, 1997
A. bifilosa	Southampton, Southampton Water, UK	Castro-Longoria and Williams, 1999
	Storfjärden, Baltic Sea, Finland	Katajisto et al., 1998
A. californiensis	Yaquina Bay, Pacific Ocean, USA	Johnson, 1980
A. clausi	Aquaculture enclosures, W-Norway	Naess, 1996
	Aquaculture enclosures, N-Norway	Naess, 1996
	Pacific Ocean, CA, USA	Marcus, 1990
	Inland Sea of Japan, Japan	Uye et al., 1979
	Mission Bay, Pacific Ocean, USA	Uye and Fleminger, 1976
A. erythraea	Inland Sea of Japan, Japan	Uye et al., 1979
A. grani	Malaga Harbour, Mediterranean, Spain	Guerrero and Rodriguez, 1998
A. hudsonica	Pettaquamscutt Estuary, USA	Marcus et al., 1994
	Narragansett Bay, Atlantic Ocean, USA	Sullivan and McManus, 1986
A. italica	Porto Cesareo, Ionic Sea, Italy	Belmonte, 1997
A. josiphinae	Porto Cesareo, Ionic Sea, Italy	Belmonte and Puce, 1994
	Otranto, Adriatic Sea, Italy	Belmonte and Puce, 1994
A. latisetosa	Adriatic Sea, Italy	Belmonte, 1992
A. pacifica	Inland Sea of Japan, Japan	Uye, 1985
A. pulmosa	Inland Sea of Japan, Japan	Uye, 1985
A. spinacaudata	Xiamen, Taiwan Strait, China	Chen and Li, unpublished in: Marcus, 1996
A. steueri	Onagawa Bay, Pacific Ocean, Japan	Uye, 1980
A. teclae	Aquaculture enclosures, W-Norway	Naess, 1996
A. tonsa	Tampa Bay, Gulf of Mexico, USA	Suderman and Marcus, 2002
	Southampton, Southampton Water, UK	Castro-Longoria, 2001
	Storfjärden, Baltic Sea, Finland	Katajisto et al., 1998
	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
	Schlei Fjord, Baltic Sea, Germany	Madhupratap et al., 1996
	Pacific Ocean, CA, USA	Marcus, 1990
	Alligator Harbor, Gulf of Mexico, USA	Marcus, 1989
	Narragansett Bay, Atlantic Ocean, USA	Sullivan and McManus, 1986
	La Jolla, Pacific Ocean, USA	Uye and Fleminger, 1976
A. tsuensis	Inland Sea of Japan, Japan	Uye, 1985
Anomalocera patersoni	Gulf of Naples, Mediterranean, Italy	Ianora and Santella, 1991
A. ornata	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
Boeckella hamata	Lake Waihola, South Island, NZ	Hall and Burns, 2001
Calanopia americana	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
C. thompsoni	Inland Sea of Japan, Japan	Uye et al., 1979
Centropages abdominalis	Inland Sea of Japan, Japan	Uye et al., 1979
C. furcatus	Alligator Harbor, Gulf of Mexico, USA	Marcus, 1989
C. hamatus	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
	Kiel Bay, Baltic Sea, Germany	Madhupratap et al., 1996
	Aquaculture enclosures, W-Norway	Naess, 1996

C. hamatus (continued)	S-North Sea	Lindley, 1990
	Drogheda, Irish Sea, Ireland	Lindley, 1990
	Margate, English Channel, England	Lindley, 1990
	Alligator Harbor, Gulf of Mexico, USA	Marcus, 1989
	White Sea, Russia	Perzova, 1974
C. ponticus	Black Sea	Sazhina, 1968
C. typicus	S-North Sea	Lindley, 1990
C. yamadai	Inland Sea of Japan, Japan	Uye et al., 1979
C. velificatus	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
Epilabidocera longipedata (= *E. amphitrites*)	Pacific Ocean, CA, USA	Marcus, 1990
	Yaquina Bay, Pacific Ocean, USA	Johnson, 1980
Eurytemora americana	Pettaquamscutt Estuary, USA	Marcus et al., 1994
E. affinis	Norrbyn, Baltic Sea, Sweden	Albertsson and Leonardsson, 2000
	Storfjärden, Baltic Sea, Finland	Katajisto et al., 1998
	Schlei Fjord, Baltic Sea, Germany	Madhupratap et al., 1996
	Aquaculture enclosures, W-Norway	Naess, 1996
	Aquaculture enclosures, N-Norway	Naess, 1996
	Pettaquamscutt Estuary, USA	Marcus et al., 1994
	Yaquina Bay, Pacific Ocean, USA	Johnson, 1980
E. pacifica	Onagawa Bay, Pacific Ocean, Japan	Uye, 1985
E. velox	Brackish water lake, SE-France	Champeau, 1970
Gippslandia estuarina	Hopkins River Estuary, Victoria, AUS	Newton and Mitchell, 1999
Gladioferens pectinatus	Lake Waihola, South Island, NZ	Hall and Burns, 2001
Labidocera aestiva	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
	Alligator Harbor, Gulf of Mexico, USA	Marcus, 1989
	Woods Hole, Atlantic Ocean, USA	Grice and Lawson, 1976
L. bipinnata	Inland Sea of Japan, Japan	Uye et al., 1979
L. trispinosa	La Jolla, Pacific Ocean, USA	Uye, 1985
L. scotti	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
	Alligator Harbor, Gulf of Mexico, USA	Marcus, 1989
L. wollastoni	S-North Sea	Lindley, 1990
	Margate, English Channel, England	Lindley, 1990
Pontella meadi	Turkey Point, Gulf of Mexico, USA	Chen and Marcus, 1997
	Gulf of Mexico, LA, USA	Chen and Marcus, 1997
	Woods Hole, Atlantic Ocean, USA	Grice and Gibson, 1977
P. mediterranea	Gulf of Naples, Mediterranean, Italy	Santella and Ianora, 1990
	Cap Ferrat, Mediterranean, France	Grice and Gibson, 1981
	Black Sea	Sazhina, 1968
Sinocalanus tenellus	Fukuyama, Japan	Uye, 1985
Sulcanus conflictus	Hopkins River Estuary, Victoria, AUS	Newton and Mitchell, 1999
Temora longicornis	Menai Bridge, Irish Sea, UK	Castellani and Lucas, 2003
	Aquaculture enclosures, S-Norway	Naess, 1996
	S-North Sea	Lindley, 1990
	Margate, English Channel, England	Lindley, 1990
Tortanus derjugunii	Xiamen, Taiwan Strait, China	Chen and Li, 1991
T. discaudatus	Pacific Ocean, CA, USA	Marcus, 1990
T. forcipatus	Inland Sea of Japan, Japan	Kasahara et al., 1974

As resting eggs are frequently found in species that are absent from the water column for portions of the year, they are often regarded as a means of securing the survival of a population in times of unfavourable environmental conditions in the plankton. Other purposes that have been suggested include the temporal partitioning of the environment (Marcus, 1984), the prevention of overcrowding (Uye, 1980), and even the slowdown of the rate of evolutionary change (Hairston and De Stasio, 1988).
Three types of resting eggs have been distinguished: quiescent subitaneous, diapause and delayed hatching eggs (Chen and Marcus, 1997), which differ in their mode of development. Subitaneous eggs hatch within a few days, but can become quiescent in response to adverse environmental conditions. As soon as these improve, eggs are capable of hatching. In contrast, diapause eggs hatch only after the completion of a refractory phase, which may last several months, even if conditions are beneficial (Grice and Marcus, 1981). During this period development and/or metabolic processes apparently cease or drop to undetectable levels (Marcus, 1996). Unlike diapause eggs, nauplii emerge from delayed-hatching eggs only gradually over an extended period of time (Chen and Marcus, 1997).
Due to their abundance, up to several million have been found per m^2 (Marcus, 1984; Guerrero and Rodriguez, 1998), resting eggs constitute an important component of bentho-pelagic coupling. Benthic processes and environmental conditions in the sediment, for example, influence survival and hatching rate of resting eggs and thereby affect the reproductive success of a species (Marcus and Lutz, 1998).
As climate may act differently (spatial, temporal) on the benthic and the pelagic systems, population dynamics of those copepod species that have resting eggs should have two control components, a benthic and a pelagic. Consequently, understanding the inter-annual variability of copepod populations in relation to climatology makes understanding egg bank dynamics a prerequisite.

CALANOID COPEPOD RESTING EGGS IN THE GERMAN BIGHT?

Nauplii of *Temora longicornis*, *Centropages hamatus*, *Centropages typicus*, *Labidocera wollastoni* and *Acartia* spp. emerged from sediment samples collected from the southern North Sea, the English Channel and the southern coast of England (Lindley, 1986; Lindley, 1990). Hatching usually continued for an extended period of time, in 50% of the samples for more than 12 months. This clearly indicated the presence of resting eggs, as embryonic development in *T. longicornis*, *C. hamatus* and *C. typicus* at an experimental temperature range of 5-10°C, should not exceed 8 days (Halsband-Lenk et al., 2002). Taking into account local oceanographic patterns, Lindley concluded, that their distribution is determined by water depth and bottom stress from tidal currents, and hence predicted copepod eggs to be abundant in bottom sediments in many areas around the British Isles including the German Bight (Figure 2) (Lindley and Hunt, 1989; Lindley, 1990).

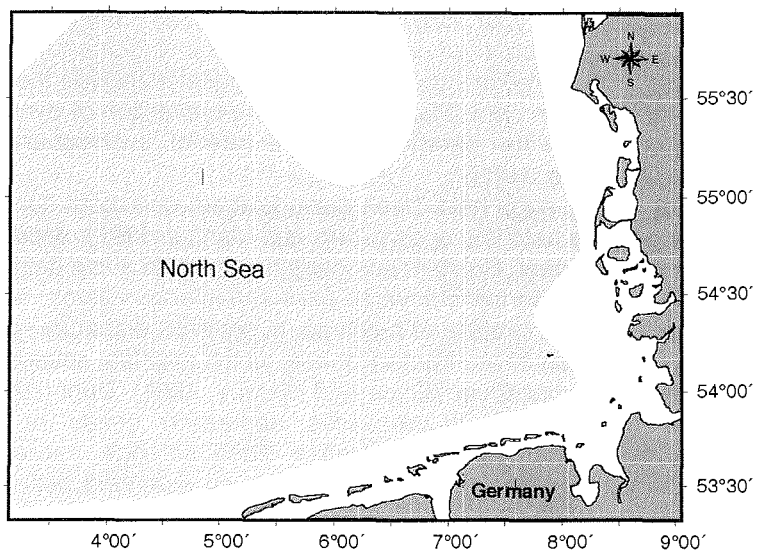

Figure 2: Shaded area indicates where calanoid copepod resting eggs are likely to be abundant in the sediment in the German Bight and adjacent waters (redrawn from Lindley, 1990)

At Helgoland Roads, a plankton monitoring site in the German Bight, *Acartia* spp., *Pseudocalanus* spp., and *T. longicornis* make up the vast majority of calanoids (Wesche, 2003; Greve and Reiners, unpublished). Other species include *C. hamatus*, *C. typicus*, *L. wollastoni*, and *Anomalocera patersoni* (Johanssen et al., 1999). Many of these undergo strong seasonal variations in abundance with maximum densities usually occurring between late spring and the beginning of autumn (Fransz et al., 1991; Greve and Reiners, unpublished). In winter numbers are significantly reduced and egg production often ceases. Species like *C. hamatus* and *C. typicus* might even be completely absent from the water column for several months every year (Halsband and Hirche, 2001). However, little is known about the overwintering strategies of copepods in this area of the North Sea. Whether resting eggs play a crucial role in the perpetuation of some of these species is unclear, as their presence has not yet been demonstrated in the German Bight.

CALANOID COPEPOD RESTING EGGS IN THE KARA SEA?

In autumn calanoid copepods usually dominate the Kara Sea zooplankton in terms of abundance (Fetzer et al., 2002) and biomass (Vinogradov et al., 1995). Most common in the 3 cruises summarised by Deubel et al. (2003) were *Limnocalanus macrurus*, *Drepanopus bungei*, *Calanus glacialis*, *Microcalanus pygmaeus*, *Pseudocalanus acuspes* and *Pseudocalanus major*.
Unfortunately data from other seasons is very limited. Due to the Kara Sea being covered by sea ice from approximately November to June (Gloersen et

al., 1992), winter expeditions are rare and consequently life cycle patterns and population dynamics of most copepod species in the Kara Sea are virtually unknown.
Nevertheless, distinct patterns are to be expected as organisms are exposed to highly variable conditions. Environmental factors like photoperiod and primary production oscillate widely in polar latitudes. Salinity also cycles strongly, especially in surface waters, due to dramatic changes in freshwater discharge from the Ob and Yenisei Rivers (Pavlov and Pfirman, 1995). Thus seasonal variability may pose a particular challenge to herbivorous and stenohaline species.

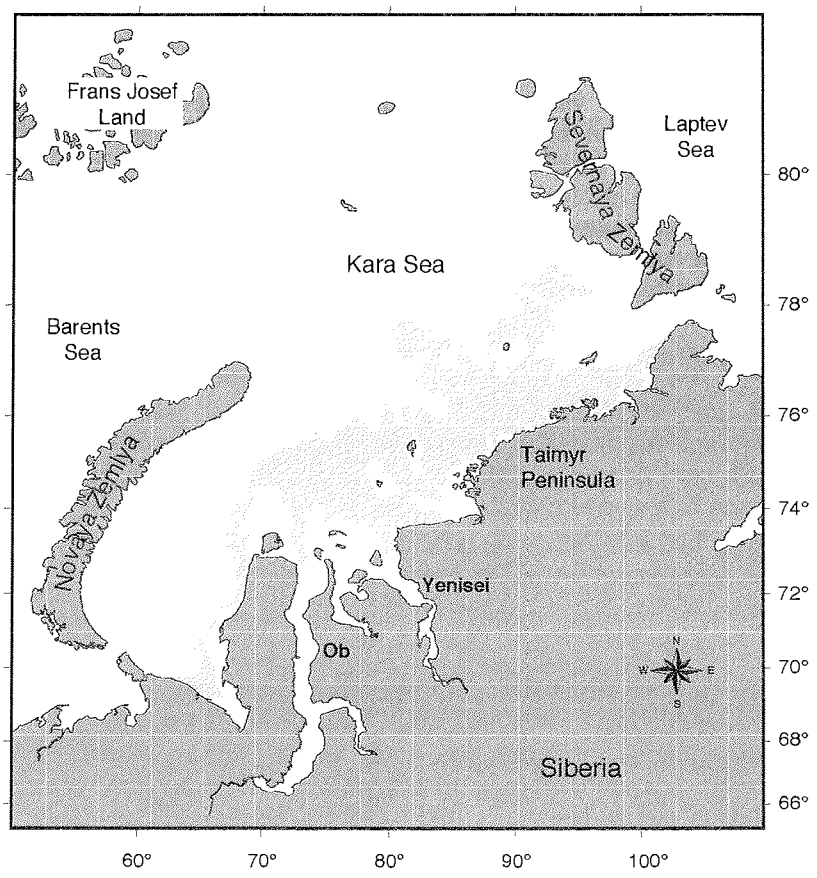

Figure 3: Areas in the Kara Sea with water depth between 20 and 50 m and bottom stress < 10 dyn cm^{-2}. Lindley (1990) predicted copepod resting eggs to be abundant in the sediment at sites around the British Isles meeting these oceanographic parameters

C. glacialis, *Calanus hyperboreus* and *Calanus finmarchicus* (the latter two also occur in the Kara Sea, but in meagre numbers) have been well studied in the Arctic Ocean (Kosobokova, 1978) and some of the shelf seas (Melle and

Skjoldal, 1998; Kosobokova and Hirche, 2001). They have been shown to store lipids as a long time energy reserve and hibernate as dormant copepodids (predominantly C4 and C5) at great depth (Conover and Siferd, 1993; Hirche, 1998). However, many of the smaller calanoids received much less attention and thus comparatively little is known about their overwintering strategies.

Only one of the 6 most common copepod species in the Kara Sea, namely *L. macrurus*, has been suggested to produce resting eggs elsewhere. But while the reports are contradictory (Roff, 1972; Torke, 1975 in: Vanderploeg et al., 1998; Kiefer and Fryer, 1978), corroborative evidence is lacking. On the other hand, it is generally accepted that the less frequent calanoids *Temora longicornis* and *Centropages hamatus* (Vinogradov et al., 1995; Fetzer et al., 2002) lay such eggs in temperate and subtropical waters and even in the White Sea (Sazhina, 1968; Perzova, 1974). However, these are the only two records of resting eggs in polar waters.

Near seabed current velocity data derived from a model developed by Harms and Karcher (1999) indicate that bottom stress caused by tidal currents (M_2 component) does not exceed 10 dyn per cm^2 in the southern Kara Sea. Thus, according to Lindley's description of the oceanographic conditions required for diapause eggs to be abundant in bottom sediments, they may well occur in the Kara Sea, particularly where water depth ranges between 20 and 50 m (Figure 3).

OBJECTIVES

Decades of monitoring have established the importance of calanoid copepods to plankton communities in the German Bight. Similar to the Kara Sea, a small number of species usually dominate the zooplankton in terms of abundance and biomass and consequently constitute a crucial component of the food web, feeding predominantly on phytoplankton and detritus while being fed on by larval fish as well as numerous invertebrate predators. It is therefore obvious that detailed information on population dynamics of common copepod species is essential in order to understand the variability and seasonal succession observable in plankton communities.
As a safeguard against environmental variability dormancy synchronises an organism's life-cycle to its environment and in doing so strongly influences population dynamics. Nevertheless copepod dormancy has hardly ever been studied in the German Bight and the Kara Sea. Resting eggs for instance have not been reported from either of the two regions so far, even though they are expected to be abundant in both areas and represent the most frequent dormant stage in the Copepoda. As inter- and intra-specific differences have repeatedly been observed, it is also difficult to draw conclusions from results obtained from a related species or a far-away location. Thus the present study focuses on calanoid copepod resting eggs in the German Bight and the Kara Sea (due to profound differences in accessibility, objectives differ between the study areas).

In the **German Bight** the aim was:

- to identify all species of calanoid copepods that produce resting eggs
- to determine the abundance of viable eggs in sea bottom sediments
- to elucidate the stimuli that induce hatching
- to study the seasonal variability of hatching
- to compare long-term (1 year) hatching patterns between resting eggs from different species
- to design, build and employ a trap capable of catching nauplii emerging from the sediment in the field
- to compare hatching results from the laboratory and the field

In the **Kara Sea** the aim was:

- to identify all species of calanoid copepods that produce resting eggs
- to determine the abundance of viable eggs in sea bottom sediments
- to analyse spatial distribution

STUDY AREA

GERMAN BIGHT

The German Bight comprises the shallow, south-eastern part of the North Sea (Figure 4). It is bordered in the southeast by extensive areas of inter-tidal mudflats (Wadden Sea), which stretch between the inshore islands and the coast and together with the post-glacial valley of the River Elbe are the most characteristic features of its bathymetry. Surprisingly, however, there is no clear-cut definition of its northern and western boundaries (Federal Maritime and Hydrographic Agency, personal communication). Therefore, in the scope of the present study, the German territorial waters in the North Sea together with the exclusive economic zone are considered as the German Bight. This area covers 41 073 km^2 (Federal Nature Conservation Agency, personal communications) and has a maximum depth of approximately 70 m at its north-western tip.

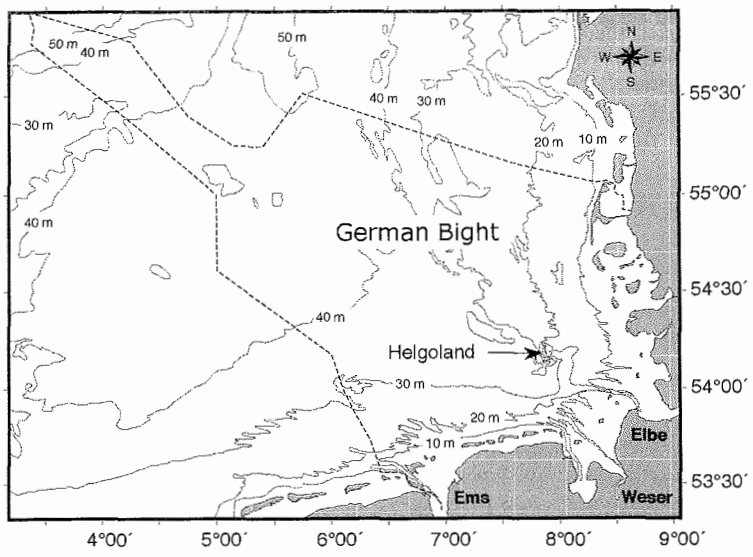

Figure 4: The bathymetry of the south-eastern North Sea (the broken line indicates the area considered as the German Bight in the present study)

According to Damm et al. (1994) Atlantic water enters the southern North Sea through the Strait of Dover and continues towards the German Bight. Here circulation is heavily dependant on wind direction, and thus nine different patterns can be distinguished. Cyclonic circulation is most frequent (Loewe et al., 2003), while two main water masses, Central Southern North Sea Water and Continental Coastal Water, prevail (Becker et al., 1992), the latter being a

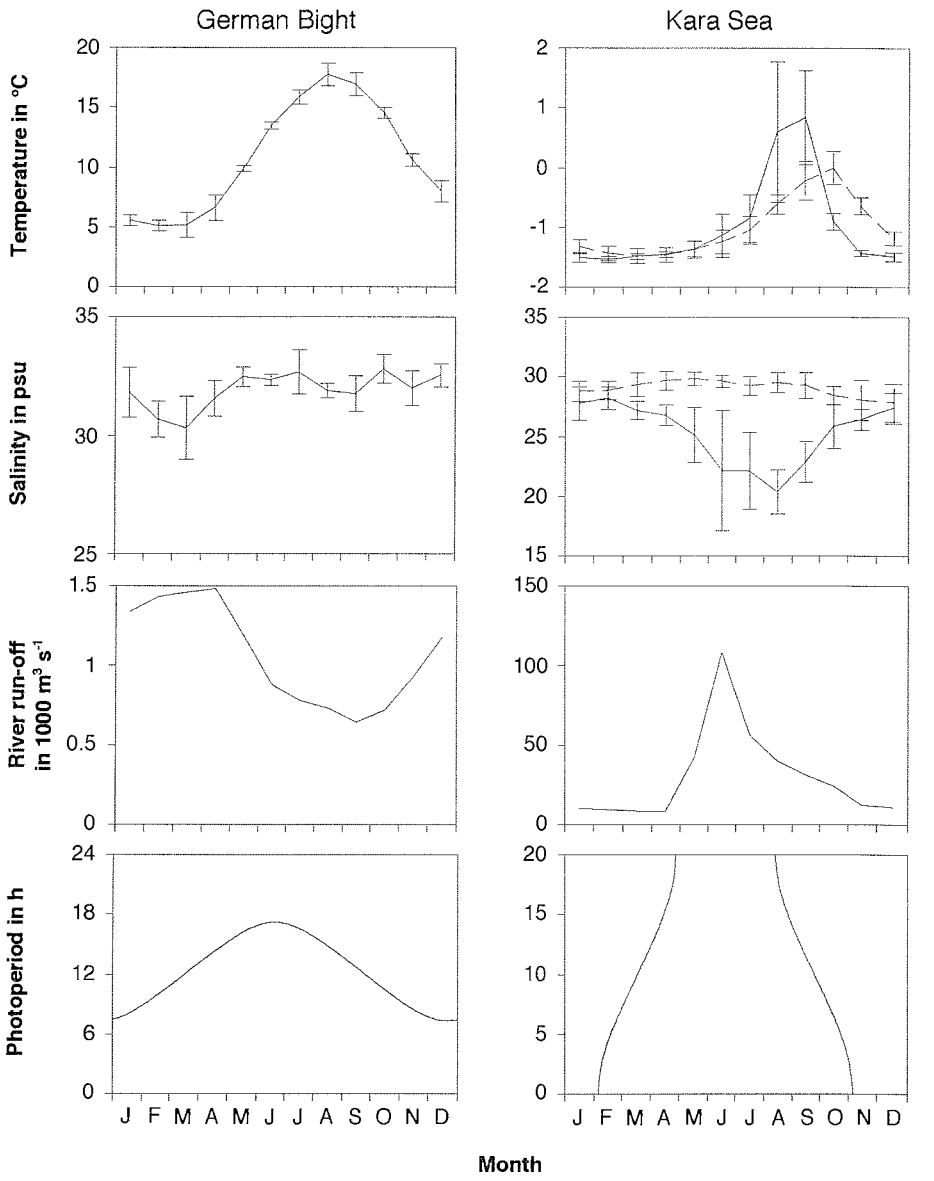

Figure 5: Annual cycles of water temperature, salinity and photoperiod in the German Bight (54°11.137′N, 7°53.909′E) and the Kara Sea (BP01-01: 74°59.12′N, 76°23.41′E). Salinity and temperature plots for the German Bight were drawn from field data from the Helgoland Roads time series (mean ± sd of monthly means from 2000-2002; surface) by courtesy of K. Wiltshire. Kara Sea salinity and temperature data (mean ± sd of monthly means from 1999-2001; solid line: 2 m below surface, broken line: 2 m above seabed) were derived from the model developed by Harms and Karcher (1999). Sunrise and sunset was computed with a tool provided by Geoscience Australia (www.ga.gov.au/nmd/geodesy/astro/sunrise.jsp). River run-off plots depict means of monthly means for discharge levels of the rivers Elbe + Weser (German Bight) and Ob + Yenisei (Kara Sea). Values were calculated from raw data available at www.sage.wisc.edu/riverdata/

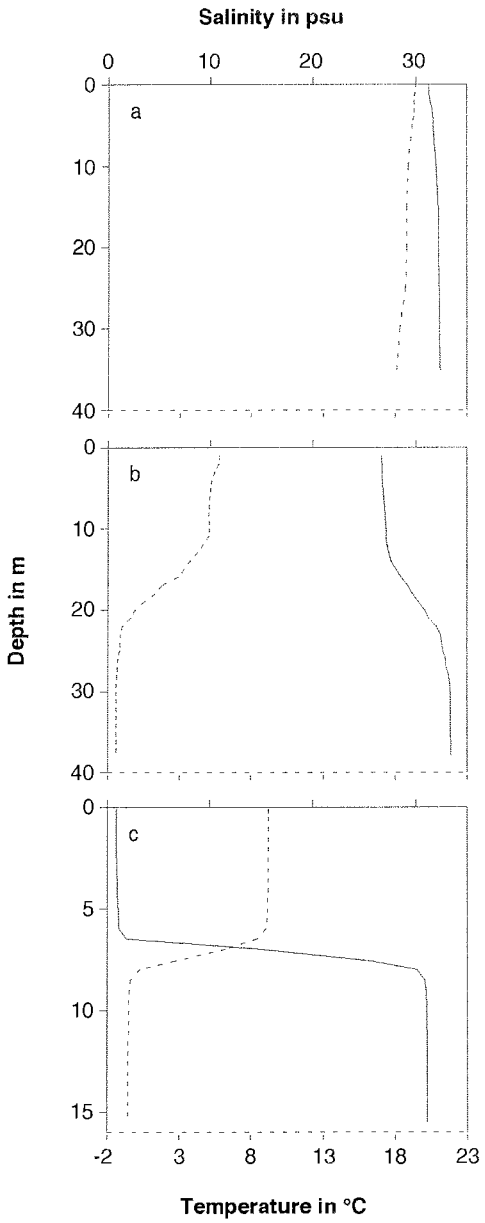

Figure 6: Salinity (solid lines) and temperature (broken lines) profiles. (a) German Bight (54°09.521´N, 7°55.931´E; 26 Aug. 2002), (b) Kara Sea (74°59.12´N, 76°23.41´E; 14 Aug. 2001 and (c) Mouth of the Ob River estuary/Kara Sea (72°40.16´N, 74°0.22´E; 7 Sep. 2001)

mixture of Atlantic water and water from the English Channel together with continental river run-off. The rivers Elbe, Weser and Ems together discharge roughly 40 km^3 of freshwater into the German Bight every year, with levels being lower in summer than in winter. Though thermal and/or haline stratification of the water column can be found in many regions at least for a few months every year (Becker et al., 1992), the discontinuity layers are rather weak (Loewe et al., 2003) (see also Figure 6a). This is due to a high tidal amplitude and low levels of river run-off compared to those encountered in the Kara Sea. The mean tidal range in the central German Bight is 2.4 m. Close to the coast and in some of the river estuaries it is well over 3 m. The seasonal cycle of water temperature in the German Bight is more pronounced than that of salinity (Figure 5). At Helgoland, sea surface salinity and temperature range between 28 and 33 psu and 2 and 20°C, respectively. Photoperiod varies between 7.33 and 17.2 h. Sediments are generally dominated by sand, but silt and clay account for more than 50% in some areas. Gravel and hard rock sea floor is rare (Figge, 1981). As surface sediments are quite mobile, they may be easily resuspended by shear currents or wave action and subsequently be transported by tidal or residual currents (Becker et al., 1992). Sediment structure is also heavily affected by intense bottom trawling (ICES, 1988).

KARA SEA

The Kara Sea is one of the Siberian Arctic Seas. It is located between 68°N and 81°N (Figure 7) and stretches from Novaya Zemlya and Frans Josef Land in the West to the Severnaya Zemlya Archipelago in the East. It encompasses an area of 883000 km^2 and has a mean depth of 111 m, though over 40% are shallower than 50 m (Volkov, 2002). Deepest regions are the Saint Anna (up to 620 m deep) and Voronin Troughs, which indent the shelf from the north, as well as the Novaya Zemlya Trough in the Southwest (Pivovarov et al., 2003).

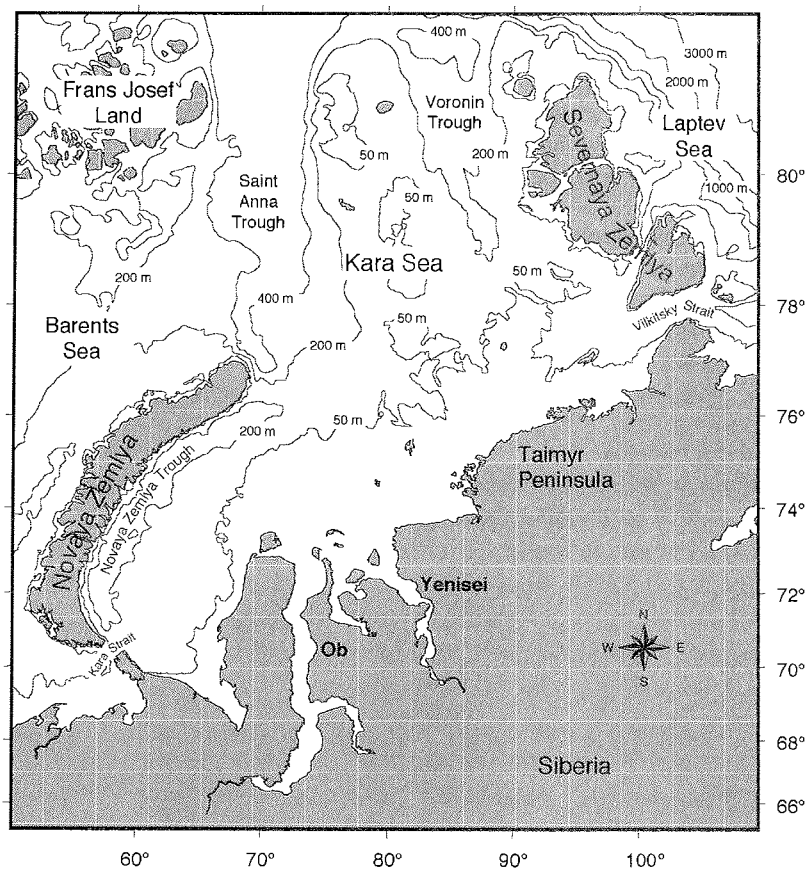

Figure 7: The bathymetry of the Kara Sea

The Kara Sea is fairly isolated from the adjoining shelf seas. It is connected to the southern Barents Sea and the Laptev Sea only through a number of comparatively narrow straits. In the North and Northwest, however, water exchange with the northern Barents Sea and the Arctic Ocean is unrestricted. Water flows in from the Barents Sea predominately through the strait between Novaya Zemlya and Frans Josef Land as well as through the Kara Strait, thus forming the Eastern Novaya Zemlya and Yamal Currents, respectively. These

two constitute the cyclonic gyre in the Southwest. The Western Taimyr Current and the eastern branch of the Yamal Current, on the other hand, transport large water masses to the north and northeast and export them to the Laptev Sea and the Arctic Ocean.

Kara Sea hydrography is strongly influenced by exceptionally high levels of river run-off from the Ob and the Yenisei, Siberia's largest streams. Including their tributaries, they drain an area of nearly 5 500 000 km^2 and, together with some minor rivers, discharge approximately 1 350 km^3 of freshwater and more than 150 million tons of suspended and dissolved organic and inorganic matter into the Kara Sea every year (Gordeev et al., 1996). Seasonal variability of river run-off is high, 80% occurs between June and September (Pavlov and Pfirman, 1995). Thus salinity and temperature cycle strongly with season, particularly in surface waters (Figure 5).

As the tidal amplitude is rather small (0.3-0.8 m), mixing of cold, highly saline bottom water and the overlying layer of warmer, low salinity river water is slow and stratification can be very distinct (Figure 6b, c). On the surface, estuarine and river plume water masses of intermediate salinity (1-25 psu) occupy all central parts of the Kara Sea in summer while they are restricted to a narrow band along the coast in winter (Pivovarov et al., 2003).

Other environmental variables also oscillate with season. At 74°59´N, in the centre of the Kara Sea sampling area, the sun remains above the horizon for 16 successive weeks in the summer and stays below it for just over 3 months in winter. Also, the Kara Sea is covered by sea ice for most of the year, usually from October until May. Consequently, photoperiod and light intensity in surface waters vary dramatically.

Bottom sediments are usually dominated by silt and clay and sediments coarser than sand (>2 mm) hardly ever occur (Steinke, 2002).

MATERIALS AND METHODS

GERMAN BIGHT: SEASONAL CYCLE OF HATCHING AND INTER-SPECIFIC VARIABILITY

Between March 2002 and February 2003, sediment cores were repeatedly collected every 6-9 weeks at 5 stations in the inner German Bight (Figure 8), near the island of Helgoland. Water depth at these stations ranged from 22 to 42 m (Table 2) and sediments were either muddy sand or sand.
Sampling was accomplished during 7 cruises with the RV Uthörn. Typically, one core was taken per cruise and station, but adverse weather conditions rendered sampling impossible at station 1 in February 2003. Thus 34 samples were collected in total.

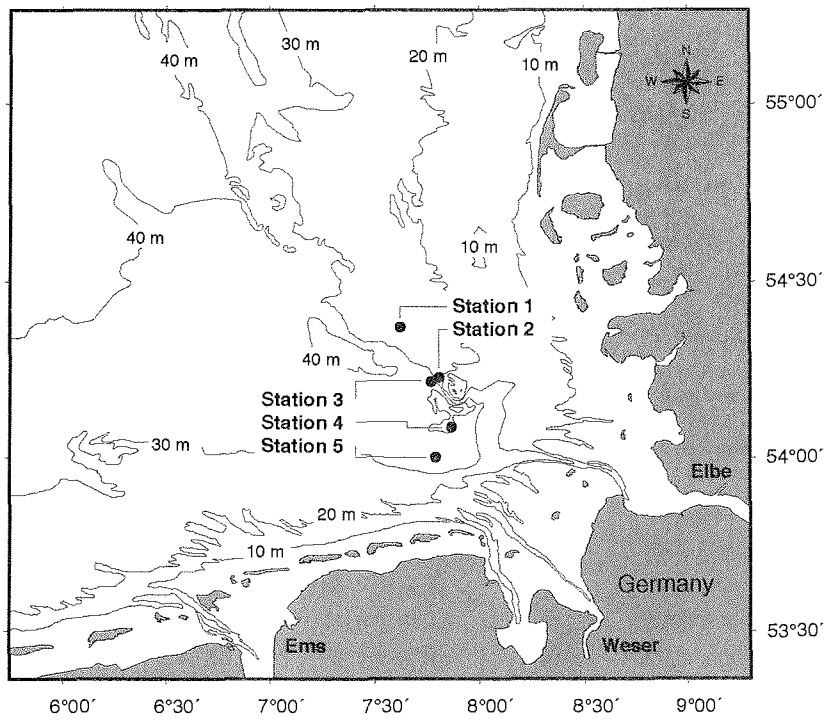

Figure 8: Map of the German Bight showing the 5 sampling stations

Sediment cores were retrieved with a minicorer or by taking subsamples from a freshly recovered box corer or a van Veen grab. For all three methods Perspex tubes with an inner diameter of 56 mm were used (i.e. a sample represented 24.6 cm^2 of seafloor). The sampling gear employed depended on sediment

type. The minicorer worked efficiently at stations 3-5, where muddy sand occurred, but was unsuitable on sandy bottom. Therefore, the box corer and the van Veen grab had to be used at stations 1 and 2.
Temperature of the overlying water was measured immediately after sampling. Subsequently, the sediment core was carefully pushed upwards in the tube using a piston. Thereby the overlying water was discarded. Once it reached the upper end of the tube, the top 5-7 cm (approx. 125-175 cm^3) of the sediment core were spooned into a transparent 500 ml Kautex bottle. The bottle was topped up with 55 μm filtered seawater and, for the rest of the cruise and during the experiments, kept at a temperature (Table 3) close to that measured at collection.

Table 2: Water depth and sediment composition at the 5 sampling stations

Station	Position	Water depth	Sediment composition		
		m	2000-63 μm	63-2 μm	< 2 μm
1	54°22.43´N 007°36.87´E	24	99.35%	0.36%	0.29%
2	54°14.49´N 007°48.86´E	22	97.50%	1.27%	1.23%
3	54°13.94´N 007°46.84´E	30	71.33%	17.51%	11.16%
4	54°05.52´N 007°51.96´E	42	74.23%	15.50%	10.27%
5	54°01.04´N 007°48.61´E	35	76.33%	12.50%	11.17%

Table 3: Sampling date, incubation temperature, stations sampled, number of screenings accomplished per sample and total number of screenings accomplished on all samples collected per sampling

Sampling date	Temperature °C	Stations sampled	Screenings per sample	Total no. of screenings
11-13 March 2002	5	1; 2; 3; 4; 5	6	30
22 April 2002	8	1; 2; 3; 4; 5	52	260
17 June 2002	16	1; 2; 3; 4; 5	9	45
21 August 2002	18	1; 2; 3; 4; 5	8	40
15 October 2002	14	1; 2; 3; 4; 5	13	65
12-13 December 2002	8	1; 2; 3; 4; 5	8	40
6 February 2003	5	2; 3; 4; 5	9	36

In the laboratory, samples collected on 22 April 2002 were incubated for 52 wk (long-term), while the remaining 29 samples were incubated for 6 to 13 wk (short-term). Light regime was LD 12:12 in all experiments. The overlying water in the Kautex bottles was carefully poured off weekly over a 55 μm sieve and the bottles were refilled with 55 μm filtered seawater. The material retained by the sieve was washed back into a plastic Petri dish and a few drops of Bengal

rose solution were added. On the following day, the Petri dish was screened for copepod nauplii using a dissecting microscope (Leica Wild M 10). Specimens of naupliar stage 2 (N2) and older were identified to species level whenever possible, but nauplii of stage 1 (N1) were pooled, as they could not be reliably assigned to species. The 34 samples were screened 516 times in total (Table 3).

Statistical analysis

Friedman's two-way analysis of variance by ranks was applied to check hatching results for statistically significant differences among stations or sampling dates in general.
Subtotals (numbers of specimens found in the first 6 screenings) were calculated for *Temora longicornis*, *Centropages hamatus*, N1 and all nauplii, for each of the 34 samples. These values were used to compute differences between sampling dates. Results from samples taken at station 1 had to be excluded, as no sample was collected at station 1 in February 2003.
Totals (numbers of specimens found in the all screenings) were calculated for *Temora longicornis*, *Centropages hamatus*, N1 and all nauplii, for each of the 34 samples. These values were used to compute differences between stations. Results from samples taken in February had to be excluded, as no sample was collected in February 2003 at station 1.

Subsequently, **Wilcoxon's matched pairs test** was applied to identify significant differences between pairs of stations or sampling dates. The data sets used in this analysis were the same as described above.

Similarity between the 34 samples in terms of species composition and abundance was computed by means of **Cluster Analysis** and **Multidimensional Scaling**. Every sample was represented by three values, the number of N1, *T. longicornis* and *C. hamatus* that were found in screenings 1-6. As absolute values ranged from zero to 710, data used to create the similarity matrix was left untransformed.

Sediment composition

For the analysis of particle size distribution, an additional, unpreserved sediment sample was collected at each of the 5 stations on the 22 April 2002. In the laboratory, approximately 5 cm^3 of each of those samples were suspended in water. Then H_2O_2 was added to dissolve any organic material present. Subsequently samples were sieved (mesh size: 63 μm) to obtain the sand fraction. Silt and clay were separated using the Atterberg technique (Atterberg, 1912; Müller, 1967), which is based on different sinking velocities of particles from different size classes.

GERMAN BIGHT: FACTORS CONTROLLING THE TERMINATION OF THE DORMANT PHASE

Temperature

On 15 October 2002 additional samples were taken to investigate the influence of temperature on hatching of copepod resting eggs. At stations 3, 4, and 5 (Figure 8) four cores each were collected in a single minicorer haul. Thus the 4 cores retrieved at one station contained sediment from an area of seabed as small as 50 cm x 50 cm and were expected to be similar with respect to grain size distribution and abundance of copepod resting eggs. Sample handling on board was equivalent to the procedure described above. In the laboratory all 12 samples were initially incubated at 14°C and LD 12:12. When the fourth screening had been completed, one sample from each of the three stations was transferred to 5°C/LD 12:12, another sample to 8°C/LD 12:12. Sample three was transferred to 18°C/LD 12:12, while the fourth sample remained at 14°C/LD 12:12. All were incubated for 9 more weeks. Samples were screened weekly for calanoid copepod nauplii. All nauplii found were identified to species level whenever possible.

Photoperiod

On 25 June 2003 a box corer haul was taken at stations 3, 4 and 5 to elucidate the impact of photoperiod on the termination of dormancy. Perspex tubes with an inner diameter of 56 mm were used to collect 4 subsamples as soon as the grab was recovered. Again, sample handling on board was equivalent to the procedure described above.
Sediments were incubated in the laboratory at LD 16:8 and 15°C for 4 weeks. Subsequently one sample per station was transferred to LD 24:0/15°C, LD 8:16/15°C and LD 0:24/15°C whereas the fourth sample was continually incubated at LD 16:8/15°C. The experiments lasted another 4 weeks. Samples were screened once per week and nauplii assigned to species whenever possible.

Oxygen concentration

In order to examine the role of the concentration of dissolved oxygen in the water on the termination of dormancy in copepod resting eggs, a second box corer haul was taken at stations 3, 4 and 5 on 25 June 2003. Subsampling and sample handling on board was identical to the procedure described above.
Samples were incubated at LD 16:8 and 15°C. The seawater used to refill the Kautex bottles with in the first 3 screenings contained approximately 7 mg $O_2 l^{-1}$. In the following 5 screenings one sample per station was topped up with water of 1 mg $O_2 l^{-1}$, 4 mg $O_2 l^{-1}$ and 14 mg $O_2 l^{-1}$, whereas the fourth sample was continually refilled with water of 7 mg $O_2 l^{-1}$. Samples were screened once per week and nauplii assigned to species whenever possible.

GERMAN BIGHT: FIELD EXPERIMENTS

In order to investigate in-situ hatching of resting eggs, traps were developed to capture nauplii emerging from the seabed.

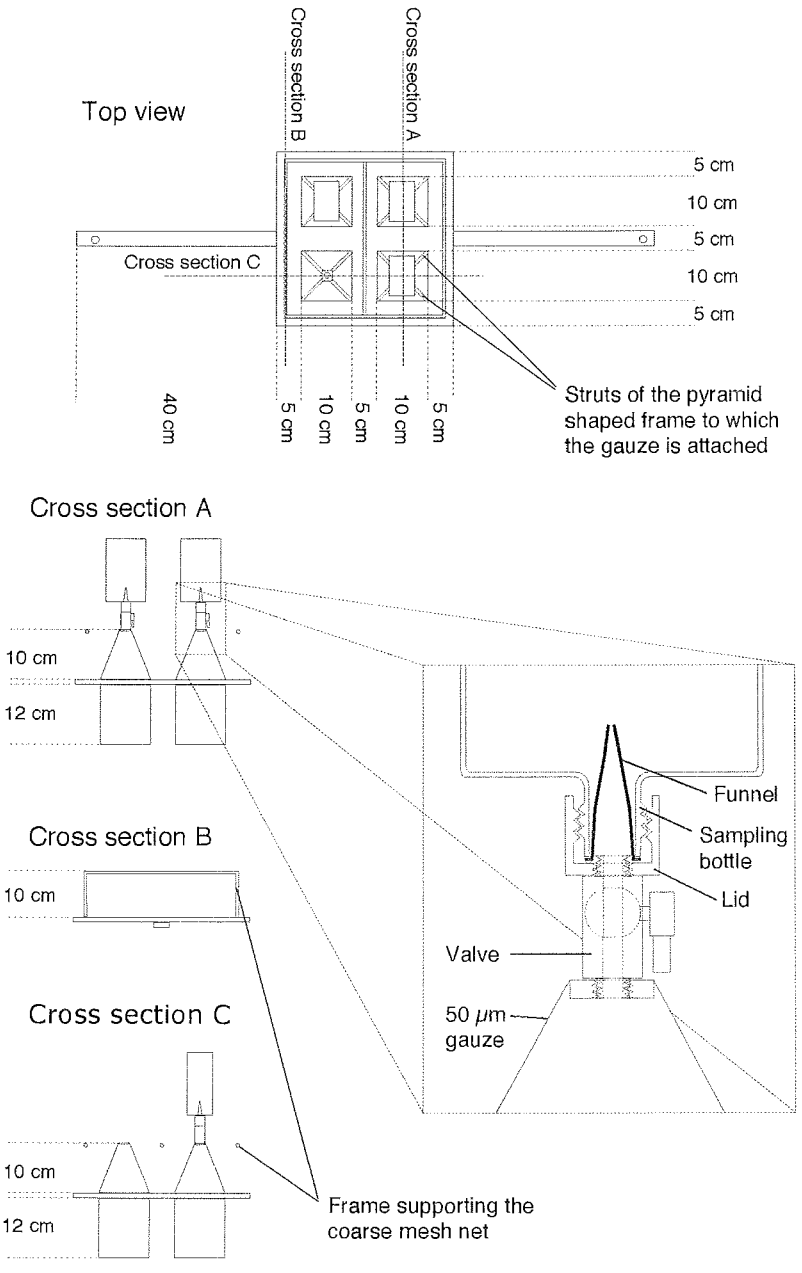

Figure 9: Drawing of the quadruple trap used in the field experiments

An approximately 12 cm long, stainless steel pipe was sealed at one end with fine mesh gauze (mesh size: 50 μm) glued to a pyramid-shaped frame. A valve was located in the apex of the pyramid. Attached to the other end of this valve was a lid, which was designed to hold a transparent 500 ml plastic bottle upside down. Four traps were embedded into a stainless steel plate (35 cm x 35 cm) (Figure 9) and covered with a coarse mesh net (mesh size: 1 cm) (Figure 10) to protect the sensitive gauze from damage.

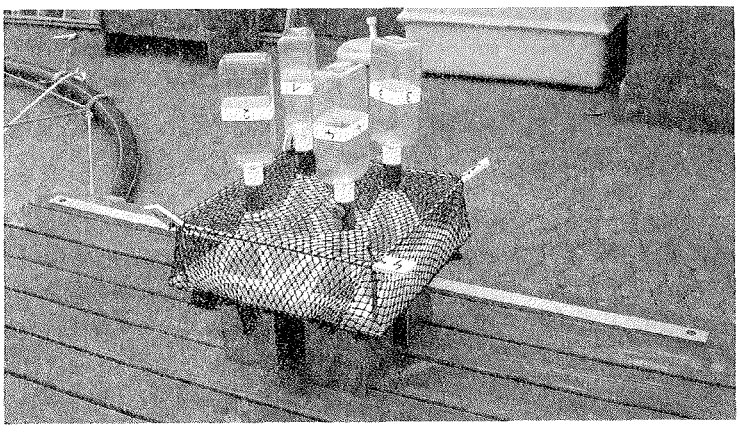

Figure 10: Picture of a quadruple trap

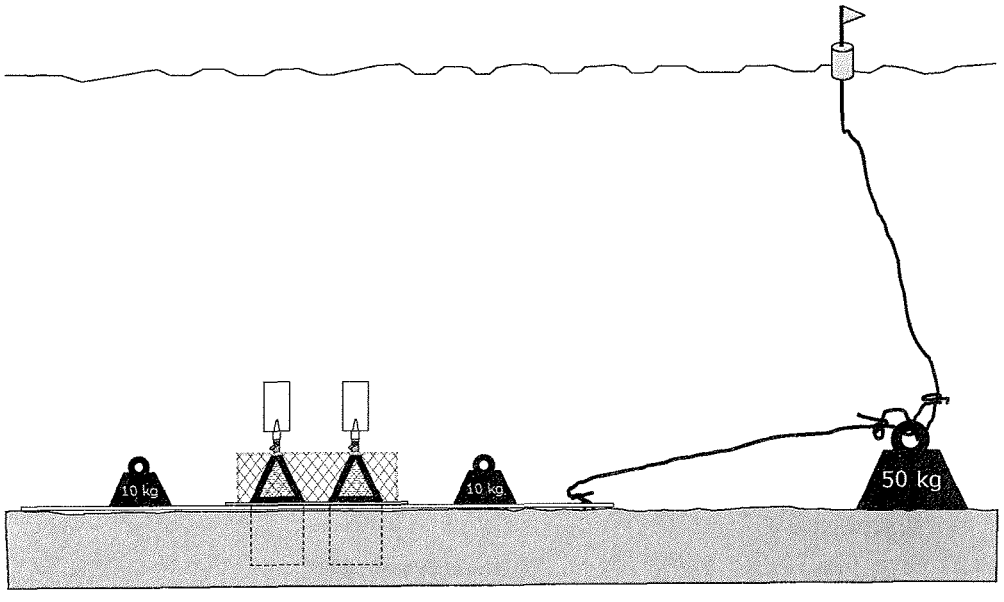

Figure 11: Sketch showing the quadruple trap in the field (not to scale)

These quadruple traps were deployed and sampled (Table 4) by a SCUBA diver. To avoid catching any adult or juvenile copepods on the way to the bottom, the trap was transported upside down through the water column. The four quadratic tubes, which protrude from the lower side of the plate, were completely sank into the sediment (Figure 11), thus enclosing 4 small patches of seafloor, each 100 cm^2 in size. This was done with the valves in the apex open, so that copepods accidentally caught would be ejected from the traps together with the surplus water.
To keep it in position, weights were placed on the steel rod that projected from the device at two sides. Additionally, the trap was connected to a heavy bottom weight holding a surface marker buoy in order to facilitate relocation.

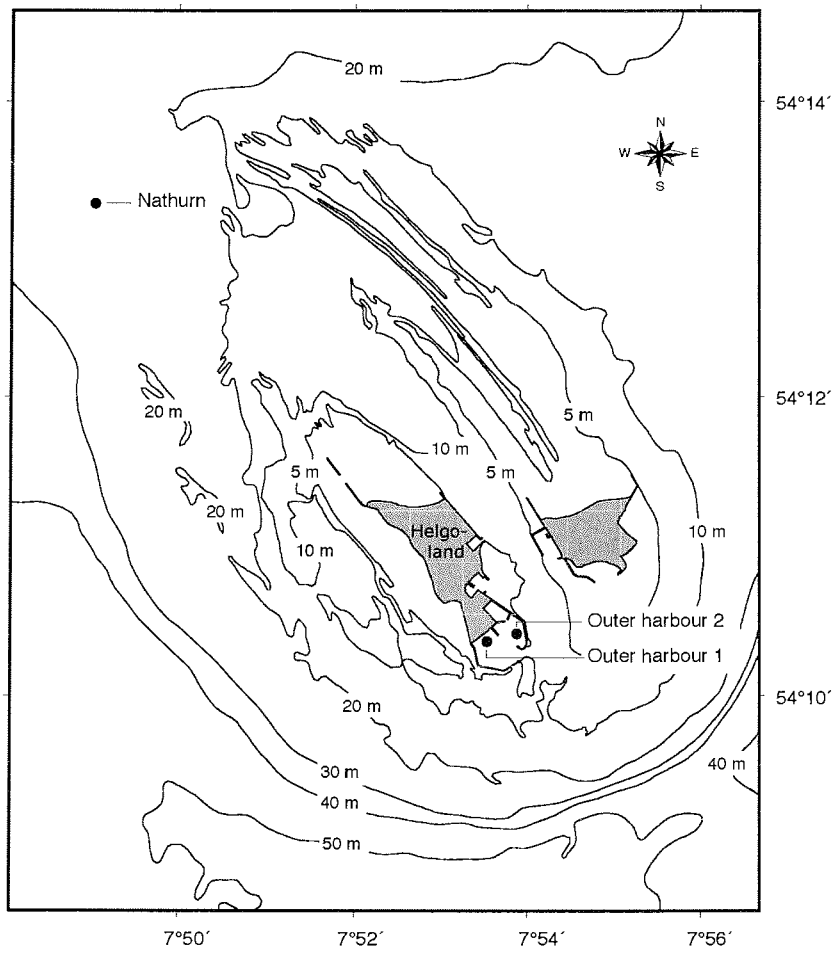

Figure 12: Map of Helgoland and adjacent waters showing the stations were in-situ experiments were performed

The sampling bottles, filled with 50 µm filtered seawater and properly closed with a plastic lid, were separately transported to the seafloor and mounted only after the trap was readily installed. The lids were taken off and the bottles immediately screwed into the lids attached to the valves of the traps.
In laboratory experiments nauplii hatching from sediment samples displayed either positive phototaxis or negative geotaxis (Engel, unpublished). Nauplii hatching from sediments in the field were therefore expected to behave similarly and to swim upwards through the valve in the apex of the pyramid and into the plastic bottle. A funnel in the neck of the bottle prevented those caught from escaping again. The valves were used to close the traps during the replacement of the sampling bottles.
Stations 1-5, where sediment cores were taken for the laboratory experiments, were either too far off Helgoland, where the nearest diving base is, to allow regular sampling or simply to deep for conventional SCUBA diving. Thus in-situ experiments had to be performed at alternative sites.

Table 4: Position, water depth and sediment type of the three stations where the emergence traps were deployed are given together with information on the sampling regime

Station	Outer harbour 1	Nathurn	Outer harbour 2
Coordinates	54°10,353´N 007°53,590´E	54°13,29´N 007°48,86´E	54°10,4´N 007°53,9´E
Water depth	6 m	27 m	6 m
Sediment type	Sand/some gravel	Muddy sand	Mud
Deployed	01 April 2003	08 April 2003	06 August 2003
1. Sampling	03 April 2003	24 April 2003	14 August 2003
2. Sampling	07 April 2003	06 May 2003	30 September 2003
3. Sampling	24 April 2003	26 May 2003	29 October 2003
4. Sampling	06 May 2003	-	13 November 2003
5. Sampling	25 May 2003	-	-

Three locations were chosen (Figure 12) according to sediment type and accessibility (water depth, distance from the island, and exposure to wind and wave action). At the station situated to the north of Helgoland (Nathurn) the sediment appeared to be very similar to that encountered at station 3 during the laboratory experiments. However, exposure and water depth rendered sampling impossible at wind speeds higher than Beaufort 4. Furthermore the strong tidal currents that prevail in the area restricted sampling to times of slack water. In contrast, the sites in the outer harbour are rather sheltered and shallow, but sediments differed somewhat compared to the stations sampled in the course of the laboratory experiments. At site "outer harbour 1" the sediment surface consisted predominantly of sand and some gravel, with the concentration of finer components increasing a few centimeters into the sediment. Anoxic mud occurred at site "outer harbour 2".

In order to compare hatching in the field to results from the laboratory, a single sediment core was taken by a SCUBA diver at each of the three stations just prior to trap deployment, using a Perspex tube and a couple of rubber stoppers. The top 5 cm of these cores were transferred to 500 ml Kautex bottles, topped up with 55 µm filtered seawater and incubated at 5°C/LD 12:12 ("Outer harbour 1" and "Nathurn") or 15°C/LD 12:12 ("Outer harbour 2"). Samples were screened for nauplii whenever the respective traps were sampled.

KARA SEA

Sediment cores from the southern and central parts of the Kara Sea as well as the Ob River and Yenisei River estuaries were collected between 14 August 2001 and 11 September 2001, during a joint Russian-German expedition of RV "Akademik Boris Petrov". With a single exception at least 3 samples were taken at each of the 32 stations (Figure 13), using a multicorer (MUC) or by subsampling intact sediments retrieved by a large box corer (LBC) (Table 5). The Perspex tubes employed in both techniques were 65 cm in length and had an inner diameter of 60 mm (i.e. a sample represented 28.3 cm^2 of seafloor). A piston was used to carefully push the sediment core upwards in the Perspex tube, thus pouring of the overlying water. Subsequently, the soft top layer (3-7 cm <-> approx. 85-200 cm^3) of each core was spooned into a 500 ml Kautex bottle. As they were intended for specific purposes, each of the three sets of samples was treated differently.

Sample A

Meant to disclose the presence of viable resting eggs of calanoid copepods in Kara Sea sediments, this sample was topped up with 0.2 µm filtered seawater (approx. 34 psu, 0°C) and placed in an incubator at 0°C and LD 20:4. The supernatant was decanted every 3-7 days by pouring it through a 55 µm sieve. The bottle was then refilled again with 0.2 µm filtered seawater (approx. 34 psu, 0°C) and returned to the incubator. The material retained by the sieve was washed back into a plastic Petri dish and a few drops of Bengal rose solution were added.
On the following day, the Petri dish was screened for copepod nauplii using a dissecting microscope (Leica Wild M 10). If present, they were transferred into a 0.5 ml Eppendorf cap and preserved in 4% borax buffered formalin for later identification and counting. Screening experiments were performed until December 2001 (19 samples) or February 2002 (13 samples, from stations: 01, 11, 14, 19, 26, 34, 40, 43, 46, 58, 67, 70, 82).

Sample B

This set of samples was to be used for direct egg counts and therefore preserved in 4% borax buffered formalin. In the laboratory, the organic material was extracted from 13 samples (see above). The saltwater-formalin solution

was carefully poured off over a 50 μm gauze screen and disposed according to regulations. The sample and the material retained by the gauze screen were transferred to a 50 μm sieve and thoroughly rinsed with freshwater to wash away salt, clay and most of the silt as well as any residual formalin.

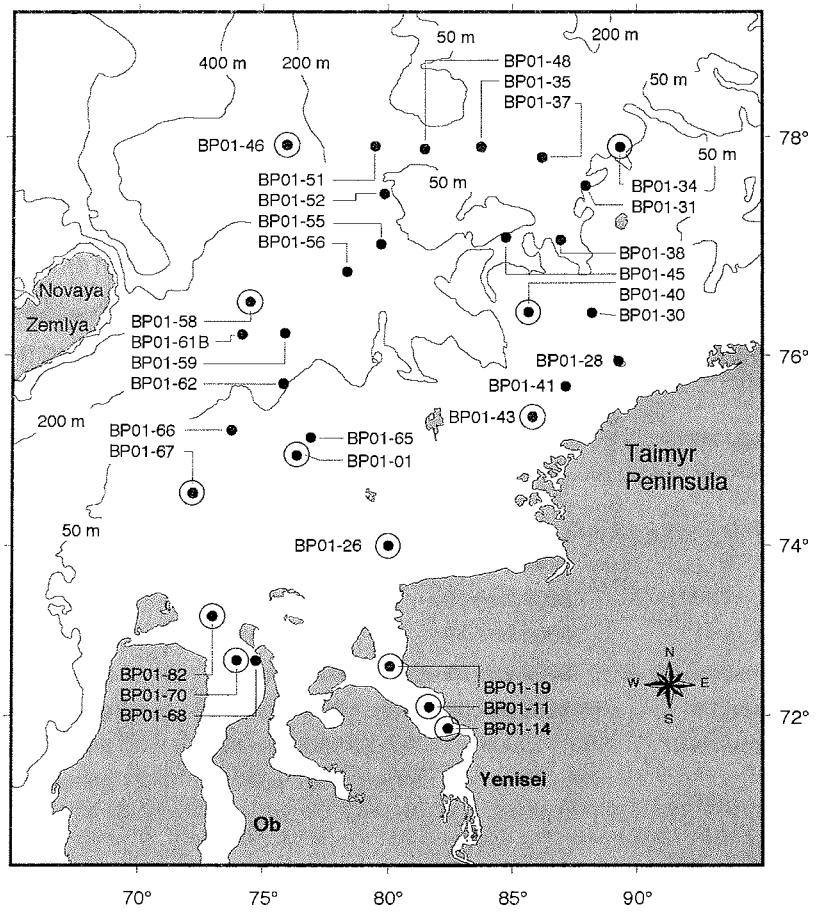

Figure 13: Map of the Kara Sea showing the 32 sampling stations. Circles indicate that all 3 samples taken at this station have been readily processed in the lab

The fraction that remained in the sieve was distributed in equal shares (20 ml at the most) to four 50 ml screw cap centrifuge tubes, which had been filled with 25 ml of Ludox®, a high-density silica sol (1.3 g ml^{-1}). The tubes were tightly closed and mixed for approximately 1 minute at full speed on a vortex mixer. Afterwards they were centrifuged at 900 g for 5 minutes. The supernatant was decanted over a 50 μm gauze screen and rinsed with freshwater to remove any remaining Ludox®. The meiobenthos was washed back into a Petri dish and examined under a dissecting microscope.

Table 5: Stations where sediment samples were collected in the Kara Sea, date and time, position, water depth, number of cores taken at each station and device used

Station	Date	Time (GMT)	Latitude N	Longitude E	Depth m	Number of cores	Device used
BP01-01	14.08.01	12:00	74°59.12′	76°23.41′	38	4	MUC
BP01-11	18.08.01	12:00	72°05.6′	81°41.8′	12	3	MUC
BP01-14	19.08.01	7:20	71°49.3′	82°27.2′	21	3	LBC
BP01-19	21.08.01	11:00	72°35.7′	80°06.4′	28	3	LBC
BP01-26	23.08.01	4:30	74°00.0′	80°01.4′	33	3	MUC
BP01-28	24.08.01	4:15	75°56.34′	89°15.9′	51	4	MUC
BP01-30	24.08.01	13:30	76°24.75′	88°10.76′	47	3	MUC
BP01-31	25.08.01	4:30	77°34.2′	87°54.5′	88	3	MUC
BP01-34	25.08.01	15:20	77°54.29′	89°20.15′	91	3	MUC
BP01-35	26.08.01	4:30	77°54.31′	83°45.94′	160	3	MUC
BP01-37	26.08.01	13:52	77°48.9′	86°11.9′	144	3	MUC
BP01-38	27.08.01	4:30	77°5.29′	86°55.48′	110	3	MUC
BP01-40	27.08.01	16:30	76°25.2′	85°39.9′	52	3	MUC
BP01-41	28.08.01	4:00	75°41.4′	87°07.8′	42	3	MUC
BP01-43	28.08.01	11:30	75°22.99′	85°49.90′	48	3	MUC
BP01-45	29.08.01	8:00	77°6.83′	84°44.0′	87	3	MUC
BP01-46	30.08.01	4:53	77°55.43′	75°57.35′	323	3	MUC
BP01-48	31.08.01	4:30	77°53.49′	81°29.94′	202	3	MUC
BP01-51	31.08.01	14:30	77°54.68′	79°29.48′	158	3	MUC
BP01-52	01.09.01	4:19	77°29.94′	79°52.0′	75	3	MUC
BP01-55	01.09.01	11:48	77°2.97′	79°43.99′	83	3	MUC
BP01-56	02.09.01	4:30	76°59.58′	75°11.48′	176	3	MUC
BP01-58	02.09.01	12:20	76°48.12′	78°21.24′	94	3	MUC
BP01-59	03.09.01	4:30	76°31.16′	74°30.95′	176	3	MUC
BP01-61b	03.09.01	13:15	76°12.9′	75°53.15′	111	3	MUC
BP01-62	04.09.01	4:30	76°12.05′	74°12.15′	135	2	MUC
BP01-65	05.09.01	4:18	75°42.98′	75°50.79′	63	3	MUC
BP01-66	05.09.01	11:28	75°10.04′	76°55.13′	55	3	MUC
BP01-67	06.09.01	4:30	75°14.65′	73°45.78′	49	3	MUC
BP01-68	06.09.01	12:25	74°35.05′	72°14.97′	31	3	MUC
BP01-70	07.09.01	7:15	72°40.16′	74°0.22′	22	3	MUC
BP01-82	11.09.01	4:17	73°11.83′	73°01.65′	29	3	MUC

Sample C

In order to be able to identify any copepod eggs present in the organic fraction of sample B, the third set of samples was intended to yield species-specific information on egg morphology, a prerequisite for direct egg counts. In order to accomplish this, the bottles were topped up with 0.2 μm filtered seawater (approx. 34 psu, 0°C) and stored in an incubator at 0°C and DD until return to

Bremerhaven. Here they were stored in an incubator at 0°C and LD 12:12. In January and February 2002 the organic compound was extracted from 13 samples (see above). The technique applied was identical to that described above with the exception that all rinsing was done with 0.2 µm filtered, pre-chilled seawater (approx. 34 psu). Egg-like objects were pooled according to external morphology and incubated in 0.2 µm filtered seawater (approx. 34 psu) at 0°C and LD 12:12 for up to 6 weeks.

RESULTS

GERMAN BIGHT: SEASONAL CYCLE OF HATCHING AND INTER-SPECIFIC VARIABILITY

Species and stage composition

A total of 13559 calanoid copepod nauplii were found in the 516 screenings performed on the 34 samples collected between March 2002 and February 2003 at stations 1-5. They were assigned to 5 different groups (Table 6): *Temora longicornis* (N2 and older), *Centropages hamatus* (N2 and older), *Acartia* spp. (N2 and older), nauplii of an unidentified species, and pooled N1. *T. longicornis* and *C. hamatus* accounted for the vast majority of all specimens that were N2 and older and it is assumed that those classified as N1 belong predominantly to these two species. Numbers of *Acartia* spp. and the unidentified species were low. By far the most frequent stage was N2 followed by N1, while older nauplii were extremely rare. Three *Acartia* spp. copepodids occurred, too, but no mature adults were found.

Table 6: Species and stage composition of all calanoid copepod nauplii that hatched from the 34 sediment samples incubated

	Species	**Abundance** %
Species composition (total: 13559)	*T. longicornis*	44.97
	C. hamatus	17.69
	Acartia spp.	0.71
	unidentified sp.	0.84
	N1	35.79

	Stage	**Abundance** %
Stage composition (total: 13445, unidentified sp. excluded)	N1	36.09
	N2	61.88
	N3	1.83
	N4	0.19
	N5	0.01
	N6	0

Between 2 and 3 161 specimens were recorded per sample (Figure 14, Table 7), disregarding the unequal number of screenings (Table 3). When only the first 6 screenings were considered (each of the 34 samples was at least screened six times), variability remained high and results ranged from 1 to 1 155. The maximum number of nauplii that were detected in a single screening was 445.

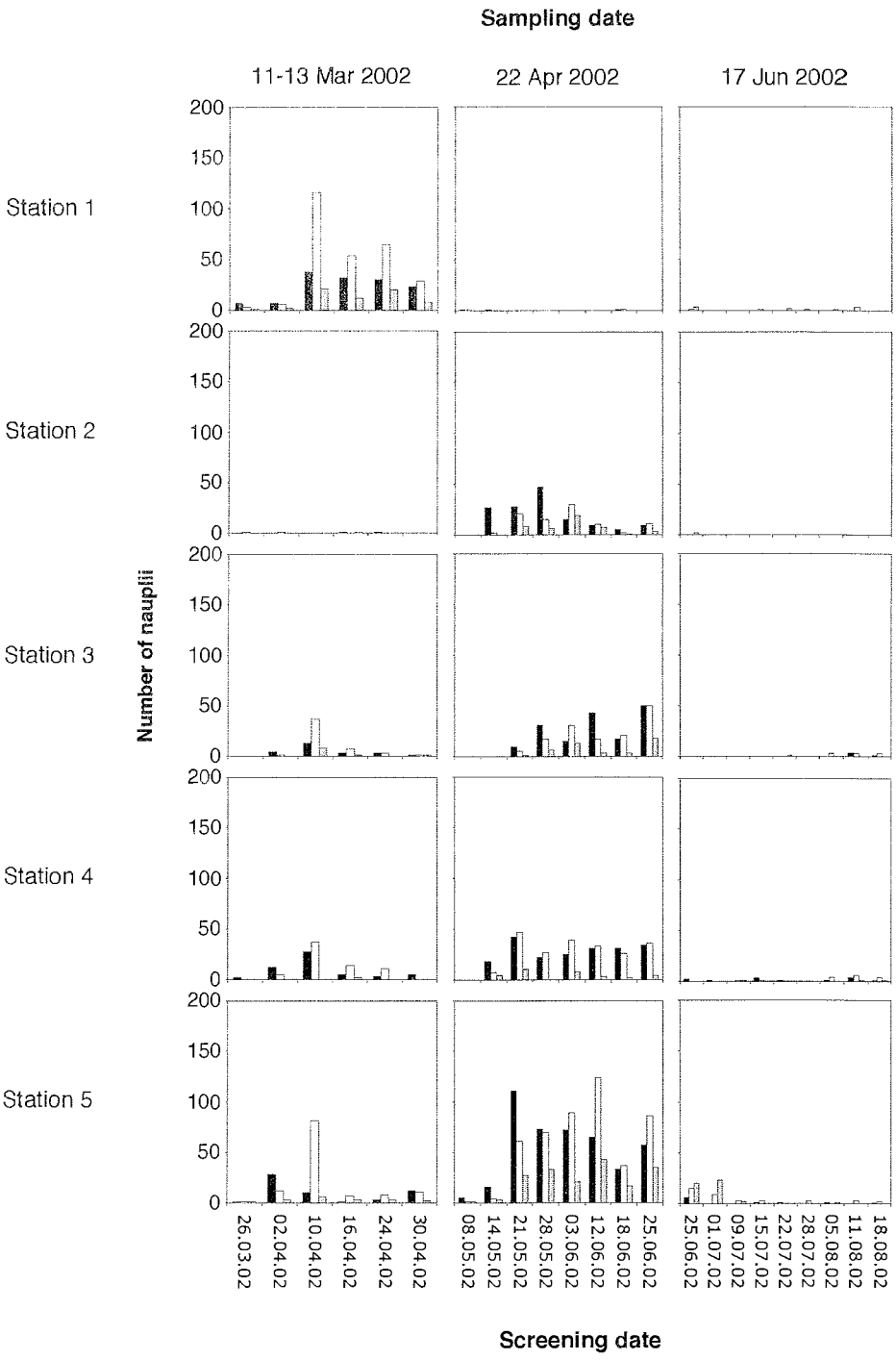

Figure 14: Number of nauplii (N1 ■, *T. longicornis* □, *C. hamatus* ▒) found per screening in all screenings accomplished (22 April 2002 ⇨ first 8 screenings only)

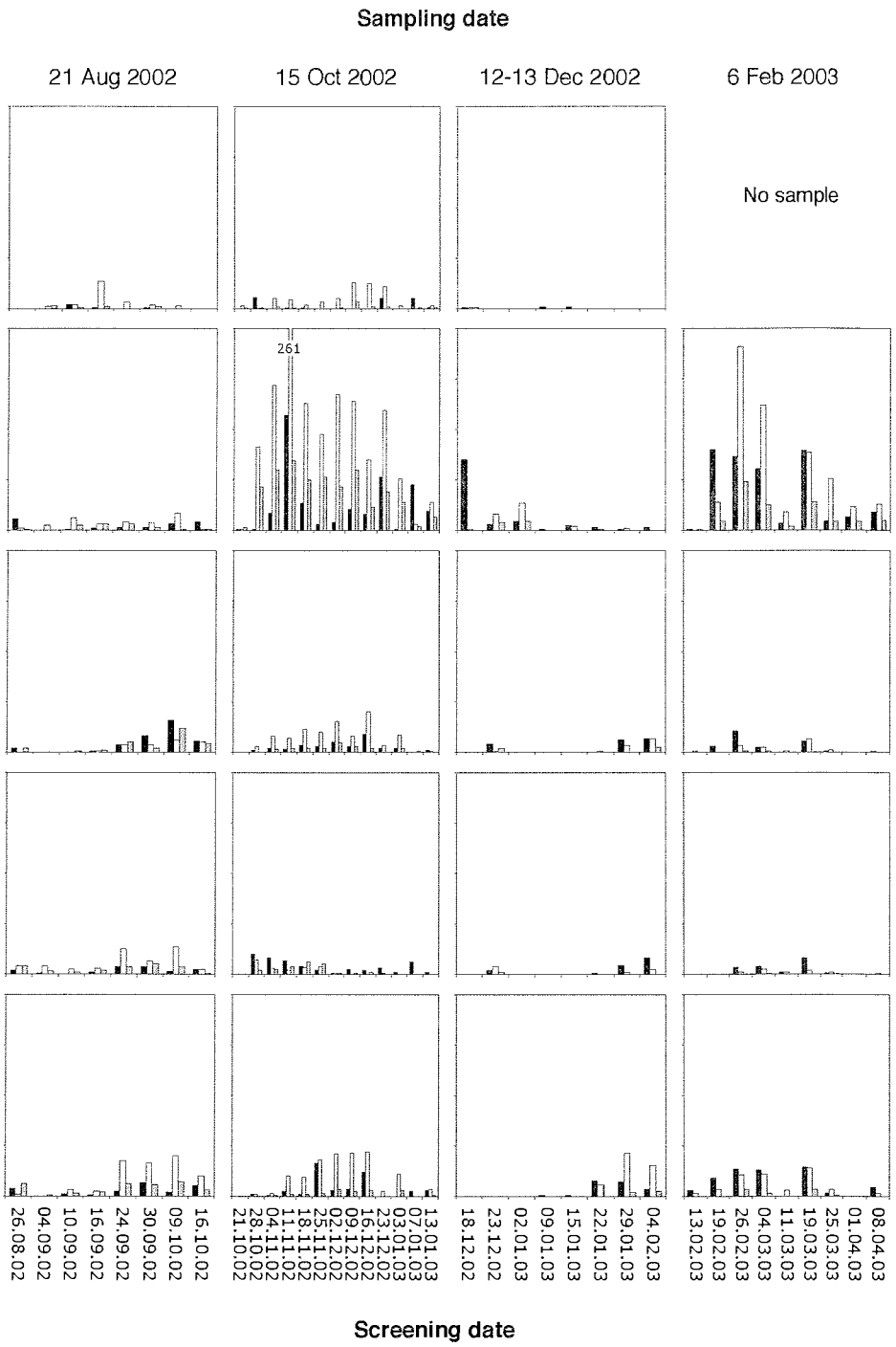
Sampling date
21 Aug 2002
15 Oct 2002
12-13 Dec 2002
6 Feb 2003
No sample
261
26.08.02
04.09.02
10.09.02
16.09.02
24.09.02
30.09.02
09.10.02
16.10.02
21.10.02
28.10.02
04.11.02
11.11.02
18.11.02
25.11.02
02.12.02
09.12.02
16.12.02
23.12.02
07.01.03
03.01.03
13.01.03
18.12.02
23.12.02
02.01.03
09.01.03
15.01.03
22.01.03
29.01.03
04.02.03
13.02.03
19.02.03
26.02.03
04.03.03
11.03.03
19.03.03
25.03.03
01.04.03
08.04.03
Screening date

Table 7: Number of *T. longicornis*, *C. hamatus*, *Acartia* spp, the unidentified species, N1 and the total number of nauplii that were found in each sample in the first 6 screenings (s.1-6) and in all screenings (all s.) the sample was subjected to (as indicated in column 4). The gear used to recover the samples is given in column 3: vVG = van Veen grab; MIC = minicorer; BC = boxcorer

Sampling date	Station	Sampling gear	Screenings	*T. longicornis*		*C. hamatus*		*Acartia* spp.		unidentified sp.		N1		Total	
				s. 1-6	all s.	s. 1-6	all s.	s. 1-6	all s.	s. 1-6	all s.	s. 1-6	all s.	s. 1-6	all s.
11-13 March 2002	1	vVG	6	273	273	64	64	0	0	0	0	137	137	474	474
	2	vVG	6	2	2	1	1	0	0	0	0	2	2	5	5
	3	MIC	6	49	49	10	10	0	0	0	0	24	24	83	83
	4	MIC	6	67	67	2	2	0	0	1	1	54	54	124	124
	5	MIC	6	120	120	18	18	0	0	0	0	55	55	193	193
22 April 2002	1	vVG	52	1	2	0	1	0	0	0	0	2	5	3	8
	2	vVG	52	78	146	40	79	1	1	2	3	126	186	247	415
	3	MIC	52	70	436	23	311	0	3	0	3	98	785	191	1538
	4	MIC	52	153	735	25	140	7	21	0	11	138	746	323	1653
	5	MIC	52	349	1126	128	705	1	3	1	30	342	1297	821	3161
17 June 2002	1	BC	9	3	6	5	6	14	14	0	0	0	0	22	26
	2	BC	9	0	0	2	2	0	0	0	0	0	0	2	2
	3	MIC	9	0	9	1	1	0	0	0	0	0	4	1	14
	4	MIC	9	2	16	1	3	0	0	0	0	7	12	10	31
	5	MIC	9	33	38	45	46	14	14	0	0	8	10	100	108
21 August 2002	1	BC	8	43	46	8	8	0	0	0	0	6	6	57	60
	2	BC	8	37	55	21	23	7	7	1	1	20	34	86	120
	3	MIC	8	19	41	17	50	9	9	1	3	28	71	74	174
	4	MIC	8	65	97	34	42	5	6	0	0	21	29	125	174
	5	MIC	8	81	141	43	63	11	11	0	9	28	42	163	266
15 October 2002	1	BC	13	35	124	5	19	0	0	0	0	13	34	53	177
	2	BC	13	710	1247	278	487	0	0	1	3	166	329	1155	2066
	3	MIC	13	79	191	15	39	0	0	0	0	22	66	116	296
	4	MIC	13	39	41	39	43	1	5	0	0	61	93	140	182
	5	MIC	13	80	243	8	33	1	1	1	1	43	91	133	369
12-13 December 2002	1	BC	8	1	1	1	1	0	0	0	0	5	5	7	7
	2	BC	8	49	51	17	17	1	1	3	3	94	98	164	170
	3	BC	8	2	23	4	9	0	0	0	0	8	34	14	66
	4	BC	8	8	15	2	2	0	0	2	2	5	30	17	49
	5	BC	8	11	85	0	9	0	0	0	1	17	38	28	133
6 February 2003	2	BC	9	429	529	115	143	0	0	24	32	301	341	869	1045
	3	MIC	9	27	29	2	2	0	0	0	0	43	45	72	76
	4	MIC	9	13	16	1	2	0	0	1	1	31	32	46	51
	5	MIC	9	87	97	17	18	0	0	10	10	106	118	220	243

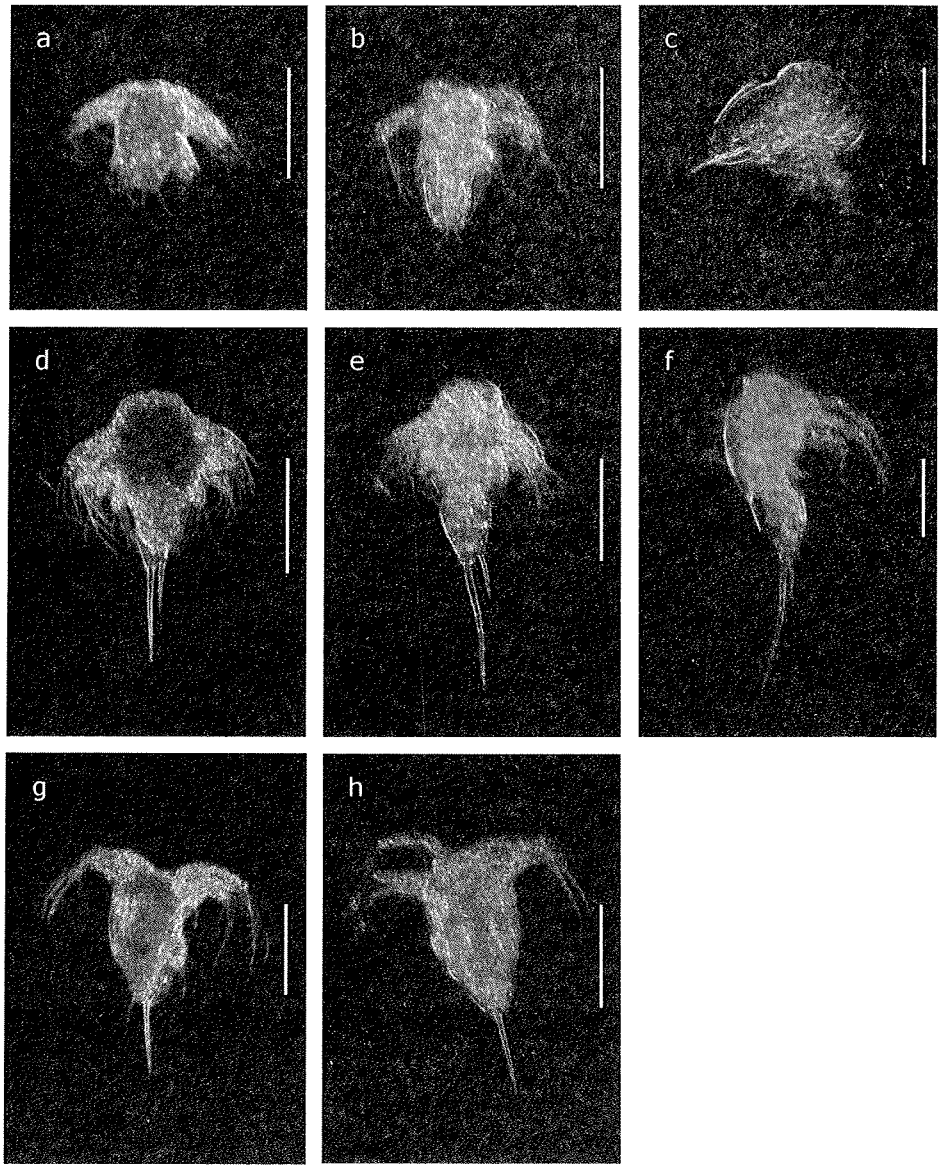

Figure 15: Photomicrographs of calanoid copepod nauplii that hatched from sediment samples collected from the German Bight. (a) N1, (b) *Acartia* sp. N2, (c) the unidentified species, (d) *T. longicornis* N2, (e) *T. longicornis* N3, (f) *T. longicornis* N4, (g) *C. hamatus* N2, (h) *C. hamatus* N3. Scale bar: 100 μm

The unidentified nauplius was laterally flattened, hunchbacked and approximately 160 μm in length (furcal appendages excluded). These appendages were of equal length and their bases, twice as long as the protruding parts, were clearly visible inside the animal's abdomen. The shape of the nauplius suggested that it belonged to the Calanoida rather than to the Cyclopoida or Harpacticoida, which are usually dorsoventrally compressed (Dussart and Defaye, 1995). In spite of intensive inquiries, the nauplius could not be unambiguously identified to species level. No attempt was made to rear the nauplius to the adult stage.
Photomicrographs of representatives from the five groups of nauplii that were distinguished are shown in Figure 15.

Spatial and seasonal variability

Numbers of nauplii varied among stations (Figure 16) and sampling dates (Figure 17). Based on the hatching results from the 30 sediment cores collected between March and December 2002[1], maximum and minimum values were detected at stations 5 and 1, respectively, for the total number of nauplii, *Temora longicornis*, *Centropages hamatus*, N1 and the unidentified species, with *Acartia* spp. being the only exception. Sums for this group peaked at station 4 and were lowest at station 2.
However, Friedman's two-way analysis of variance by ranks indicated statistically significant differences between the 5 sampling stations only for *Temora longicornis* ($\hat{\chi}_R^2$ = 9.20; critical value for χ_R^2 = 9.08 [k = 5; n = 6; p = 0.05]; Sachs, 1978).
Wilcoxon's matched pairs test showed differences between stations 1 and 5 on the 95% confidence level for the total number of nauplii ($\hat{\chi}_R^2$ = 15; critical value for χ_R^2 = 14.9 [k = 5; n = 6; p = 0.05]; Sachs, 1978) and *T. longicornis* ($\hat{\chi}_R^2$ = 15).

Cluster analysis (Figure 18) and multidimensional scaling (Figures 19), based on three values per sample (N1, *T. longicornis* and *C. hamatus* found in screenings 1-6; all 34 samples were considered) rather than just one, did not group the samples according to station. Species composition and abundance was obviously not sufficiently dissimilar between samples from the 5 different stations.

Hatching results (first 6 screenings) from the 28 sediment cores collected between March 2002 and February 2003 at stations 2 to 5[2] indicate seasonal variability (Figure 17). Values peaked in April (the total number of nauplii, *T. longicornis* and N1), October (*C. hamatus*), August (*Acartia* spp.) and February (unidentified sp.). Minima were observed in June (the total number of nauplii, *T. longicornis*, N1 and unidentified sp.), December (*C. hamatus*), March and February (*Acartia* spp.).

[1] As no sample was taken at station 1 on 6 February 2003, nauplii that emerged from samples taken on that date at stations 2-5 were omitted.
[2] As no sample was taken at station 1 on 6 February 2003, nauplii that emerged from samples taken at station 1 on other sampling dates were omitted.

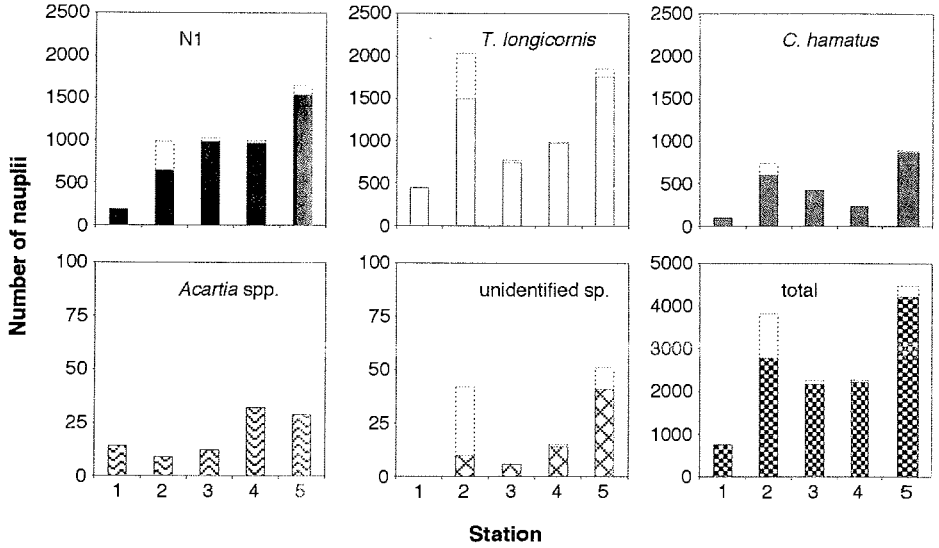

Figure 16: Spatial variability of hatching. Columns are the total number of nauplii that hatched per station in samples collected between March and December 2002 (column border: solid line) and in February 2003 (column border: broken line). Data from all screenings, a sample was subjected to are considered

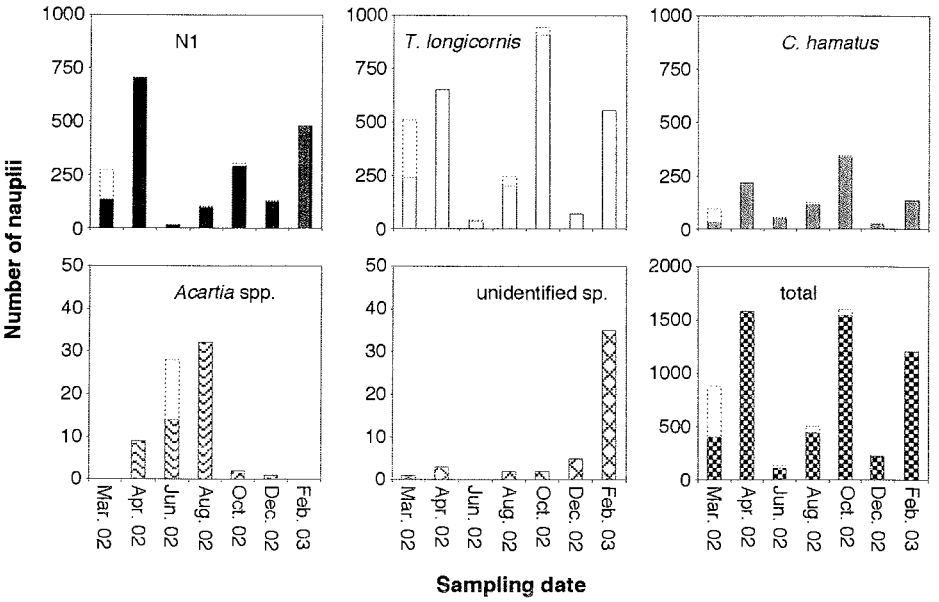

Figure 17: Seasonal variability of hatching. Columns are the total number of nauplii that hatched per sampling date from samples collected at stations 2-5 (column border: solid line) and station 1 (column border: broken line). Data from the first 6 screenings a sample was subjected to are considered

Friedman's two-way analysis of variance by ranks clearly indicated statistically significant differences between the 7 sampling dates for the total number of nauplii ($\hat{\chi}^2_R$ = 16.607; critical value for χ^2_R = 14.19 [k = 7; n = 4; p = 0.01]; Sachs, 1978), *T. longicornis* ($\hat{\chi}^2_R$ = 15.53) and N1 ($\hat{\chi}^2_R$ = 17.78).

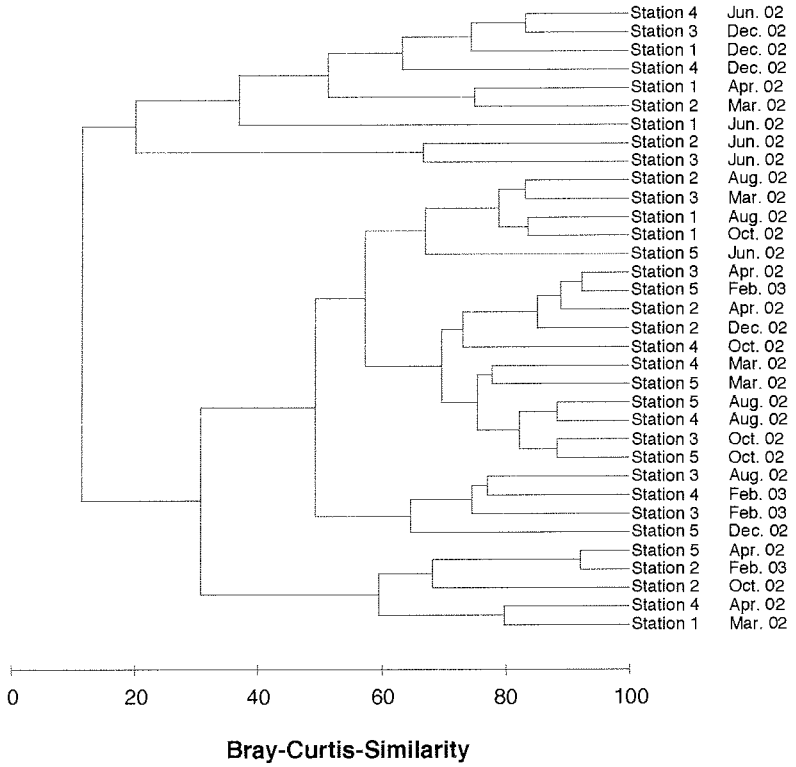

Figure 18: Dendrogram indicating similarity in terms of species composition and abundance among the 34 sediment samples. The matrix used for this analysis was based on the untransformed numbers of N1, *T. longicornis* and *C. hamatus* nauplii found in screenings 1-6

Wilcoxon's matched pairs test showed differences between sampling dates April and June 2002 for the total number of nauplii ($\hat{\chi}^2_R$ = 21; critical value for χ^2_R = 18 [k = 7; n = 4; p = 0.05]; Sachs, 1978), *T. longicornis* ($\hat{\chi}^2_R$ = 20) and N1 ($\hat{\chi}^2_R$ = 21), as well as between February and June for N1 ($\hat{\chi}^2_R$ = 18).
Differences in hatching between sampling dates are also suggested by cluster analysis (Figure 18) and multidimensional scaling (Figure 20). Although samples are not strictly grouped according to sampling date, those collected in February and April are clearly separated from those taken in June.

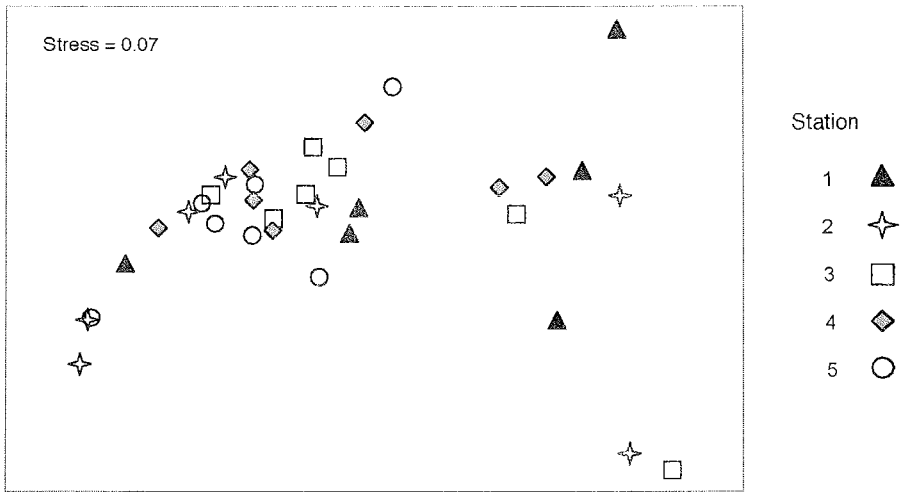

Figure 19: MDS plot based on the same similarity matrix as the dendrogram in Figure 18. The distribution of symbols, which represent the 34 sediment samples and are marked according to station, again indicates similarity in terms of species composition and abundance

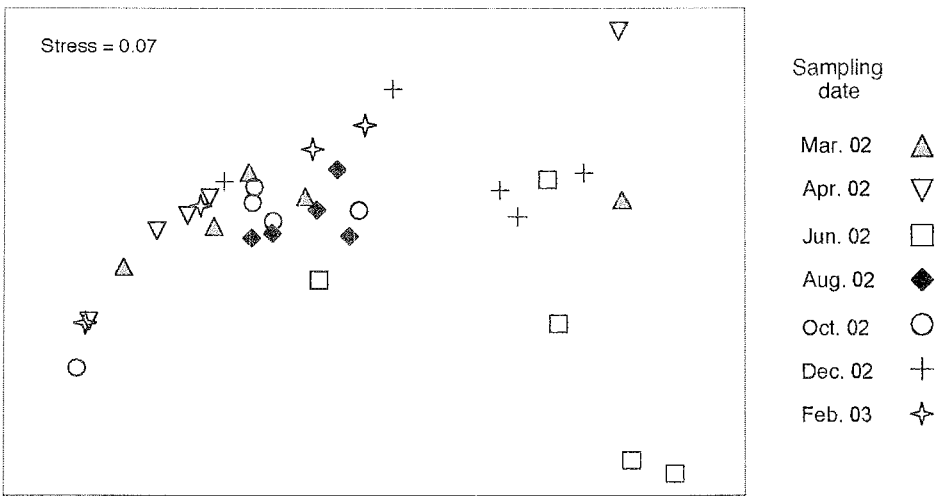

Figure 20: MDS plot based on the same similarity matrix as the dendrogram in Figure 18. The distribution of symbols, which represent the 34 sediment samples and are marked according to sampling date, again indicates similarity in terms of species composition and abundance

A more detailed picture of the seasonal variation in hatching can be obtained by looking at each station separately. Patterns were almost identical at stations 3, 4, and 5 where abundance maxima occurred in April (Figure 21). Values accounted for 34.7 to 49.5% of the sum of nauplii (all species) that were found in the first 6 screenings of all samples collected at the corresponding stations. Numbers dropped to lower levels in June before rising again in autumn, forming a second, wider peak of intermediate height. The maximum at station 2 was found in the sample taken in October (45.6%). This was the only site that did not have its abundance maximum in spring, but the second highest number of nauplii at this station hatched from the sample collected in February. Seasonal variability of *Temora longicornis* nauplii is comparable to the pattern that can be observed when all species are regarded (Figure 21). The seasonal cycle of hatching of *Centropages hamatus* was most variable between different sites. When only N1 stages are considered, abundance generally peaked early in the year.

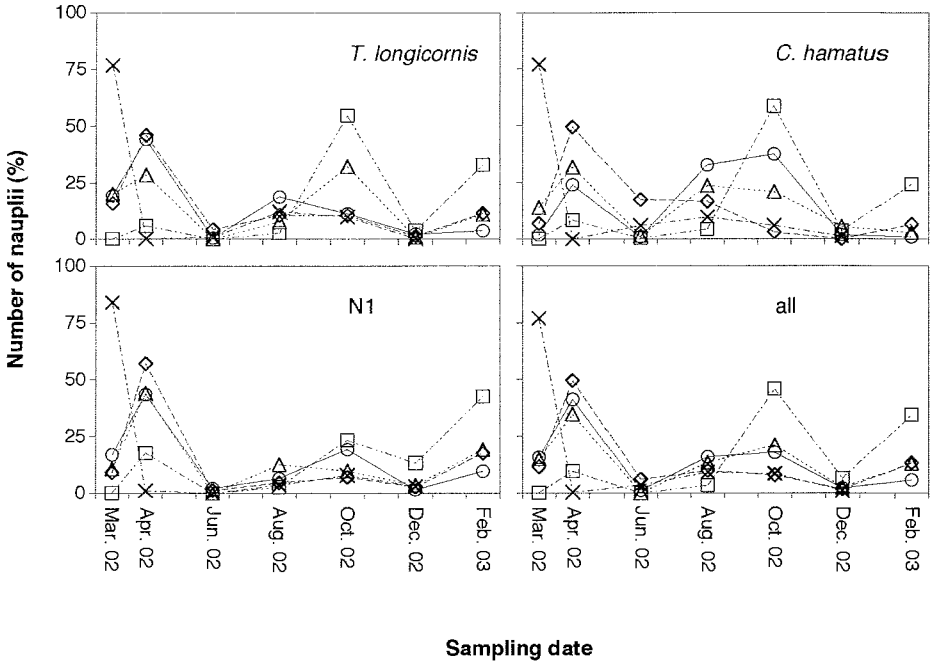

Figure 21: Seasonal variability of hatching at individual stations. Values are the number of nauplii that hatched from a sample collected at a particular station (station 1: --x--; station 2: ----□----; station 3: --△--; station 4: —o—; station 5: --◇--) and sampling date as percentage of the total number of nauplii that hatched from all samples that were collected at that station during this study. Only nauplii that were found in the first 6 screenings were considered. (a) all nauplii; (b) *T. longicornis*; (c) *C. hamatus*; (d) N1

Hatching patterns

a. Short-term incubations

In the majority of samples, numbers of nauplii were low in screening 1, but increased over the following two to three weeks. This was particularly true for the

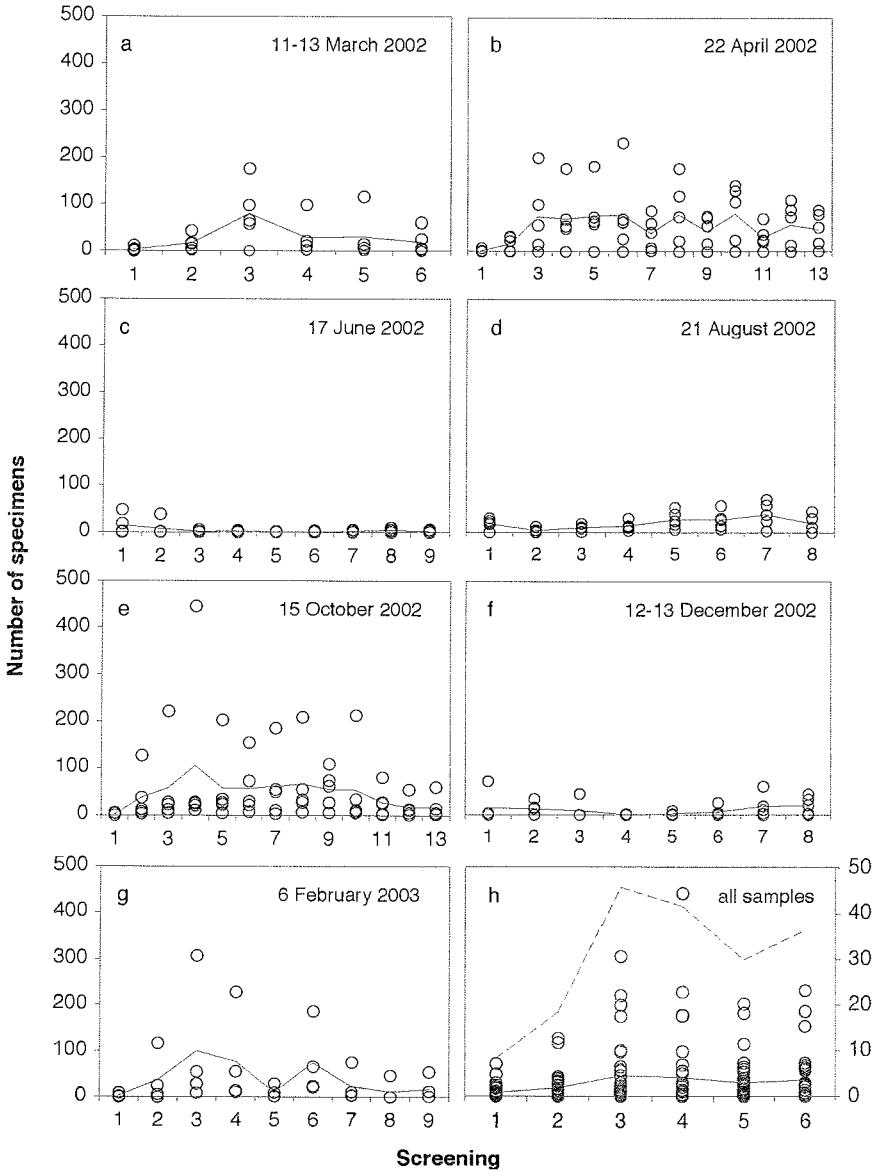

Figure 22: Onset of hatching. (a)–(g) Number of nauplii that hatched per screening from all samples (Apr. 02: screenings 1-13 only). Results are arranged according to sampling date (open circles = values of individual samples; black line = mean); (h) Number of nauplii that hatched per screening from all 34 samples (open circles = values of individual samples; solid line = mean; broken line = mean based on secondary value axis)

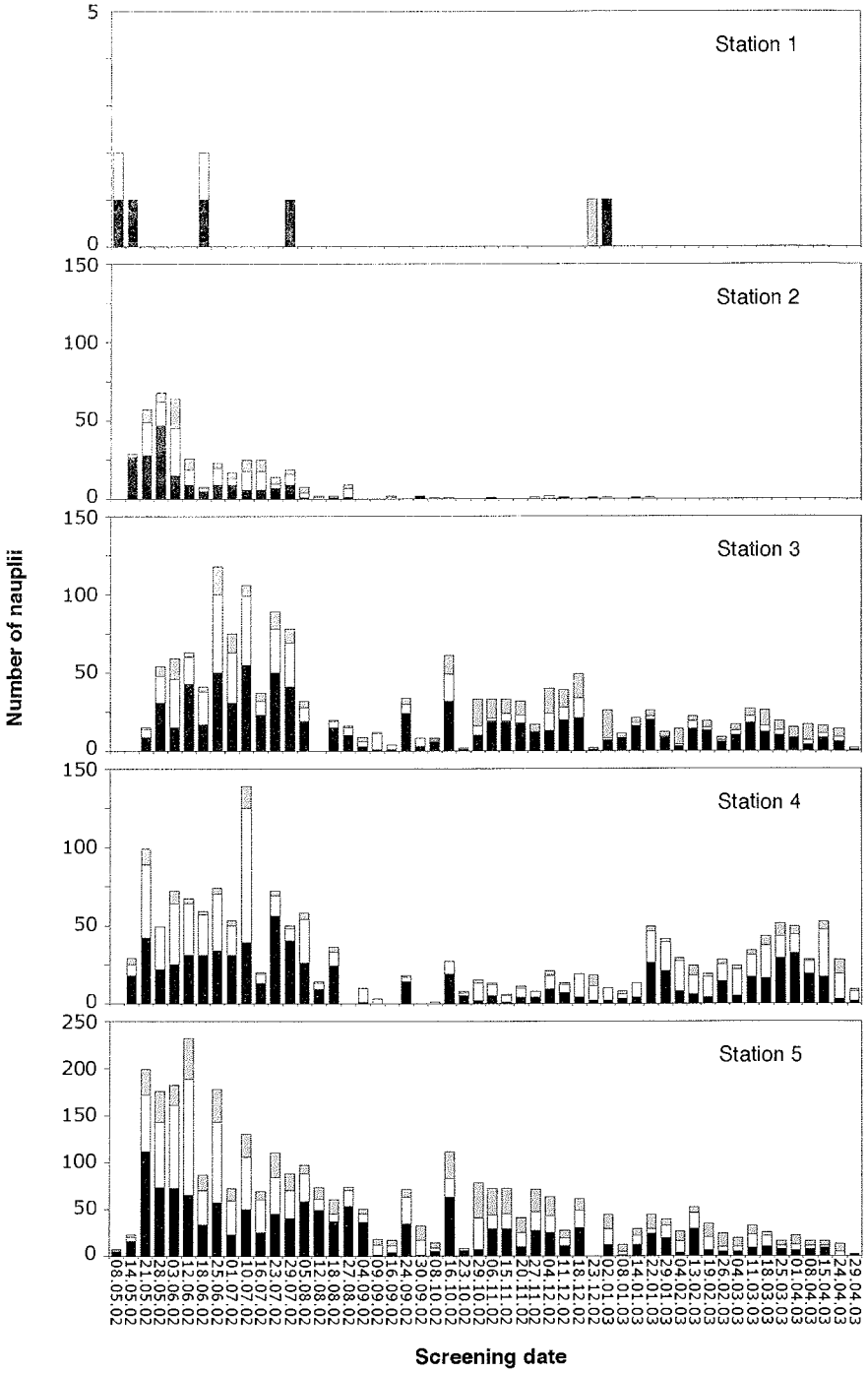

Figure 23: Number of nauplii (N1 ■, *T. longicornis* □, *C. hamatus* ▒) found per screening in the samples collected on 22 April 2002

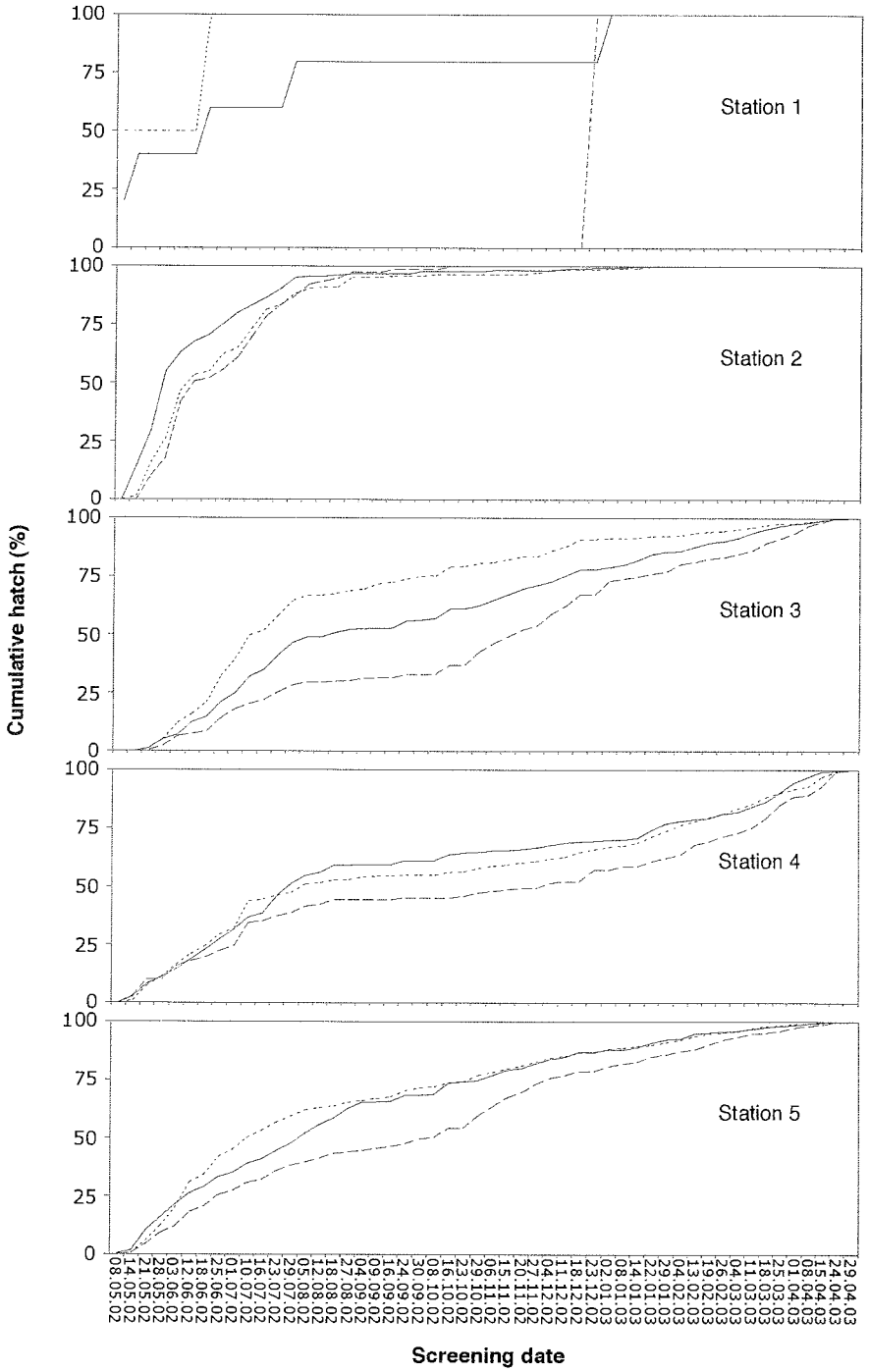

Figure 24: Cumulative number of nauplii (——— N1, ------- *T. longicornis*, — — — *C. hamatus*) in samples collected on 22 April 2002

samples taken in March, April, October and February (Figure 22). Usually hatching continued for the entire experimental period. The pattern in the samples collected in June, August and December, however, was quite different. Average numbers were comparatively high in screening 1, but declined thereafter. Towards the end of the incubation period values rose again gradually, especially in the samples collected in August and December.

b. Long-term incubation

In three out of the 5 samples that were incubated for 52 wk nauplii hatched continually until the end of the experiment (Figures 23, 24), while in the samples from stations 1 and 2 no nauplii were found later than in week 38. Interspecific differences were clearly expressed in the time required for 50% nauplii to hatch: *Temora longicornis* needed less than half the time (mean: 12 wk, Figure 25) required by *Centropages hamatus* (mean: 27 wk). N1 stages reached this level after 14 wk. Hatching rate was not constant, but changed with time in both species; it was higher in the beginning and changed after approximately 13 wk. While *T. longicornis* seemed to have 2 phases of different hatching rates, *C. hamatus* displayed a third intermediate phase between weeks 13 and 25 characterised by an extremely low hatching rate. The rate was initially higher in *T. longicornis* but the situation changed after week 25. Only 27 *Acartia* spp. nauplii and 47 unidentified specimens hatched from all four stations. The last *Acartia* spp. was found after week 51 and the last unidentified in week 47.

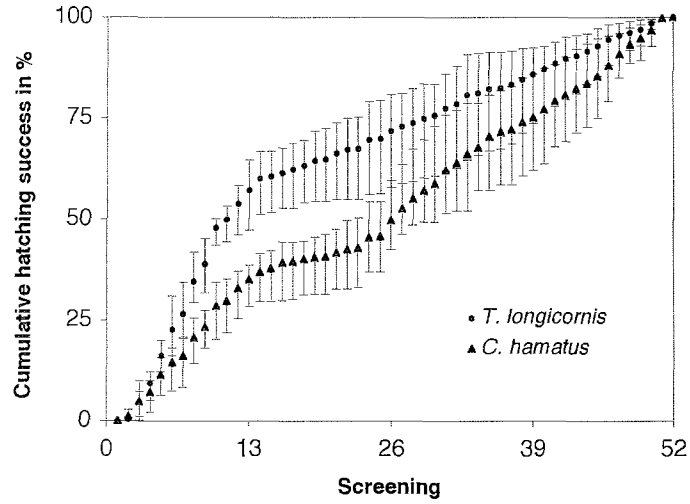

Figure 25: Cumulative number of hatched nauplii in % (mean, range) for (●) *T. longicornis* and (▲) *C. hamatus* across samples that were taken at stations 3, 4, and 5 on the 22 April 2002

Maximum abundance and recruitment potential

The maximum number of nauplii found in one sample in a single screening was 445. Of those 261 were *Temora longicornis*, 69 *Centropages hamatus* and 114 specimens of naupliar stage N1, equivalent to 105 968 ind. per m^2, 28 015 ind. per m^2 and 46 285 ind. per m^2, respectively. The 445 nauplii must have hatched within 7 days as the previous screening was done exactly a week earlier. One square meter of sediment at the site where that sample was taken (station 2; water depth: 22 m) could therefore be able to release 688 *T. longicornis* and 182 *C. hamatus* nauplii plus another 300 nauplii of stage N1 (probably for the most part also *T. longicornis* or *Centropages* spp.) into every overlying cubic meter of water per day. The maximum number of nauplii found in one sample in 52 screenings was 3 161. Of those 1 126 were *T. longicornis*, 705 *Centropages* spp. and 1 297 specimens of naupliar stage N1, equivalent to 457 166 ind. per m^2, 286 236 ind. per m^2 and 526 594 ind. per m^2, respectively.

GERMAN BIGHT: FACTORS CONTROLLING THE TERMINATION OF THE DORMANT PHASE

Temperature

In 156 screenings a total of 4 245 nauplii were found (Table 8). *Temora longicornis* accounted for 49.56% of those, *Centropages hamatus* for 11.5% and N1 for 37.15%. Specimens of *Acartia* sp. and the unidentified species were also detected, but only in meagre numbers (0.38% and 1.41%, respectively).
Although the 12 samples were initially incubated under identical conditions, hatching varied widely in the first five weeks (Figure 26), even among those collected at the same station. This suggests that the distribution of eggs in the sediment is rather patchy on a small scale, as all 4 samples taken at one station originate from an area of seafloor merely 0.5 m x 0.5 m in size.
In terms of numbers of nauplii, treatments 1-3 (14°C → 18°C; 14°C → 14°C; 14°C → 8°C) seem to have little impact on hatching, as a clear trend (increase or decrease) across stations is not discernable. Cooling to low temperatures (14°C → 5°C) appears to be effective in two types of ways:

First, the number of nauplii (all nauplii and N1) found in screenings 6-10 (25 November-23 December 2002) was higher than in the first 5 screenings, independent of sampling station. Results for *T. longicornis* and *C. hamatus* were more mixed.

Second, a clear pattern is discernable. Hatching dropped to very low levels 2 weeks after the temperature was down regulated. Subsequently, another 2 weeks later on the 16 and 23 of December, a synchronous, significant increase in numbers of nauplii was recorded.
Interestingly, the unidentified species is found almost exclusively in the samples that have been cooled to 5°C or 8°C.

Table 8: Numbers of nauplii found in each of the 36 samples used to test the effect of some physical parameters on hatching in the initial phase of the experiments (s. 1-4/5) and after the shift in temperature, photoperiod or dissolved oxygen (4-8; 6-10)

Parameter	Treatment	Station	*T. longicornis*		*C. hamatus*		*Acartia* spp.		unidentified sp.		N1		Total	
			s. 1-5	s. 6-10	s. 1-5	s. 6-10	s. 1-5	s. 6-10	s. 1-5	s. 6-10	s. 1-5	s. 6-10	s. 1-5	s. 6-10
TEMPERATURE	14°C → 18°C	3	63	63	20	26	0	1	0	0	15	13	98	103
	14°C → 18°C	4	54	11	8	4	4	0	0	0	42	8	108	25
	14°C → 18°C	5	29	78	8	20	0	0	0	0	12	49	49	153
	14°C → 14°C	3	59	114	11	23	0	0	0	0	16	44	89	209
	14°C → 14°C	4	31	10	29	14	1	3	0	0	57	20	124	48
	14°C → 14°C	5	44	170	5	21	0	1	1	0	10	70	60	262
	14°C → 8°C	3	45	65	10	12	0	0	1	6	35	44	99	140
	14°C → 8°C	4	111	70	29	20	0	1	0	2	130	62	271	156
	14°C → 8°C	5	198	146	44	35	0	0	0	2	33	124	289	313
	14°C → 5°C	3	40	153	7	17	0	0	0	21	23	194	76	386
	14°C → 5°C	4	46	33	10	9	2	1	0	5	49	88	107	136
	14°C → 5°C	5	80	123	33	12	0	0	0	17	29	134	146	287
			s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8
PHOTOPERIOD	LD 16:8 → LD 24:0	3	0	3	0	0	0	0	0	0	0	0	0	3
	LD 16:8 → LD 24:0	4	9	1	3	1	0	0	0	0	1	10	13	12
	LD 16:8 → LD 24:0	5	8	6	5	0	1	0	0	0	6	11	20	17
	LD 16:8 → LD 16:8	3	0	3	0	0	0	0	0	0	0	1	0	4
	LD 16:8 → LD 16:8	4	5	12	2	0	1	1	0	0	5	7	13	20
	LD 16:8 → LD 16:8	5	2	52	0	16	0	0	0	0	1	27	3	95
	LD 16:8 → LD 8:16	3	2	1	3	1	0	0	0	0	0	0	5	2
	LD 16:8 → LD 8:16	4	4	30	2	2	0	1	0	0	1	15	7	48
	LD 16:8 → LD 8:16	5	34	63	37	26	1	0	0	0	11	17	83	106
	LD 16:8 → LD 0:24	3	2	0	2	1	0	0	0	0	1	0	5	1
	LD 16:8 → LD 0:24	4	7	6	2	0	1	0	0	0	11	0	21	6
	LD 16:8 → LD 0:24	5	41	17	22	7	0	0	0	0	16	3	79	27
			s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8	s. 1-4	s. 5-8
OXYGEN	7 mg/l → 14 mg/l	3	3	23	0	3	0	0	0	0	6	14	9	40
	7 mg/l → 14 mg/l	4	1	9	0	4	0	0	0	0	3	3	4	16
	7 mg/l → 14 mg/l	5	43	171	8	18	0	0	0	0	22	41	73	231
	7 mg/l → 7 mg/l	3	0	0	0	0	0	0	0	0	2	1	2	1
	7 mg/l → 7 mg/l	4	3	0	2	0	0	0	0	0	6	0	11	0
	7 mg/l → 7 mg/l	5	29	80	18	15	0	0	0	1	32	31	79	126
	7 mg/l → 4 mg/l	3	3	6	1	0	1	0	0	0	3	5	8	11
	7 mg/l → 4 mg/l	4	1	7	0	3	1	0	0	0	0	9	2	19
	7 mg/l → 4 mg/l	5	116	118	10	8	2	0	0	0	55	73	183	199
	7 mg/l → 1 mg/l	3	3	2	0	0	0	0	0	0	1	1	4	3
	7 mg/l → 1 mg/l	4	34	15	10	3	0	0	0	0	55	12	99	30
	7 mg/l → 1 mg/l	5	133	39	25	7	0	0	0	0	92	43	250	89

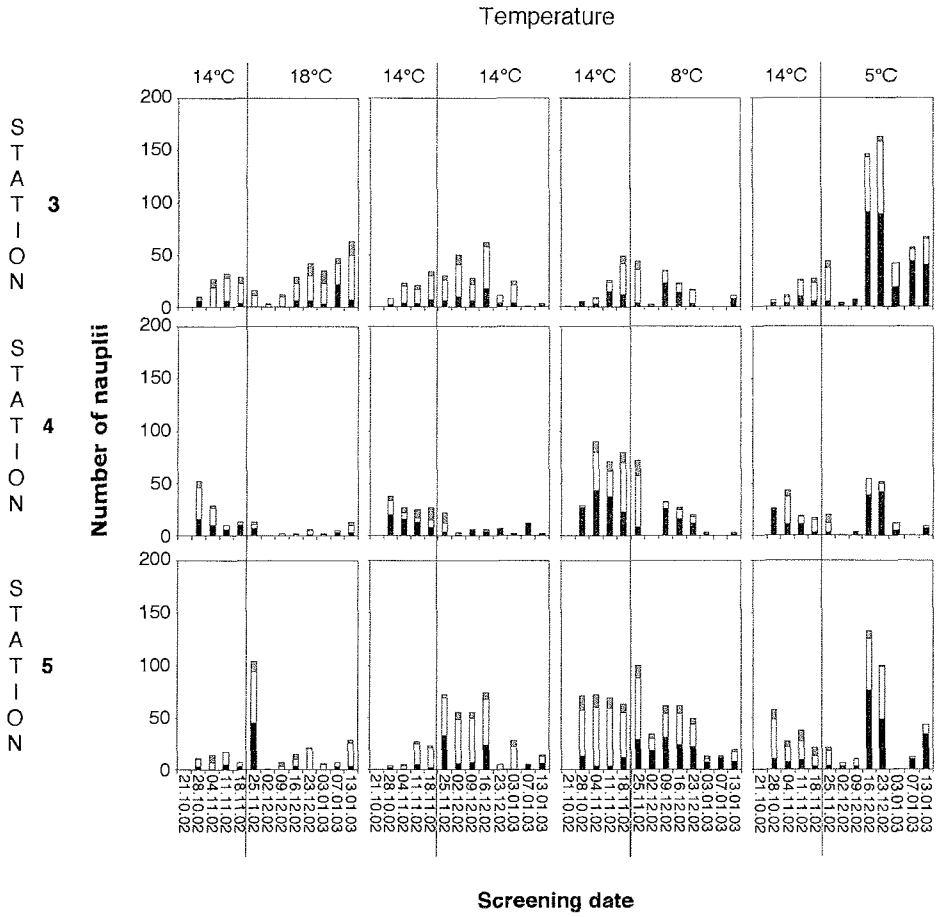

Figure 26: Screening results from the 12 samples used to test the effectiveness of a change in temperature as an environmental cue capable of terminating dormancy. Stacked columns are numbers of nauplii (N1 ■, *T. longicornis* □, *C. hamatus* ▒) found per screening

Photoperiod

Compared to the experiment that focused on the effect of temperature on dormancy termination (see above), distinctly lower numbers of nauplii emerged from the samples (Figure 27). Only 590 nauplii were found in the 96 screenings. 52.20% were *T. longicornis*, 22.37% *C. hamatus*, N1 24.41% and *Acartia* sp. 1.02%. No unidentifiable specimens were found. Nevertheless, results, in particular for station 5, again indicate small-scale patchiness (counts of nauplii from the first four screenings vary widely between samples from one station, though the experimental conditions were identical). Furthermore, significant differences (Friedman's two-way analysis of variance by ranks: $\hat{\chi}^2_R = 6.5$; critical value for $\chi^2_R = 6.0$ [k = 3; n = 4; p = 0.10]; Sachs, 1978) between stations hint to

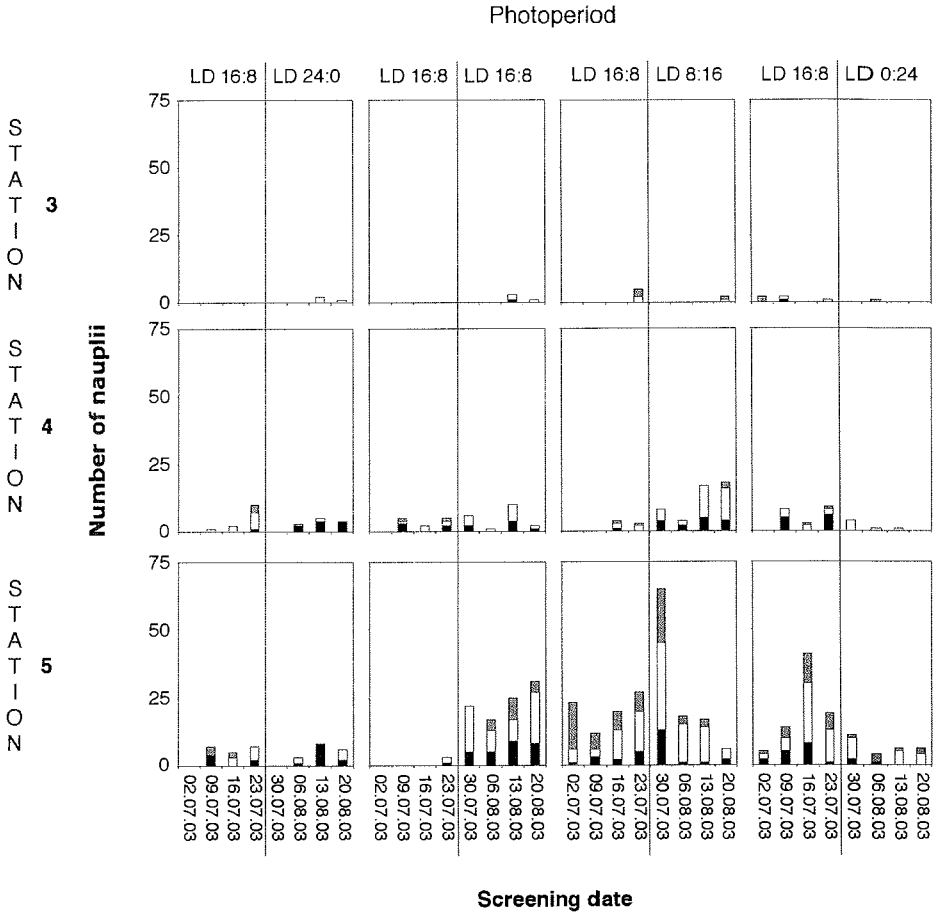

Figure 27: Screening results from the 12 samples used to test the effectiveness of a change in photoperiod as an environmental cue capable of terminating dormancy. Stacked columns are numbers of nauplii (N1 ■, *T. longicornis* □, *C. hamatus* ▒) found per screening

large-scale patchiness. The provided cue, the shift in photoperiod, does not seem to have a strong impact on the termination of dormancy. It neither boosts nor synchronises the emergence of nauplii. However, hatching appears to be stimulated by prolonged incubation at LD 16:8 and inhibited by complete darkness.

Oxygen concentration

In relation to the two previous incubations, an intermediate number of nauplii were found. Within the 8-week experimental period a total of 1 489 specimens emerged from the 12 samples. 56.34% were *T. longicornis*, 9.07% *C. hamatus*,

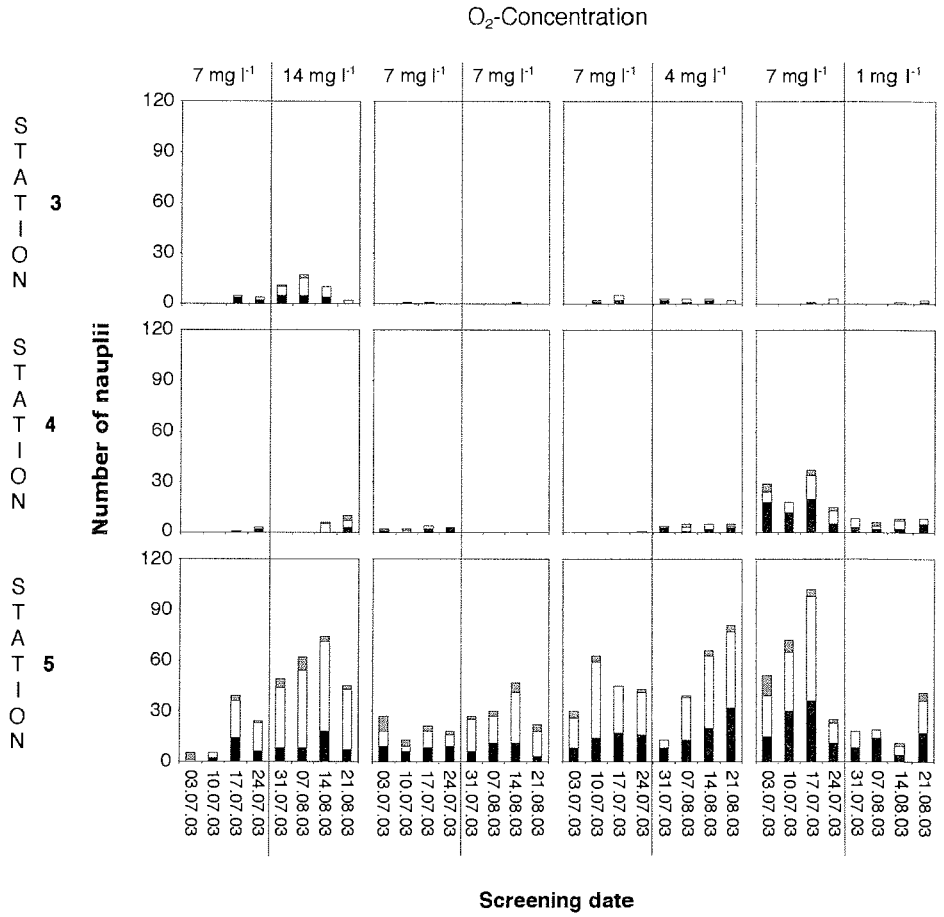

Figure 28: Screening results from the 12 samples used to test the effectiveness of a change in the concentration of dissolved oxygen as an environmental cue capable of terminating dormancy. Stacked columns are numbers of nauplii (N1 ■, *T. longicornis* □, *C. hamatus* ▒) found per screening

0.27% *Acartia* sp., 0.07% unidentified sp., and 34.25% N1. Counts of nauplii from the first four screenings once again indicate large-scale patchiness (Friedman's two-way analysis of variance by ranks: $\hat{\chi}^2_R = 6.0$; critical value for $\chi^2_R = 6.0$ [k = 3; n = 4; p = 0.10]; Sachs, 1978). Similarly small-scale patchiness is easily recognisable.

Results suggest an increase in hatching at elevated levels of oxygen concentration (Figure 28). Sums for all groups of nauplii either increase or remain at least constant after a shift to 14 mg l^{-1}. They also hint to a decrease in hatching at strongly reduced levels of dissolved oxygen. Numbers of nauplii decreased or remained constant after a shift to 1 mg l^{-1}. Inter-specific differences were not detected.

GERMAN BIGHT: FIELD EXPERIMENTS

Though it was intended to replace the sampling bottles on the emergence traps every 7-10 days, intervals were usually longer. All in all the contents of 51 bottles was analysed. Taking into account the size of seafloor covered by each pyramid (100 cm^2) and the results obtained from the laboratory incubations described above, the number of nauplii was extremely small (Tables 9-11). Only 47 specimens were found. They were either *Temora longicornis*, *Pseudocalanus elongatus* or *Acartia* spp. or were assigned to the group that comprised all calanoid nauplii of stage 1. The majority was found early in the experiments. 75-93% occurred in the first set of samples recovered from each station. Hatching in the samples that were collected in close proximity to the traps but incubated in the laboratory was equally low.

Table 9: Species (Tl = *Temora longicornis*), stage and number of calanoid copepod nauplii found in the field experiment performed at the station "Outer harbour 1" and the respective lab sample

Outer harbour 1
Trap deployed: 01 April 2003
Lab sample collected: 01 April 2003

Sampling date	Pyramid 1	Pyramid 2	Pyramid 3	Pyramid 4	Lab sample	Screening date
03 Apr. 03	N1: **8**	N1: **3**	N1: **4**	N1: **7**	-	03 Apr. 03
07 Apr. 03	-	Tl (N2): **2**	-	-	-	07 Apr. 03
24 Apr. 03	N1: **1**	-	-	-	Tl (N2): **1** N1: **1**	24 Apr. 03
06 May 03	Tl (N3): **1**	Tl (N4): **1**	Tl (N6): **1**	-	No screening	06 May 03
25 May 03	-	-	-	-	No screening	25 May 03

Table 10: Species (Tl = *Temora longicornis*, Pe = *Pseudocalanus elongatus*, A sp. = *Acartia sp.*), stage and number of calanoid copepod nauplii found in the field experiment performed at the station "Nathurn" and the respective lab sample

Nathurn
Trap deployed: 08 April 2003
Lab sample collected: 08 April 2003

Sampling date	Pyramid 1	Pyramid 2	Pyramid 3	Pyramid 4	Lab sample	Screening date
24 Apr. 03	N1: **1**	Tl (N3): **1** Pe (N5): **1** A sp. (N2): **1** N1: **1**	Pe (f+eggs): **1** Pe (N1): **5** Pe (N2): **1** Pe (N3): **1** N1: **1**	Pe (N2): **1**	N1: **1**	24 Apr. 03
06 May 03	Tl (N2): **1**	-	-	-	-	06 May 03
26 May 03	-	-	-	-	Tl (N2): **1** N1: **1**	26 May 03

Table 11: Species (TI = *Temora longicornis*, A spp. = *Acartia* sp.), stage and number of calanoid copepod nauplii found in the field experiment performed at the station "Outer harbour 2" and the respective lab sample

Outer harbour 2
Trap deployed: 06 August 2003
Lab sample collected: 06 August 2003

Sampling date	Pyramid 1	Pyramid 2	Pyramid 3	Pyramid 4	Lab sample	Screening date
14 Aug. 03	A sp. (N4): **1** A sp. (N5): **1**	-	-	A sp. (N5): **1**	-	14 Aug. 03
22 Aug. 03	-	-	-	-	-	22 Aug. 03
30 Sep. 03	No sample	-	-	-	No screening	30 Sep. 03
29 Oct. 03	-	-	-	-	No screening	29 Oct. 03
13 Nov. 03	-	-	-	TI (N2): **1**	No screening	13 Nov. 03

KARA SEA

Hatching experiments

The incubation of sediments collected in the Kara Sea yielded results entirely different from those described for the German Bight. Even though the 32 unprocessed samples (Sample A) were incubated for 3 to 6 months and screened 633 times in total, only 10 calanoid copepod nauplii were found. Eight hatched from the sample taken at the deepest of the Kara Sea stations (BP01-46, 323 m), despite the fact that resting eggs are believed to be particularly common in shallow waters. They were detected in three successive screenings (Figure 29), were 415-430 μm in length and probably naupliar stage 1. Six of them lacked any caudal armature and thus differed from the two found on 25 September (Figure 30).

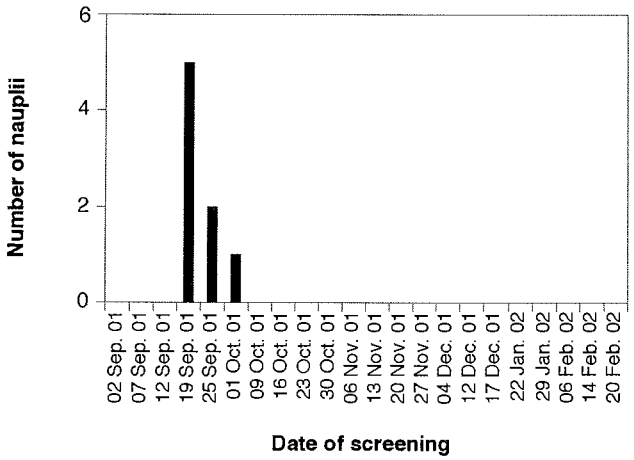

Figure 29: Number of nauplii found per screening in Sample A from station BP01-46

Apart from these 8 specimens, one nauplius each emerged from the samples collected at stations BP01-19 (28 m) and BP01-37 (144 m). They were detected on 2 October 2001 and 7 November 2001, respectively. The nauplius from BP01-37 resembled those from BP01-46, while the one from BP01-19 was much smaller (140 μm) (Figure 30). Nevertheless, they, too, were assumed to be N1.

The incubation of the second set of unpreserved samples (Sample B) was even less successful. Approximately 240 objects that resembled copepod eggs in terms of shape and size were isolated from 13 of the 32 samples, grouped according to external morphology and incubated for up to 6 weeks. Whether any of those actually were calanoid eggs remains unknown, as no calanoid copepod nauplii hatched at all. However, 12 harpacticoid nauplii were found, which probably emerged from subitaneous eggs (adult harpacticoids were abundant in the samples).

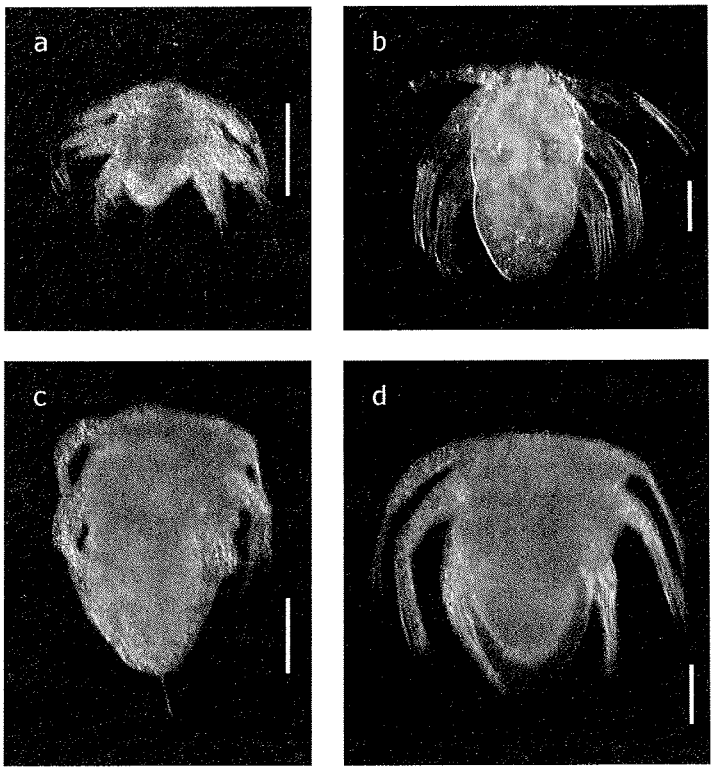

Figure 30: Photomicrographs of calanoid copepod nauplii that hatched from sediment samples collected from the Kara Sea. (a) from station BP01-19, (b) from station BP01-37, (c, d) from station BP01-46. Scale bar: 100 μm

Direct egg counts

The third, preserved set of samples (Sample C) was meant to be used for direct egg counts. The protocol for the separation of meiofauna, which was successfully employed by Burgess (2001), was followed closely in order to isolate copepod eggs from 13 of the sediment samples, but did not produce satisfactory results. Hardly any inorganic material was found in the organic fraction, but much of the meiofauna was still associated with the pellet at the end of the extraction cycle. Separation remained incomplete even when the pellet was subjected to another 2-3 extraction cycles. Thus the analysis was quantitatively not reliable. In addition, as no calanoid copepods nauplii were found during the incubation of potential eggs extracted from the second set of samples (Sample B), it was not possible to unequivocally identify any objects found as copepod eggs.

DISCUSSION

METHODOLOGY

In numerous species of marine calanoid copepods freely spawned eggs tend to sink, as their mass density is greater than that of seawater (Marcus and Fuller, 1986; Miller and Marcus, 1994; Tang et al., 1998; Knutsen et al., 2001), and those that do not hatch before reaching the seafloor will accumulate in the sediment. The analysis of sediment samples is therefore the standard approach in the search of resting eggs. But as these are often difficult to assign to species and their mere presence does not guarantee viability, hatching experiments should produce more meaningful results than direct egg counts.

Two different experimental set-ups have been used in the past. Eggs were either extracted prior to incubation (Marcus, 1989; Naess, 1991; Katajisto et al., 1998), or complete samples were incubated (Lindley, 1986; Hall and Burns, 2001). Here the latter method was applied, which ensures that eggs remain largely untouched. Although sonication and centrifugation do not appear to have an effect on viability (Onbe, 1978; Marcus, 1984), extraction procedures may alter the physiology of hatching. Also environmental conditions are more natural in unprocessed samples. The incubation of those should hence mirror the situation on the seafloor more closely than the incubation of isolated eggs would. However, handling considerably stirred up the samples, so that sediment stratification did not necessarily resemble the situation in the field. Nevertheless, the method is assumed to provide an estimate of the number of eggs likely to hatch in the event of only limited disturbance, comparable to normal tidal flushing (Lindley et al., 1998).

Its main drawback is, that it remains unclear how many viable resting eggs actually were buried in the sediment, as the experimental conditions may not have induced hatching in all eggs present. For example, nauplii hatched continually for one year from 3 samples collected in the German Bight in April 2002, though hardly any were found to emerge from those that were taken at the equivalent stations in June. Hatching might have been suppressed by unfavourable conditions during the incubation. Alternatively, refractory diapause eggs may have dominated in the samples or sediments were depleted, if all resting eggs in the field hatched before June.
Still, numbers of nauplii found during the long-term incubations (maximum values were equivalent to 1.28×10^6 per m^2), were the same order of magnitude as direct egg counts in other studies (Guerrero and Rodriguez, 1998; Katajisto et al., 1998). It is therefore believed that these results are a good approximation of the abundance of calanoid copepod resting eggs in the sediments of the German Bight, although hatching had not entirely ceased after 52 wk.
In order to support this assumption, direct egg counts were attempted. The protocol suggested by Burgess (2001) for the separation of meiofauna and sediment, using the colloidal silica sol Ludox®, was tested, but turned out to be

unsatisfactory, as much of the organic material remained in the pellet. However, the identification of eggs by visual inspection would have been very difficult anyway, particularly for the Kara Sea samples, as detailed information on egg morphology is scarce and several copepod species in this area do not spawn in autumn (Fetzer and Arndt, 2000; Hirche et al., 2003). As a result of this, a comprehensive collection of eggs produced by Kara Sea calanoids, intended as a reference database, could not be created at the time the cruise took place.

A second, equally important aspect in the analysis of sediment samples concerns the device employed. Numerous authors have pointed out that meiofaunal composition in sediment cores collected from the seabed can vary significantly with sampling gear. The main factor affecting sampler bias is the loss of superficial sediment (Blomqvist, 1991). Thus it would have been desirable to use a single technique to take all the samples analysed in the present study. However, water depth, sediment characteristics and gear availability made this impossible.
Direct collection by SCUBA divers, using transparent Perspex tubes with rubber stoppers is considered to be the best way for taking sublittoral sediment samples (Fleeger et al., 1988). But some of the sites were simply to deep for conventional SCUBA diving.
A minicorer, which is equipped with four transparent Perspex tubes, is capable of collecting similarly undisturbed samples, yet it is only suitable for soft sediments. It is comparatively light and does not penetrate hard sand to a sufficient depth. Furthermore, the mounting of the minicorer with extra weights frequently caused the Perspex tubes to disintegrate on impact on the seafloor.
Consequently more robust sampling gear was necessary on sandy bottom. Though box corers are widely used for the retrieval of seemingly undisturbed samples, there is evidence for bow-wave induced bias in the operation of such a device (Blomqvist, 1991; Bett et al., 1994). But Somerfield and Clarke (1997) demonstrated that differences in meiofauna composition and abundance were more pronounced between samples collected with a van Veen grab, which many authors regard as inappropriate for quantitative sampling (Elmgren, 1973; Heip et al., 1977; Blomqvist, 1991), and a Craib corer (similar to a minicorer) than between those taken with a box corer and a Craib corer. The use of the van Veen grab was therefore kept to the absolute minimum.

Despite the fact that the same experimental approach was used in the German Bight and the Kara Sea in order to identify calanoid copepod species that produce resting eggs, very different results were obtained:

GERMAN BIGHT: SEASONAL CYCLE OF HATCHING AND INTER-SPECIFIC VARIABILITY

Even though 6 of the calanoid copepod species that occur regularly in the German Bight (Johannsen et al., 1999) have been reported to lay resting eggs elsewhere (*Acartia clausi*: Kasahara et al., 1974; *Temora longicornis*, *Centropages hamatus*, *Centropages typicus*, *Labidocera wollastoni*: Lindley,

1986; *Anomalocera patersoni*: Ianora and Santella, 1991), only nauplii of *T. longicornis*, *C. hamatus* and *Acartia* spp. were found in this study, along with a few specimens of an unidentified species.

Temora longicornis

Resting eggs of *T. longicornis* are known to be common in the English Channel and the southern North Sea (Lindley, 1986; Lindley, 1990), but are missing in the western Baltic Sea (Madhupratap et al., 1996). Results from the present study prove that they are also abundant in the German Bight.
Here the percentage of spawning females and the egg production rate (EPR) in *T. longicornis* are particularly low in November and December, but nevertheless reproduction occurs all year round (Halsband and Hirche, 2001). This suggests that the primary purpose of these eggs may probably not be to secure survival during the winter. But what is the benefit of resting eggs to this species in the German Bight?
Supposing *T. longicornis* produces morphologically distinct "non-hatching" eggs predominantly in late spring/early summer, as described by Castellani and Lucas (2003) for this species in the Irish Sea, the aim may rather be to minimize mortality from predation and to prevent intra-specific competition.
The decline of copepod numbers observed by Greve and Reiners (1980) in the inner German Bight in June 1979 has been attributed to the predatory ctenophore *Pleurobrachia pileus*. Furthermore the phagocytic dinoflagellate *Noctiluca miliaris*, which peaks in the German Bight in July (approximately 200-300 cells l^{-1}) (Uhlig and Sahling, 1982), has been shown to feed on copepod eggs on a big scale (Daan, 1987). However, Daan noted that digestion time of these eggs by *N. miliaris* was very long. It is therefore reasonable to assume that the differences in egg shell thickness between subitaneous and "non-hatching" eggs (Castellani and Lucas, 2003) should make the latter, more robust type, a less easily digestible food item. Diapause eggs from other copepod species have even been shown to survive ingestion unharmed (Marcus, 1984). Consequently, *T. longicornis* would benefit from the production of "non-hatching" eggs at the peak of the reproductive season in May in at least three ways:

First, it would minimize mortality of post-embryonic stages by decreasing the number of nauplii that hatch in times when predators are abundant. Second, the embryonic stages would be less easily digestible in times when predators feeding on copepod eggs are abundant. Third, intra-specific competition for food among nauplii and early copepodids (adults are known to be omnivorous; Marshall, 1949) is decreased in times when the phytoplankton concentration in the water column dramatically declines at the end of the spring bloom (Halsband and Hirche, 2001). It is important to note that statements 1 and 2 include mortality caused by cannibalism.

Some of the results obtained support the assumption that *T. longicornis* produces morphologically distinct "non-hatching" eggs predominantly in late spring/early summer in order to minimize mortality from predation and to

prevent intra-specific competition. The hatching pattern visible in samples collected in June and August indicates that resting eggs, if present, may be refractory diapause eggs. Thus hardly any hatching occurs after a comparatively high number of nauplii, which possibly originated from non-quiescent subitaneous eggs, were found in the first screening. The presence of such eggs on the seafloor is particularly likely in June as EPR is high in *T. longicornis* and *Centropages hamatus* at this time of year (Halsband and Hirche, 2001). Substantial hatching in October might also indicate that resting eggs are an adaptation to unfavourable conditions in summer, rather than winter, but it is uncertain whether these results reflect in-situ dynamics, as a new generation is usually not observed for *T. longicornis* in late autumn (Hirche, unpublished).
However, as *T. longicornis* nauplii in the present study still hatched from sediment samples after an experimental period of one year, resting eggs may at least be capable of securing year-after-year survival. Additionally, maximum hatching rates in April indicate an important role in spring recruitment.
An alternative approach trying to explain the benefit of resting eggs to *T. longicornis* in the German Bight focuses on an improved utilisation of the spring bloom. Data presented by Halsband and Hirche (2001) suggest, that EPR in this species is related to phytoplankton abundance, though a time lag is distinguishable in spring. EPR peaks in May, approximately one month after the maximum in phytoplankton carbon is observed. Unlike many polar species (Table 16), *T. longicornis* does not store large amounts of lipids (Kattner et al., 1981; Evjemo et al., 2003) and thus the nutritional status of females at the end of the winter may be inadequate for immediate reproduction, despite the fact that their diet is not restricted to phytoplankton. A few weeks of intensive feeding seem to be required for EPR to increase accordingly. Thereby the bulk of eggs are produced in times when primary production strongly declines. Resting eggs hatching a week or two prior to the onset of the spring bloom would counter this mismatch of food abundance and reproductive potential, as nauplii would reach the first feeding stage (N2; van Duren and Videler, 1995), just as primary production starts to increase.
Strictly speaking, both scenarios would perfectly intertwine and may not be antagonisms at all, provided that resting eggs are produced at the height of the reproductive season.

Centropages hamatus and inter-specific differences

Second most numerous to emerge from the samples were nauplii of *C. hamatus*. In subtropical waters resting eggs enable this species to survive adverse conditions in summer (Marcus and Lutz, 1994). In the temperate German Bight however, they are more likely to insure the perpetuation of the species during the winter, as adults are absent from the plankton from December to March (Halsband and Hirche, 2001). But convincing evidence in support of this assumption is scarce in the results. The seasonal pattern of hatching displayed by *C. hamatus* was similar to that found in *Temora longicornis*, although one would expect a comparatively larger peak in spring in a species which exclusively depends on recruitment from resting eggs at that

time of the year. Moreover pelagic populations of *C. hamatus* were observed to hibernate in other areas of the North Sea (Lindley and Hunt, 1989), and thus resting eggs may not be vital to the population in the study area, as planktonic stages may be advected to this region every year anew. However, relative to the abundance of post-embryonic stages in the plankton (monthly means of *T. longicornis* near Helgoland are roughly ten times as high as in *C. hamatus*: Greve and Reiners, unpublished), the proportion of resting eggs in the sediment was considerably higher in *C. hamatus* than in *T. longicornis*. This militates in favour of their particular importance to this species.

Significant inter-specific differences were also visible in the long-term incubations. After an initial period of intensive hatching, which lasted 13 weeks, rates dropped simultaneously in both species and in *T. longicornis* stayed remarkably constant for the remaining 39 weeks. In contrast, hatching in *C. hamatus* almost ceased and did not re-increase before another 3 months had passed. This resembles a refractory phase, which is typical for diapause and was found to last as long as 6 months in eggs of *C. hamatus* from the Gulf of Mexico (Chen and Marcus, 1997). But if the resting eggs present in the samples collected in April were spawned during the previous reproductive season (April-November), it is unlikely that they were still in need of time to complete diapause in August the following year.

Table 12: Numbers of nauplii that hatched in 52 weeks from 3 samples taken on the 22 April 2002 at sites 3, 4 and 5. Ratios (specimens found in screenings 27-52 compared to those discovered in the first 26 screenings) are given together with mean values. Figures in the lower part of the table show results from a similar experiment done by Lindley (1986; 1990). Means were calculated from 8 samples per species. Note that samples represent only 2 cm^2 of seafloor rather than 24.63 cm^2

		T. longicornis (N2-N6)	*C. hamatus* (N2-N6)	N1
	Week 1-26	352	132	490
Station 3	Week 27-52	84	179	295
	Ratio	**4.2:1**	**0.7:1**	**1.7:1**
	Week 1-26	425	66	482
Station 4	Week 27-52	310	74	264
	Ratio	**1.4:1**	**0.9:1**	**1.8:1**
	Week 1-26	867	420	969
Station 5	Week 27-52	259	285	328
	Ratio	**3.3:1**	**1.5:1**	**2.9:1**
	Week 1-26	548	206	647
Ø Stations 3-5	Week 27-52	217.7	179.3	295.7
	Ratio	**2.5:1**	**1.1:1**	**2.2:1**

		T. longicornis (N1-N6)	*Centropages* spp. (N1-N6)
Lindley, 1990	Month 0-6	19.9	9.9
Ø 8 samples per species)	Month 6-12	9.9	9.5
	Ratio	**2:1**	**1:1**

Long-term hatching also varied in other respects. Sums of *C. hamatus* nauplii decreased by only 30% in the second half of the experimental one-year period, while numbers of *T. longicornis* nauplii declined by 65%. Similar results were evident in a study by Lindley (1990). When he incubated sediments from the English Channel twice as many *T. longicornis* emerged in the first 6 months of the experiment compared to the subsequent 6 months (Table 12). In contrast, numbers of *C. hamatus* nauplii were almost identical in the two successive 6 months periods. Analogue ratios were found in the present study.

However, it is rather difficult to elucidate the exact mechanisms underlying the patterns observed. A major obstacle is that the egg types involved are unknown. Quiescent subitaneous and diapause eggs of *C. hamatus* have been reported to co-occur in sediments from the Gulf of Mexico (Marcus and Lutz, 1998). Similarly, *T. longicornis* from the Irish Sea is known to produce two morphologically distinct types of eggs, one subitaneous and the other probably diapause (Castellani and Lucas, 2003). Unfortunately, it has neither been established whether in the North Sea resting eggs of these two species include quiescent subitaneous and diapause eggs, nor what their seasonal production cycle is like. The problem is, that quiescent subitaneous eggs and post-refractory diapause eggs hatch soon after conditions become favourable and are therefore difficult to distinguish in hatching experiments. It is also important to keep in mind, that, should both egg types co-occur in one species, they would not necessarily have to be sensitive to the same cues, nor would they have to be protective measures against adverse levels of the same environmental variable.

The cues, which initiated hatching in the incubations, are also unclear, but the findings suggest, that sample handling or sampling provided a signal that induced the eggs to commence hatching, as numbers of nauplii were often low in screening 1, but increased over the following two to three weeks. This was particularly true for those taken in March, April, October and February. Physical parameters like oxygen concentration and light have been identified as potential triggers for copepods eggs from different areas (Uye and Fleminger, 1976; Uye et al., 1979).
In the present study, temperature remained constant in individual samples but the sediment surface was stirred up in every screening when bottles were refilled with seawater. Thus resting eggs were re-suspended and exposed to new, possibly beneficial levels of environmental variables. In contrast to Marcus and Lutz (1998) a threshold temperature for hatching of *C. hamatus* resting eggs was not observed.
Differences between station 2 and stations 3, 4, and 5 in the long-term experiments may have been caused by the reduced longevity of diapause eggs at normoxia (Marcus and Lutz, 1998). Alternatively, a certain amount of dissolved oxygen may be essential for hatching. Due to the grain size distribution the upper few centimetres of the sediment at station 2 are likely to be well oxygenated and may thus contain only refractory diapause eggs. Those that had completed the refractory phase would have hatched already and subitaneous eggs may not have become quiescent in the first place.

Results also suggest that hardly any eggs were present in the sample collected at station 1 in April as only 8 nauplii were found in 52 screenings. Here the sediment was particularly coarse and contained very little organic material. Thus it was probably particularly well oxygenated. Therefore all nauplii might have hatched in the 6 weeks between the cruise in March, when eggs were abundant in the sample collected at station 1, and the cruise in April. On the other hand high winds may have caused bottom current velocity at station 1 to increase to levels that induce re-suspension and dislocation of any resting eggs that had still been buried in the sediment at that site.

Centropages typicus

If not hidden in the N1-group, no *Centropages typicus* nauplii emerged from the samples, although adults of this species are absent from the water column around Helgoland from February to August (Halsband and Hirche, 2001). Smith and Lane (1987) did not find evidence for diapause egg production in *C. typicus* either, but Lindley (1990) reported that some, though only very few nauplii of this species emerged from sediment samples from the English Channel and southern North Sea.
The lack or scarcity of resting eggs and the absence of the species from the plankton for part of the year suggests that *C. typicus* is expatriated in the German Bight and depends on advection with Atlantic water, as already hypothesised by Krause et al. (1995). CPR (Continuous Plankton Recorder) data, however, suggests that the species overwinters in the German and the Southern Bights (Lindley and Reid, 2002).

Acartia spp.

Acartia clausi is by far the most abundant species of this genus around Helgoland (Krause et al., 1995) and present in the plankton all year round, though it may not reproduce during the winter (Halsband and Hirche, 2001). Its resting eggs have been reported from the Pacific (Kasahara et al., 1974; Uye and Fleminger, 1976; Marcus, 1990), but appear to be particularly vital to populations living in warmer waters (T > 22°C), where they guarantee survival during the summer, when the species is absent from the plankton (Uye, 1985). They also occur in areas of the Pacific, where water temperature is lower (even below 0°C during the winter), but are probably of less importance there, as planktonic populations are perennial in these regions (see Koyama, 1975 in Uye, 1985; Uye, 1982). In the Atlantic clear evidence is missing.

Because *A. clausi* is as abundant in the German Bight as *Temora longicornis* (Greve and Reiners, unpublished), corresponding numbers of resting eggs are to be expected in the sediment. The marginal portion of nauplii found here is therefore more likely to originate from the eggs of a congener. Regrettably, the occurrence of *Acartia* species other than *A. clausi* near Helgoland is purely documented. *A. bifilosa* has been named by Bradford-Grieve (1999) as an inhabitant of the North Sea and has occasionally been observed in the study

area (Knotz, unpublished). It is known to produce resting eggs in the northern Baltic Sea (Katajisto et al., 1998) and in Southampton Water (Castro-Longoria and Williams, 1999) and might do so in the German Bight as well. As *A. longiremis*, which also occurs at Helgoland Roads (Greve and Reiners, unpublished), has never been reported to produce resting eggs yet, the *Acartia* nauplii found in the present study were most likely *A. bifilosa*.

Labidocera wollastoni and *Anomalocera patersoni*

From the 49 species known to produce resting eggs worldwide (Table 1) another two, i.e. *L. wollastoni* and *A. patersoni*, occur in the study area, but in very low numbers. Monthly means are < 0.1 m^{-3} and < 1 m^{-3}, respectively (Greve and Reiners, unpublished). As the specimens classified as unidentified did not resemble their nauplii (Grice and Gibson, 1982; Sazhina, 1985) these two species may either not lay resting eggs in the German Bight, or the eggs have simply eluded sampling.

The unidentified species

The specimens that were assigned to this group of nauplii could not unambiguously be identified to species, despite intensive enquiries. They were easily distinguishable from the other 4 groups found in this study, but did not resemble the juvenile stages of *Labidocera wollastoni* (Grice and Gibson, 1982), *Anomalocera patersoni* (Sazhina, 1985) or *Centropages typicus* (Lawson and Grice, 1970) either; species that occur in the German Bight and have been shown to produce resting eggs elsewhere.
As a matter of fact they may have erroneously been assigned to a separate group. There is evidence to suggest that they were indeed *Temora longicornis* nauplii in an early postmolt phase. What has been described as the "bases of the furcal appendages" (see RESULTS) looked like shafts of not yet completely emerged setae and/or like setal tracks, which remain visible for some time in the surrounding tissue after the new setae have emerged (Dexter, 1981; Mauchline, 1998).
For all the differences in external morphology, particularly caudal armature, the unidentified nauplii resembled the juvenile stages of *T. longicornis* more closely than those of *Centropages hamatus* (Oberg, 1906) or one of the *Acartia* species (Oberg, 1906; Klein Breteler, 1982). Equal length of the caudal armature, however, is atypical for naupliar stages 2-6 of *T. longicornis*, but may be explained by the still incomplete emergence of one of the furcal appendages. Also the furcal appendages appeared to be of equal thickness. This applies to all nauplius stages of *T. longicornis*, but only to N1 in *C. hamatus*. Due to its size of approximately 160 μm (furcal appendages excluded), the unidentified species is far to big for being *C. hamatus* N1. It is more likely to be *T. longicornis* N2 or N3. Further support in favour of the assumption that the unidentified specimens were *T. longicornis* nauplii after all, comes from the hatching results. Maximum numbers of unidentified specimens frequently co-occurred with maximum numbers of *T. longicornis* particularly at low incubation

temperatures (the more *T. longicornis* nauplii are present, the greater the chance of discovering some that have just finished ecdysis; the lower the incubation temperature, the more time it will take for a nauplius to complete a molting cycle and thus the better the chances of detecting specimens are in an early postmolt phase). Though there is no significant correlation, a trend is clearly discernable (Figure 31).

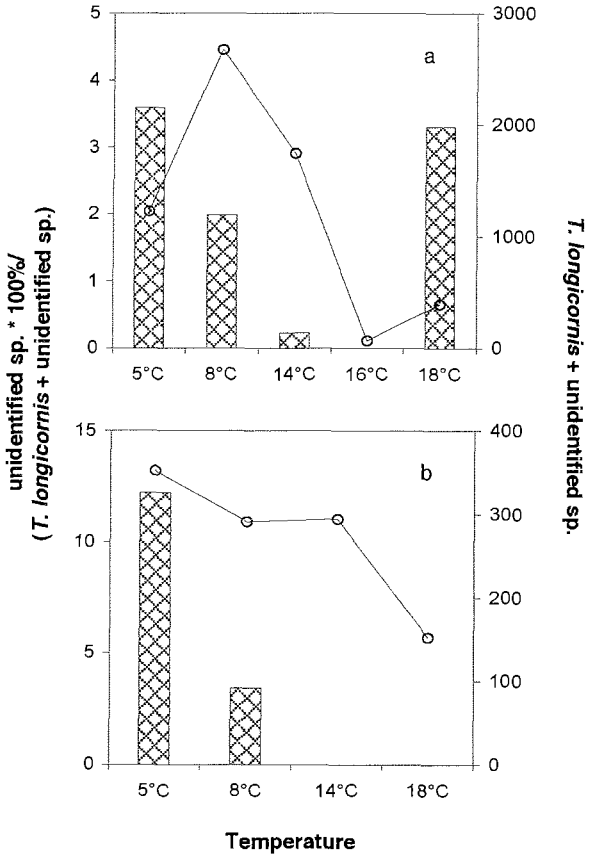

Figure 31: Sum of *T. longicornis* + unidentified sp. (line) and number of unidentified sp. as percentage of the sum of *T. longicornis* + unidentified sp. (columns) in relation to the incubation temperature. Data originate from (a) the 34 samples incubated in the first set of experiments performed in the German Bight (all screenings) and (b) the 12 samples incubated in order to identify the influence of temperature on hatching (screenings 6-10)

Pooled N1

Calanoid copepod nauplii ranked as stage 1 accounted for over one third of all 13559 specimens that emerged from the 34 samples collected at stations 1-5 between March 2002 and February 2003. They could not reliably be assigned to species, but it was assumed that they were for the most part *Temora longicornis* and *Centropages hamatus*, as those two accounted for the vast majority of all nauplii of stage 2 and older. A few probably were *Acartia* spp..

Table 13: Stage duration (days) of N1 instars, at different temperatures, for some of the calanoid copepods that occur in the German Bight. Values are taken from the literature

Species	Stage duration (N1) in days, at:				Reference
	5°C	10°C	15°C	20°C	
Acartia clausi	4.2	2.1	0.9	0.8	Klein Breteler and Schogt, 1994
Acartia tonsa	-	-	0.75	-	Landry, 1983
Centropages hamatus	-	-	1.04	0.66	Halsband-Lenk et al., 2002
Centropages typicus	-	2.04	1.08	0.89	Halsband-Lenk et al., 2002
Pseudocalanus elongatus	0.91	0.6	0.41	-	Thompson, 1982
Temora longicornis	-	-	0.98	0.5	Halsband-Lenk et al., 2002

In principal, specimens belonging to entirely different species may have been present, too. However, the chances, that this was the case, are minute. The length of time of embryonic and post-embryonic development in copepods is closely related to temperature. Within certain physiological levels an increase in temperature speeds up development. At 15°C, for example, the stage duration of N1 instars is down to approximately one day in several German Bight calanoids (Table 13). Thus it would be reasonable to assume that with usually 7 days between successive screenings at least some specimens of every species should manage to develop to a stage beyond N1. But only four groups of nauplii, other than N1, emerged from the samples (*T. longicornis*, *C. hamatus*, *Acartia* spp. and the unidentified species).

Maximum abundance and recruitment potential

As aforementioned, the main benefit of resting eggs appears to differ between *Temora longicornis* and *Centropages hamatus*. They may guarantee perpetuation from year to year, minimize mortality at times when predators are abundant or enable a species to take advantage of favourable conditions in the plankton (spring bloom) in times when reproductive females are absent or present in low numbers only. But regardless of the way by which a species might profit from the production of such eggs, their impact will always depend on the ratio of the number of nauplii emerging from resting eggs on the seabed to those hatching at the same time from freshly spawned eggs.
Using multi-year seasonal abundance data for *T. longicornis* and *C. hamatus* from Helgoland Roads (Figure 32a, f)(Greve and Reiners, unpublished) as well as EPR data for both species (Figure 32b, g) recently published in a comprehensive paper by Halsband-Lenk et al. (2004), it was possible to estimate the number of eggs likely to be spawned per cubic meter of water and day in the German Bight (Figure 32c, h). Similarly, the number of nauplii emerging from resting eggs to every overlying cubic meter of water per day (Figure 32d, i) was calculated from the results obtained in the present study (mean of 4-5 samples collected per cruise; values are numbers of *T. longicornis* or *C. hamatus* detected in screenings 2-6 divided by water depth at the particular station and number of days between screenings 1-6).

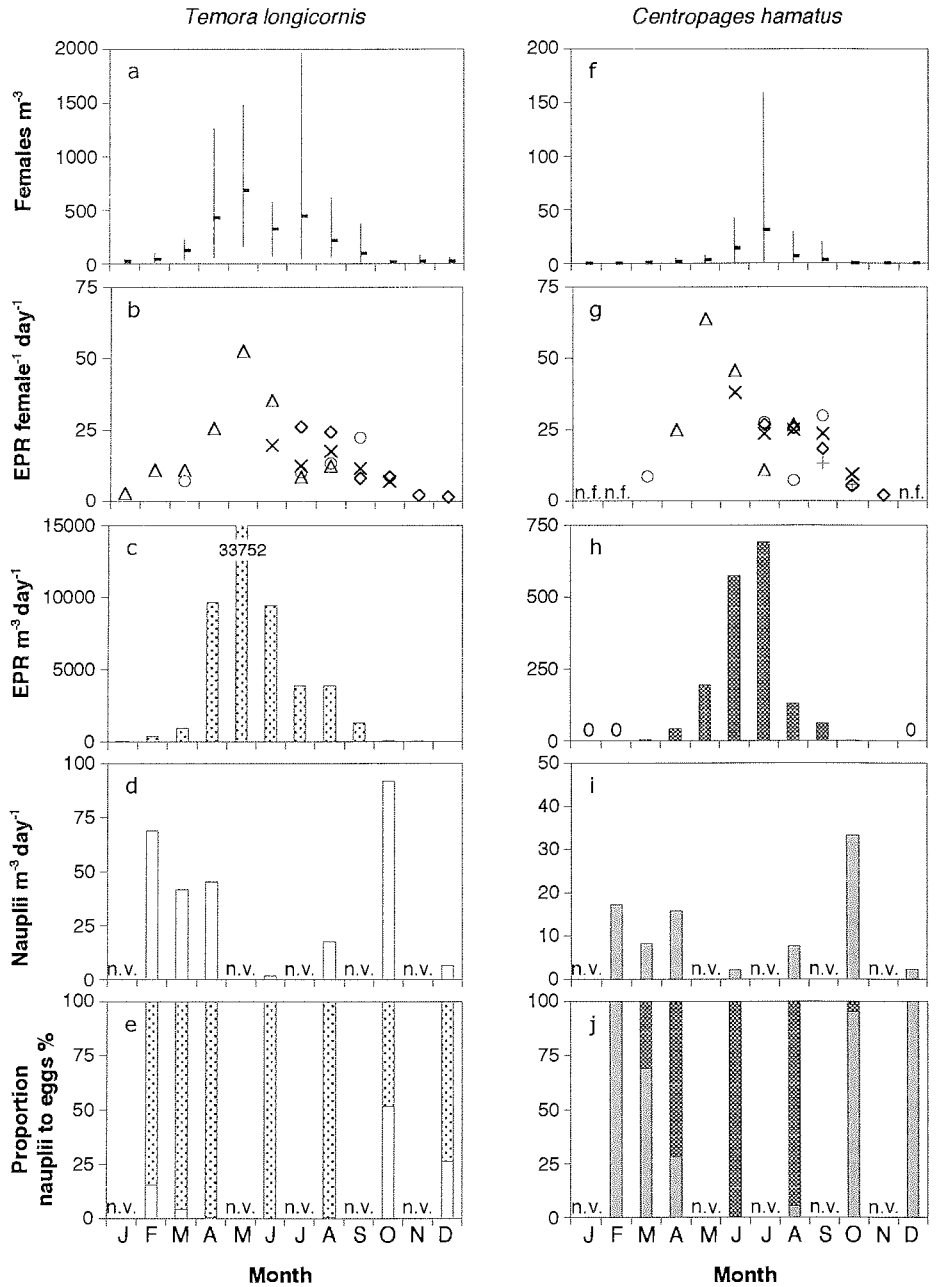

Figure 32: (a-e) *T. longicornis* and (f-j) *C. hamatus*. **a+f** Seasonal abundance of females at Helgoland Roads (mean and range of monthly means 1995-2001; Greve and Reiners, unpublished). **b+g** Egg production rate (monthly means) for specimens from Helgoland Roads (data from several years: ◊: 1995, Δ: 1996, +: 1998, x: 1999; o: 2000; Halsband-Lenk et al., 2004). **c+h** Egg production per m^3 and day (calculated from the values displayed in graphs a and b and f and g, respectively). **d+i** Number of resting egg derived nauplii emerging into every m^3 of the water column per day (values computed from the results of the present study). **e+j** Proportion of c to d and h to i, respectively. n.v.= no value; n.f.= no females present

Thus it was possible to estimate the proportion of resting egg derived nauplii to freshly spawned eggs, a measure for the potential impact on recruitment of either source (Figure 32e, j).
Maximum EPR $m^{-3}day^{-1}$ (*T. longicornis*: 33752; *C. hamatus*: 690) clearly exceeded the maximum emergence of nauplii $m^{-3}day^{-1}$ (*T. longicornis*: 92; *C. hamatus*: 33) in both species and at the peak of the reproductive season the share of resting egg derived nauplii was down to a few percent or less. But from late autumn to spring, when planktonic recruitment plummeted or ceased entirely their relevance increased significantly. Though the seasonal pattern appeared to be comparable in both species, the importance of nauplii hatching from resting eggs as a recruitment source was much higher in *C. hamatus* than in *T. longicornis*. And their impact on recruitment might even have been underestimated in these calculations, for two reasons:

First, the vast majority of specimens classed as N1 will most certainly be either *T. longicornis* or *C. hamatus*. But only those beyond naupliar stage 1 have been considered in the calculations.
Second, numbers of eggs are compared to numbers of nauplii. Hatching success below 100% (some eggs will inevitably come to rest on the seafloor, if they do not, it would be difficult to explain where the resting eggs in the sediment samples came from) and egg mortality (predation, cannibalism, etc.) might reduce naupliar recruitment from freshly spawned eggs and thereby increase the relative importance of nauplii hatching from eggs resting in the sediment. Daan (1987) for example calculated that predation by *Noctiluca miliaris* alone, which is abundant in the German Bight during the summer (Uhlig and Sahling 1982), can account for over 50% of copepod egg mortality. And Peterson and Kimmerer (1994) calculated egg mortality in *T. longicornis* from the Long Island Sound to range from 37-99%. Mortality of N1 will have a similar effect.

The recruitment potential of sediments around Helgoland appears to be similar to that of the southern North Sea. Lindley (1990) found numbers of nauplii equivalent to 285 000 specimens per m^2 for *T. longicornis* (N1-N6) and also for *Centropages hamatus* (N1-N6) to hatch from sediment samples from this area over a period of 12 months. Though the values found in the present study were higher, they were in the same order of magnitude.

In conclusion, the results suggest that in the German Bight resting eggs are an important component of the life cycles of *Temora longicornis* and *Centropages hamatus*. However, to clearly identify their contribution to population dynamics a better understanding of the physiology of the different egg types and the factors that control hatching of these eggs in the North Sea is necessary.

GERMAN BIGHT: FACTORS CONTROLLING THE TERMINATION OF THE DORMANT PHASE

Numerous, predominantly abiotic environmental variables have been shown to influence maintenance and termination of dormancy in calanoid copepod resting eggs (Grice and Marcus, 1981; Marcus, 1996). But the effectual parameters and their threshold values can vary with latitude and/or between species.
In the present study, all three physical factors tested for their impact on hatching proved to be effective in one way or another. But the interpretation of the patterns observed is somewhat difficult. As freshly hatched nauplii were abundant in the samples prior to the shift in temperature, oxygen concentration or photoperiod, conditions must have already been beneficial in the initial phase of the incubations. This suggests that sample handling itself provided the trigger(s) responsible for the termination of dormancy. Replacement of the overlying water during screening caused partial re-suspension of the sediment and reshuffled the eggs, exposing them to light and higher levels of oxygen concentration, though not temperature. Nevertheless, the last of these three physical factors turned out to be the most effective cue in this set of experiments.

Temperature

Though a variety of investigators have reported a strong impact of temperature on copepod resting eggs (Marcus, 1980, 1987, 1989; Uye, 1985; Sullivan and McManus, 1986; Ban and Minoda, 1991; Guerrero and Rodriquez, 1998), no consistent pattern is discernable.
In the present study a marked drop synchronized and enhanced hatching. Four weeks after transfer to 5°C numbers of nauplii, predominantly *Temora longicornis* and N1, peaked simultaneously for two consecutive screenings in all three samples. In contrast to *Labidocera aestiva* from Woods Hole (Marcus, 1980) or *Acartia tonsa* from Narragansett Bay (Zillioux and Gonzalez, 1972), a re-increase in temperature was not necessary for synchronisation.
Provided that resting eggs are intended to improve a species' capability to utilize the spring bloom, this seems to be ecologically reasonable. The analysis of seasonal data from the German Bight suggests that a rise in near-bottom water temperature is an inadequate cue, as it does not properly attune hatching of diapause eggs to the vernal boost of primary production. At least several successive days of increasing values should be necessary to signal a reliable uptrend. Assuming that development resumes immediately after that period of time, it will take 4-7 days for the eggs to hatch (Table 14) and another couple of days for the nauplii to develop to the first feeding stage (N2; Landry, 1983; Fryd et al, 1991; van Duren and Videler, 1995). Thereby they would have occurred 7 weeks after the onset of the spring bloom in 2001 and 5 weeks prior to it in 2002 (Figure 33, broken lines and arrows). In comparison N3 would have already become abundant 2-3 weeks after the onset of the spring bloom in 2001 and only 3 weeks prior to it in 2002, if hatching took place 4-5 weeks after temperatures fell to approximately 5°C (Figure 33, solid lines and arrows).

Although this pattern of dormancy termination is not ideal either, it would be more suitable than the one described previously.

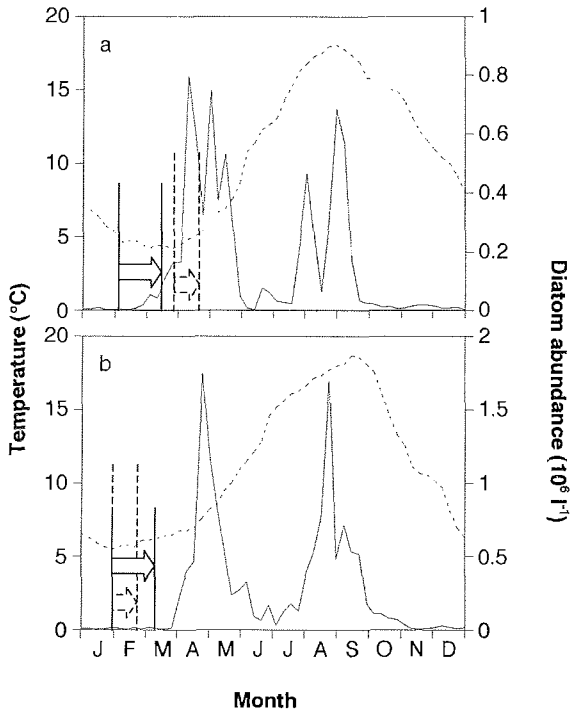

Figure 33: Seasonal cycles of diatom abundance (solid line) and near-bottom water temperature (broken line) in the German Bight for (a) 2001 and (b) 2002. Values are weekly means. Diatom data originates from Helgoland Roads (54°11.137′N, 7°53.909′E; Wiltshire and Dürselen, in press). Temperature readings are from the 30 m probe of the Marnet monitoring site "Feuerschiff Deutsche Bucht" (54°10′N, 07°27′E; depth: 33 m; www.bsh.de). The effect of two different patterns of dormancy termination in copepod eggs is indicated (see text for details)

But how exactly does temperature affect dormancy? In *Acartia hudsonica*, resting eggs that did not hatch at 20°C, did so synchronously 7-10 days after transfer to 4°C (Sullivan and McManus, 1986). This suggests that the temperature shift itself is the trigger. In the present study, however, a month passed between the date temperature was lowered and the date the peaks were recorded, despite the fact that even at 5°C embryonic development in *T. longicornis* and *Centropages hamatus* normally does not take longer than one week (Table 14). Thus simultaneous hatching would be expected to occur much earlier, unless the majority of eggs were still in the refractory phase and did not complete this integral part of diapause until another three weeks had passed. But why should so many eggs complete their refractory phase at the same time? Have they been spawned at the same time? And is it likely, that at the end of October significant numbers of eggs have still not completed the refractory phase?

These questions are difficult to answer and a similar hatching pattern has not previously been described in the literature. Moreover, alternative interpretations of the underlying mechanisms are equally conceivable in order to explain the patterns observed in the present study. For example, the eggs that hatched synchronously may have been post-refractory diapause eggs, sensitive to

temperatures below a certain threshold value, say 5°C. Once this value is reached (in the German Bight around the end of January) it triggers some internal timepiece of the eggs, which then initiates the resumption of development approximately one month later. Thus they would hatch in time with the onset of the spring bloom. It may also be possible that a certain number of days at temperatures characteristic for winter conditions may be required to cause simultaneous hatching.

Table 14: Duration of embryonic development, at different temperatures, for some of the calanoid copepods that occur in the German Bight. Values were calculated using Belehrádek equations from the literature

Species	Equation	Duration of embryonic development in days, at:				Reference
		5°C	10°C	15°C	20°C	
Acartia clausi	$D=1442.0(T+10.49)^{-2.05}$	5.2	3.0	1.9	1.3	McLaren, 1978
Centropages hamatus	$D=1148.9(T+6.9)^{-2.05}$	7.2	3.5	2.1	1.3	Halsband-Lenk et al., 2002
Centropages typicus	$D=1535.3(T+11.6)^{-2.05}$	4.8	2.8	1.8	1.3	Halsband-Lenk et al., 2002
Temora longicornis	$D=2469.5(T+18.2)^{-2.05}$	3.9	2.6	1.9	1.4	Halsband-Lenk et al., 2002

According to results obtained by Wiltshire and Manly (2004), a mismatch of food abundance and reproductive potential should be most successfully avoided, if hatching of copepod resting eggs was triggered by the temperature regime in the last quarter of the preceding year, as the analysis of seasonal data on temperature and phytoplankton abundance from the past 40 years revealed, that in the German Bight the onset of the spring bloom is linked more strongly to this component of the seasonal temperature cycle than to spring values.

Obviously, additional, more sophisticated experiments are necessary to solve this matter. What seems to be indisputable, is that temperature has to be lowered to values characteristic for winter in order to synchronize hatching of calanoid copepod resting eggs in the German Bight, as no such effect was observed when temperature was merely reduced to 8°C. In addition results support the assumption that a drop in temperature mediates the status of another important environmental variable, as cold itself does not appear to be disadvantageous to postembryonic stages of *T. longicornis* (otherwise eggs should have remained dormant).
The drop to 5°C did not only synchronize hatching, it had an enhancing effect, too. The effect was, however, not consistent between the different groups of nauplii. While it was clearly evident in the overall number of specimens and in the number of those that were naupliar stage 1, the results for *T. longicornis* and *C. hamatus* were more mixed. It also seemed to be essential for specimens of the unidentified species to occur. However, as previously suggested, they may have been early postmolt *T. longicornis* and thus their appearance might be attributable to decelerated development (see above) rather than a triggering stimulus. A rise in temperature hardly affected hatching.

Photoperiod

Photoperiod is an important environmental trigger inducing the production of diapause eggs in several species of fresh-water (Hairston et al., 1990) and marine (Uye, 1985; Marcus, 1982; Chinnery and Williams, 2003) calanoid copepods. To date, there is however little evidence to suggest, that it also functions as a cue terminating the dormant phase of such eggs. This is not to say that light has no impact on hatching; hatching of eggs of some copepod species can be suppressed by continuous darkness (Landry, 1975; Pasternak and Arashkevich, 1999), but it is unknown whether the mere presence of light is sufficient to break dormancy or whether a specific light-dark-cycle is required.
In the present study sediment samples were exposed to a light-dark-cycle (LD 16:8; LD 8:16), continuous light or continuous darkness. From the results obtained it seems that a special photoperiodic regime is not essential. But as continuous darkness caused a decrease in numbers of nauplii emerging from the samples, light appears to stimulate hatching.
It is arguable whether these results mirror the situation in the field. Water depth at stations 3, 4 and 5 ranged from 30 to 42 m, while in the laboratory, sediments were covered by little more than 5 cm of seawater. Electromagnetic radiation (e.g. visible light, ultraviolet radiation) is attenuated and scattered by water. The spectrum of wavelengths narrows and light intensity decreases with increasing depth. Consequently, light quality and quantity at the water-sediment interface differ strongly between the laboratory incubations and the seabed. Furthermore a large share of the eggs is likely to be buried in more than a few millimetres of sediment (Viitasalo and Katajisto, 1994; Belmonte et al., 1995; Katajisto, 1996) and will thus not receive any light at all, unless re-suspended.
Yet this may exactly be the point. It will presumably be difficult, if not impossible, for freshly hatched calanoid nauplii to squeeze themselves through centimetres of closely packed, fine-grained sediments trying to reach the water column. Therefore continuous darkness would be a suitable cue for being in a place inappropriate for hatching, while light would signal the direct opposite. Kasahara et al. (1975) reported that resting eggs of *Tortanus forcipatus* did not hatch when buried in mud. However, when the eggs were incubated without mud but in continuous darkness, hatching was not suppressed. Nevertheless this role of light would also explain why photoperiod is not important.
The photoreceptors involved remain to be identified. Astaxanthin and xanthophyll esters have been found in copepod eggs (Kleppel and Lessard, 1992), but the presence of melatonin, a key substance in the perception and transduction of photoperiodic information in animals and plants, has not yet been demonstrated, though it is said to be ubiquitous (Hardeland and Fuhrberg, 1996) and known to occur in crustacea (Tilden et al., 1997).

Oxygen concentration

Near anoxic conditions have been suggested to slow down the developmental rate of copepod resting eggs (Lutz et al., 1994) and thereby suppress or even inhibit hatching. Eggs of *Acartia clausi*, *Acartia erythraea*, *Calanopia thompsoni* and *Labidocera bipinnata*, for example, did not hatch when incubated in

seawater containing 0.04-0.1 ml O_2 l^{-1}, but did hatch after transfer to normoxic conditions (Uye et al., 1979). Similar results were obtained by Uye and Fleminger (1976), Lutz et al. (1992, 1994) and Marcus and Lutz (1994). Generally speaking, concentrations lower than 0.2 ml O_2 l^{-1} were effective.
In the present study, strongly reduced levels of dissolved oxygen also caused a decline in nauplii emergence, while elevated levels resulted in an increase in hatching.
When attempting to interpret these results it is important to bear in mind that complete samples were incubated and that the seawater used to refill the bottles contained plankton smaller than 55 μm. Consequently, respiration, biodegradation and photosynthesis will have influenced the concentration of dissolved oxygen during the 7-day periods between successive screenings. Levels were not continually monitored, but one-time measurements produced readings between 0.5 and 3.5 ml O_2 l^{-1} after 7 days, across the 4 different treatments.
Although Uye and Fleminger (1976) noted substantial hatching of resting eggs incubated without sediment at oxygen levels as low as 0.26-0.47 ml l^{-1}, here nauplii emergence was significantly suppressed in samples that were refilled weekly with seawater containing roughly 2 to 4 times as much oxygen (1 mg O_2 l^{-1}). The inconsistency of these results may have arisen from inter-specific differences in the susceptibility of the eggs to hypoxia. Alternatively, biodegradation and respiration of the benthic infauna may have caused the oxygen level at the water-sediment interface to drop to values close to 0.2 ml O_2 l^{-1} and to even lower levels underneath the sediment surface (Revsbech et al., 1980).
Despite the fact that resting eggs are known to hatch at levels of oxygen that are insufficient for nauplii to survive on (Uye and Fleminger, 1976), the decrease observed here is likely to result from a decline in hatching rather than from premature death of nauplii.
Anoxia/hypoxia may influence hatching of resting eggs in at least two ways. First, like continuous darkness, it might be a signal for conditions inappropriate for hatching. And second, age-dependent susceptibility of copepod eggs to the lack of oxygen (Lutz et al., 1992, 1994) suggests that it is essential in certain quantities for successful embryogenesis.
Increased hatching was observed in samples that were refilled weekly with oxygen-enriched seawater (14 mg O_2 l^{-1}). Several beneficial effects of this treatment can be assumed. The depth of the sediment to which advantageous environmental conditions prevail may expand. It will take longer before oxygen drops to unfavourable levels at or just below the water-sediment interface. Embryonic development may speed up.

Regardless of the environmental factor that eventually triggers the termination of dormancy, the time required by copepod eggs for embryonic development at low temperatures (Table 14), particularly in *Centropages hamatus*, suggests that its registration and hatching of naupii is frequently more than a single screening event apart. This is endorsed by the high abundance of nauplii older than stage 1.

Though the effect of only 3 environmental factors was tested, the results presented here suggest that hatching of calanoid copepod resting eggs in the German Bight is governed by more than one.

GERMAN BIGHT: FIELD EXPERIMENTS

The main goal of the field experiments was to evaluate the significance of the results obtained in the laboratory. Do they really mirror the situation on the seafloor? This question could have been most easily answered by deploying the emergence traps at the 5 stations where sediment samples had been repeatedly collected for the incubations discussed above. Unfortunately, this was not feasible, as water depth, exposure to wave action, and distance from the dive base (Helgoland) would have rendered sampling extremely difficult. Therefore alternative sites had to be chosen, which were shallower, more sheltered and closer to the island.

In the past, emergence traps have been successfully used in field studies to demonstrate seasonal hatching of copepod (DeStasio, 1989; Hairston et al, 2000) and cladoceran (Caceres, 1998) resting eggs in the sediment of freshwater ponds and lakes. According to Marcus (1996), similar efforts in the marine system have failed, due to turbulence and clogging. Nevertheless, a variety of emergence traps have proved to be effective for use in the sea (Youngbluth, 1982; Jacoby and Greenwood, 1988). Though these traps had not specifically been conceived to collect juvenile Crustacea emerging from benthic resting eggs, copepod nauplii were found in them whenever the design (particularly mesh size) was appropriate to retain such minute organisms. These traps were, however, used on sandy bottom and remained on the seafloor for a maximum of 4 consecutive nights only. Thus clogging of the gauze by suspended particles or fouling was unlikely to occur.
In the present study the experimental period was considerably longer as the field studies were intended to resemble the laboratory incubations in terms of duration. When the traps were retrieved from the bottom of the sea after 2-3 months, sea squirts (*Ascidiella* sp.) were found to grow on the outer coarse mesh net in great quantities. Additionally, much of the fine mesh gauze was covered with an orange-brown substance (probably also fouling organisms), but the net was not completely clogged. Turbulence did not appear to be a major problem either, despite the fact that strong, tide-induced currents (maximum velocity 0.7-1.2 m s^{-1}: Mittelstaedt et al., 1983) prevail in the study area.
Still it is probable that small mesh size and fouling do influence numerous environmental factors. Current speed, which controls re-suspension, and light intensity are likely to be reduced. Water exchange will also be affected and consequently oxygen concentration may decrease. Dana et al. (1988) reported that levels of dissolved oxygen inside their emergence traps dropped in laboratory tests at a rate of 1 mg l^{-1} every 24 h when the circular ports in the funnel of their trap were covered with 80 μm Nitex screen. DeStasio (1989), in contrast, did not find statistically significant differences in the concentration of dissolved oxygen between the traps interior and its immediate vicinity, when he

deployed the device in a freshwater pond for 3 successive years. Instead values were very similar (8.37-8.55 mg l^{-1}), even though his traps obviously lacked any ports that might have facilitated the exchange of water and dissolved gases.

The bearing that the trap, which was used in the present study, had on the hatching results is unfortunately difficult to determine, as it was not clarified whether or not the values of crucial environmental variables (i.e. those that initiate hatching) were significantly altered by the presence of the trap. Due to the lack of in situ measurements it is uncertain whether the environmental conditions inside the trap deviated from those beyond. In addition, the parameters that trigger hatching in those calanoid copepod resting eggs that occur in the German Bight have not unambiguously been identified.
The number of calanoid copepod nauplii found in the field experiments was exceptionally low. Based on the assumption that the results obtained from the incubation of 34 sediment samples from the German Bight (described above) are a good approximation of the number of viable eggs in the sediment, conspicuously higher values were expected. This is particularly true as 100 cm^2 of seafloor were covered by a single trap (pyramid), roughly four times the area represented by one of the samples that were incubated in the laboratory. But nauplii were not only rare in the samples retrieved from the traps but also in the samples collected nearby and subsequently incubated in the laboratory. Therefore eggs were presumably scarce in the sediment at the stations where the emergence traps were deployed.
This is confirmed by the emergence pattern. In each of the three field tests the majority of the few nauplii that were discovered in the cod end bottles of the emergence traps were detected in the first set of samples retrieved. They included several specimens of *Pseudocalanus elongatus*, a species that does not spawn its eggs freely into the water column, but carries them in an egg sac until the nauplii hatch. As *P. elongatus* has never been reported to produce resting eggs, it is reasonable to assume that the nauplii found in these experiments have been captured in the trap when it was transported to the seafloor by the diver who deployed it, rather than originating from eggs resting in the sediment.

KARA SEA

Including the Ob River and Yenisei River estuaries, at least 26 species of calanoid copepods occur in the Kara Sea (Tables 15-18), though some of them only in negligible numbers. Nineteen species were reported by Fetzer et al. (2002) from two autumn cruises in 1997 and 1999. Another seven were detected in plankton samples collected in fall 2000 and 2001 (Hirche et al., unpublished).
Despite the considerable diversity of calanoids in this area of the Siberian Arctic, freshly hatched nauplii were extremely rare in the incubations. This may be due to at least a couple of reasons.
First, inappropriate experimental conditions may have prevented hatching. For example, in every screening seawater of 33 psu was used to refill the sample

bottles, and incubations were carried out at 0°C, though in-situ conditions (water temperature and salinity close to the seafloor) at the time of sampling ranged from −1.4°C to 12.8°C and 0.04 psu to 34.9 psu between the 32 stations. Supposing brackish water species produce resting eggs in autumn, when levels of river discharge plummet and planktonic stages face a continuously shrinking habitat, as zones of intermediate salinity narrow dramatically. In a situation like this freshwater input would be critical to those species and consequently low or decreasing levels of salinity would be an adequate cue for the termination of egg dormancy, signalling the improvement of environmental conditions. It is unlikely that such eggs would have hatched, even if they had been present in the samples. However, the postembryonic stages of several of the species occurring in the Kara Sea do not seem to be very sensitive to changes in salinity and, for that matter, temperature, either (Table 18).
Second, alternative physiological adaptations for surviving in seasonal environments replace resting eggs in the Kara Sea. The storage of lipids is widespread and only a small number of species is exclusively herbivorous (Table 17), so that the extreme seasonality of primary production, which is the key factor governing polar ocean ecosystems (Hagen, 1999), may not pose a great threat. In addition numerous species have been shown to undergo diapause in a developmental stage other than the egg stage (Table 15). Thus there is little evidence to suggest that resting eggs are an important component of copepod life history in the Kara Sea.

Limnocalanus macrurus

L. macrurus is a cold-water stenotherm (Roff and Carter, 1972), euryhaline (Hirche et al., 2003) species, common in Arctic coastal waters (Johnson, 1956; Lischka et al., 2001; Fetzer et al., 2002) as well as brackish (Bowman and Long, 1968; Van Hove et al. 2001) and freshwater lakes (Vanderploeg et al., 1998) in the northern hemisphere. It also occurs in the Baltic and the Caspian Seas (Holmquist, 1970). Of the six most abundant calanoid copepods in the Kara Sea (*Drepanopus bungei*, *L. macrurus*, *Pseudocalanus major*, *P. acuspes*, *Calanus glacialis* and *Microcalanus pygmaeus*; Deubel et al., 2003), *L. macrurus* is the only species that has been suggested to produce dormant eggs, at least in freshwater (Ekman, 1907; Hutchinson, 1967; Kiefer and Fryer, 1978). But the authors fail to give corroborative evidence in favour of their statement, while others disagree (Roff, 1972).
Nauplii resembling those of *L. macrurus* also hatched from resting eggs found in sediment samples collected from brackish waters of the northern Baltic Sea (Viitasalo and Katajisto, 1994; Katajisto, 1996). Regrettably, however, the remarkable likeness of the first developmental stages of *L. macrurus* and *Temora longicornis* (Lindquist, 1959) on the one hand and *L. macrurus* and *Eurytemora affinis* (Katajisto, 1996) on the other hand hampered identification. But when the nauplii, which were believed to be either *L. macrurus* or *E. affinis*, were reared to identifiable stages, solely specimens belonging to the latter species were found (Katajisto, 1996). In addition, in a subsequent study performed in the same region only *E. affinis* and *Acartia* spp. nauplii were found

Table 15: Dormancy in the life cycle of the 26 species of calanoid copepods occurring in the Kara Sea (n.s. = not specified)

Species	Dormancy stage	Location	Reference
Acartia longiremis	f	Balsfjorden, Norway	Norrbin, 1994, 1996
Calanus finmarchicus	CIV+CV	Barents Sea, Arctic	Pedersen et al., 1995
	CV	Greenland Sea, Arctic	Hirche, 1989
	CIV+CV	Balsfjorden, Norway	Tande and Slagstad, 1982
Calanus glacialis	1st winter: CIII+CIV; 2nd winter: CV	Barents Sea, Arctic	Tande et al., 1985
Calanus hyperboreus	CV	Greenland Sea, Arctic	Hirche, 1989
Centropages hamatus	Resting eggs	German Bight	This study
	Resting eggs	North Sea	Lindley, 1990
	Resting eggs	Alligator Harbor, USA	Marcus, 1989
	Resting eggs	White Sea	Perzova, 1974
Chiridius obtusifrons			
Diaptomus glacialis			
Diaptomus gracilis	No resting stage	Three lakes, Germany	Santer et al., 2000
	No resting eggs	n.s.	Kiefer and Fryer, 1978
Drepanopus bungei			
Eurytemora gracilis			
Eurytemora herdmani	Probably no resting eggs	n.s.	Redden and Daborn, 1991
Heterocope appendiculata	Resting eggs likely (species frequently absent from the plankton in winter)	Northern Europe	Tollinger, 1911
Jaschnovia brevis			
Jaschnovia tolli			
Limnocalanus macrurus	Resting eggs	n.s.	Kiefer and Fryer, 1978
	None	Lake Michigan, USA	Torke, 1975, in Vanderploeg et al., 1998
	No resting eggs	Meretta Lake, CAN	Roff, 1972
Metridia longa	Probably none (active during winter)	Balsfjorden, Norway	Grønvik and Hopkins, 1984

Microcalanus pygmaeus	None	Weddell Sea, Antarctic	Pasternak and Schnack-Schiel, 2001
	Probably none (species seems to reproduce and grow year-round)	Weddell Sea, Antarctic	Schnack-Schiel and Mizdalski, 1994
	Probably none (species seems to reproduce year-round)	Loch Striven, Scotland	Marshall, 1949
Neoscolecithrix farrani			
Pareuchaeta glacialis			
Pareuchaeta norvegica	Probably none (egg production occurs almost all year round, despite 2 peaks)	Loch Etive, Scotland	Mauchline, 1994
	Probably none (egg production occurs almost all year round, despite 1 peak)	Rockall Trough, Atlantic	Mauchline, 1994
Pseudocalanus acuspes	CIV + CV	Balsfjorden, Norway	Norrbin, 1994, 1996
	CIII + CIV	Resolute Bay, Arctic	Conover and Huntley, 1991
	CIII + CIV	Bedford Basin, Canada	McLaren et al., 1989
Pseudocalanus major			
Senecella siberica			
Spinocalanus longicornis			
Spinocalanus longispinus			
Temora longicornis	Resting eggs	German Bight	This study
	Resting eggs	North Sea	Lindley, 1990
	Resting eggs	White Sea	Perzova, 1974

Table 16: Lipid content and dominant lipid class of the 26 calanoid species occurring in the Kara Sea (n.s. = not specified)

Species	Stage	Total lipids (% of dry mass)	Dominant lipid class and % of total lipids	Location	Reference
Acartia longiremis	F	n.s.	TAG, max 55%	Balsfjorden, Norway	Norrbin et al., 1990
Calanus finmarchicus	Adults	24.7±0.6%	n.s.	Vestfjorden, Norway	Evjemo et al., 2003
	CIV+CV	23.2±0.3%	n.s.	Vestfjorden, Norway	Evjemo et al., 2003
	F	n.s.	WE, usually > 90%	Fram Strait, Arctic	Albers et al., 1996
Calanus glacialis	F	n.s.	WE, usually > 90%	Fram Strait, Arctic	Albers et al., 1996
	F	24%	WE, 64.2%	Barents Sea, Arctic	Tande and Henderson, 1988
	CV	48%	WE, 76%	Barents Sea, Arctic	Tande and Henderson, 1988
	CIV	19%	WE, 74.2%	Barents Sea, Arctic	Tande and Henderson, 1988
	CIII	47.9%	WE, 81.4%	Barents Sea, Arctic	Tande and Henderson, 1988
Calanus hyperboreus	F	36.4-46.1%	n.s.	Fram Strait, Arctic	Auel et al., 2004
	CV	40.9-44.6%	n.s.	Fram Strait, Arctic	Auel et al., 2004
	F	n.s.	WE, usually > 90%	Fram Strait, Arctic	Albers et al., 1996
	n.s.	41%	WE, 53.4%	Barents Sea, Arctic	Scott et al., 1999
	F	29-74%	WE, 34-91%	T-3, Arctic	Lee, 1974
Centropages hamatus	F, M, CV	n.s.	TG, PL, FA (WE < 5%)	North Sea	Kattner et al., 1981
Chiridius obtusifrons	F	Ø = 18.7%	n.s.	Greenland Sea, Arctic	Auel, 1999
	CV	Ø = 26.1%	n.s.	Greenland Sea, Arctic	Auel, 1999
	CIV	Ø = 34.7%	n.s.	Greenland Sea, Arctic	Auel, 1999
Diaptomus glacialis					
Diaptomus gracilis					
Drepanopus bungei	CV + F	n.s.	WE, 60.3-92.1%	Laptev Sea, Arctic	Peters, 2001
Eurytemora gracilis					
Eurytemora herdmani	Late Cs + F	Neutral lipids: 10-15%	n.s.	St. Lawrence estuary, CAN	Mayzaud et al., 1992
Heterocope appendiculata					
Jaschnovia brevis	MCV	~ 40%	TAG, 80.2±7.7%	Arctic	Scott et al., 2002
	FCV	~ 70%	TAG, 81.9±2.9%	Arctic	Scott et al., 2002

Jaschnovia tolli					
Limnocalanus macrurus	M+F	n.s.	WE, Ø = 87.1%.	Kara Sea, Arctic	Hirche et al., 2003
	F	10.5-67.3%	WE, 10-80%	Lake Michigan, USA	Vanderploeg et al., 1998
	F	Ø = 42.3-67.3%	WE, ~ 80%	Lake Michigan, USA	Cavaletto et al., 1989
	M	Ø = 44.7-50.0%	WE, ~ 80%	Lake Michigan, USA	Cavaletto et al., 1989
Metridia longa	CIV-CVI	n.s.	WE, 27-83.5%	Balsfjorden, Norway	Falk-Petersen et al., 1987
	n.s.	57%	WE, 76%	T-3, Arctic	Lee, 1975
Microcalanus pygmaeus	Cs + F	n.s.	WE, Ø = 52%	Weddell Sea, Antarctic	Kurbjeweit, 1993
Neoscolecithrix farrani					
Pareuchaeta glacialis	F	Ø = 33.9%	n.s.	Greenland Sea, Arctic	Auel, 1999
	n.s.	43%	WE, 72%	T-3, Arctic	Lee, 1975
Pareuchaeta norvegica	F	Ø = 42.4%	n.s.	Greenland Sea, Arctic	Auel, 1999
	F	26.4-47.3%	n.s.	Korsfjorden, Norway	Båmstedt, 1980
	M	32.5-42.9%	n.s.	Korsfjorden, Norway	Båmstedt, 1980
	CV	25.9-43.4%	n.s.	Korsfjorden, Norway	Båmstedt, 1980
Pseudocalanus acuspes	CIV+CV	n.s.	WE, 55-72%	Balsfjorden, Norway	Norrbin et al., 1990
Pseudocalanus major					
Senecella siberica					
Spinocalanus longicornis					
Spinocalanus longispinus					
Temora longicornis	CV+CVI	10.7±0.2%	n.s.	Vestfjorden, Norway	Evjemo et al., 2003
	F, M, CV	n.s.	TG, FFA (WE < 5%)	North Sea	Kattner et al., 1981

Table 17: Nutritional preferences of the 26 calanoid species occurring in the Kara Sea (n.s. = not specified)

Species	Feeding	Location	Reference
Acartia longiremis	Omnivorous	Disko Bay, Greenland	Levinsen et al., 2000
	Omnivorous	n.s.	Conover and Huntley, 1991
	Omnivorous/carnivorous	Balsfjorden, Norway	Davis, 1977
Calanus finmarchicus	Herbivorous	Greenland Sea, Arctic	Barthel, 1988
Calanus glacialis	Herbivorous	Greenland Sea, Arctic	Barthel, 1988
	Ice algae	Hudson Bay, CAN	Runge and Ingram, 1988
Calanus hyperboreus	Herbivorous	Greenland Sea, Arctic	Barthel, 1988
Centropages hamatus	Omnivorous	n.s.	Marshall, 1949
Chiridius obtusifrons	Omnivorous	Greenland Sea, Arctic	Auel, 1999
Diaptomus glacialis			
Diaptomus gracilis	Herbivorous	Two reservoirs, England	Kibby, 1971
Drepanopus bungei	Herbivorous	Laptev Sea, Arctic	Hanssen, 1997
Eurytemora gracilis			
Eurytemora herdmani			
Heterocope appendiculata			
Jaschnovia brevis	Probably herbivorous	Arctic Ocean	Scott et al., 2002
Jaschnovia tolli			
Limnocalanus macrurus	Predacious	Ellesmere Island, CAN	Van Hove et al., 2001
	Predacious	Lake Michigan, USA	Warren, 1985
Metridia longa	Phytoplankton/ *C. hyperboreus* eggs	n.s.	Conover and Huntley, 1991
	Ice algae	Hudson Bay, CAN	Runge and Ingram, 1988
	Artemia nauplii	Gulf of Maine, USA	Haq, 1967
Microcalanus pygmaeus	Herbivorous/detritivorous	Weddell Sea, Antarctic	Pasternak and Schnack-Schiel, 2001
	Herbivorous/ detritivorous	Croker Passage	Hopkins, 1985
Neoscolecithrix farrani			

Pareuchaeta glacialis	Carnivorous	North Water, Arctic	Hobson et al., 2002
	Carnivorous	Greenland Sea, Arctic	Auel, 1999
Pareuchaeta norvegica	Carnivorous	Greenland Sea, Arctic	Auel, 1999
	Carnivorous	Korsfjorden, Norway	Yen, 1987
Pseudocalanus acuspes	Herbivorous	Barrow Strait, CAN	Fortier et al., 2001
	Herbivorous	Laptev Sea, Arctic	Hanssen, 1997
Pseudocalanus major	Herbivorous	Laptev Sea, Arctic	Hanssen, 1997
Senecella siberica			
Spinocalanus longicornis			
Spinocalanus longispinus			
Temora longicornis	Omnivorous	n.s.	Marshall, 1949

Table 18: Salinity and temperature tolerance in the 26 calanoid species occurring in the Kara Sea (n.s. = not specified)

Species	Salinity tolerance	Temperature tolerance	Location	Reference
Acartia longiremis				
Calanus finmarchicus	Not below 20 psu	n.s.	Kara Sea, Arctic	Fetzer and Arndt, 2000
	n.s.	LD_{50} after 24h: 21°C	Greenland Sea, Arctic	Hirche, 1987
Calanus glacialis	Not below 20 psu	n.s.	Kara Sea, Arctic	Fetzer and Arndt, 2000
	n.s.	LD_{50} after 24h: 18°C	Greenland Sea, Arctic	Hirche, 1987
Calanus hyperboreus	Not below 20 psu	n.s.	Kara Sea, Arctic	Fetzer and Arndt, 2000
	n.s.	LD_{50} after 24h: 16°C	Greenland Sea, Arctic	Hirche, 1987
Centropages hamatus	n.s.	LD_{50} after 36h: 20°C; 2-5°C < 30% dead after 120h	North Sea	Halsband-Lenk et al., 2002
Chiridius obtusifrons				
Diaptomus glacialis				
Diaptomus gracilis				
Drepanopus bungei	Max. abundance 17-20 psu	n.s.	Laptev Sea, Arctic	Timofeev, 1998
	Abundant at almost 0 psu	n.s.	Laptev Sea, Arctic	Abramova, 1998
	Present in less than 3 psu	n.s.	Ellesmere Island, CAN	Bowman and Long, 1968
	LD_{50}: < 8.6 and > 31.25 psu (m)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
	LD_{50}: < 11.9 and > 23.1 psu (f)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
Eurytemora gracilis				
Eurytemora herdmani	Present in 22-32 psu	Present in 0-21°C	Various localities	George, 1985 and references therein
	Reprod. ceased at S < 15 psu	Reprod. ceased at T > 18°C	Nahant, USA	Katona, 1970
Heterocope appendiculata	n.s.	Warm water species	n.s.	Kiefer and Fryer, 1978
Jaschnovia brevis	LD_{50}: < 8.5 and > 30.3 psu (m)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
	LD_{50}: < 6.2 and > 30.8 psu (f)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
	LD_{50}: < 2.5 and > 32.5 psu (CV)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
Jaschnovia tolli	Max. abundance 17-20 psu	n.s.	Laptev Sea, Arctic	Timofeev, 1998
	LD_{50}: < 6.8 and > 34.6 psu (m)	n.s.	Kara Sea, Arctic	Fetzer, unpublished
	LD_{50}: < 4.7 and > 32.5 psu (f)	n.s.	Kara Sea, Arctic	Fetzer, unpublished

Limnocalanus macrurus	Present in 1.7-33 psu	n.s.	Kara Sea, Arctic	Hirche et al., 2003
	5-35 psu	n.s.	Kara Sea, Arctic	Fetzer and Arndt, 2000
Metridia longa	n.s.	LD_{50} after 24h: 19°C	Greenland Sea, Arctic	Hirche, 1987
Microcalanus pygmaeus				
Neoscolecithrix farrani				
Pareuchaeta glacialis				
Pareuchaeta norvegica				
Pseudocalanus acuspes				
Pseudocalanus major	Max. abundance 17-20 psu	n.s.	Laptev Sea, Arctic	Timofeev, 1998
	Present in approx. 1-32.8 psu	n.s.	Kara Sea, Arctic	Vinogradov et al., 1995
Senecella siberica	Present in 1-22 psu	-0.48 to +8°C	Kara and Laptev Seas	Vyshkvartzeva, 1994
Spinocalanus longicornis				
Spinocalanus longispinus				
Temora longicornis	n.s.	LD_{100} after 24h: 25°C; 2-22.5°C < 30% dead after 120h	North Sea	Halsband-Lenk et al., 2002

to hatch from calanoid eggs recovered from the sediment (Katajisto et al., 1998). Thus it appears to be disputable whether *L. macrurus* actually does produce resting eggs.
Population dynamics as well as adult lipid content and composition object to this assumption. The prevailing opinion is that *L. macrurus* invaded fresh water during the Pleistocene glaciation, but retained its marine arctic life cycle, producing only a single generation per year (Ekman, 1907; Carter, 1969; Roff and Carter, 1972; Selgeby, 1975). According to Roff (1972) it does not produce any resting eggs, though subitaneous eggs may take 30 days to hatch. Subsequently, the new generation moves through all developmental stages without diapausing (Vanderploeg et al., 1998). As reproduction does not start until several months after molting to C6, populations may consist exclusively (Roff and Carter, 1972; Hove et al., 2001), or almost exclusively (Hirche et al., 2003) of adults at certain times of the year.
In Lake Michigan the concentration of lipids in C5 females is initially low but increases continually during summer and fall, before reproduction commences (Vanderploeg et al., 1998). Maximum values were about 67% of dry mass. Wax esters, which are regarded as a long-time energy reserve, can account for over 80% of total lipids in *L. macrurus* from the Kara Sea (Hirche et al., 2003), a species, that is omnivorous or carnivorous (Warren, 1985).

In short, *L. macrurus* has a high salinity tolerance and has never been reported to occur only seasonally in the plankton in any particular location. As an omnivorous or even predacious species it does not directly depend on primary production, and is even able to store large amounts of lipids, mainly wax esters (Cavaletto et al., 1989; Hirche et al., 2003). There may certainly be environmental factors other than food availability or salinity that would make the production of resting eggs a useful or even inevitable strategy to secure population survival, but population dynamics and physiological abilities suggest, that *L. macrurus* does not depend on resting eggs and probably does not produce any.

Drepanopus bungei

This small-sized, neritic, brackish-water copepod can be very common in the southern Kara Sea, occasionally accounting for more than 50% of total zooplankton abundance in autumn (Fetzer et al., 2002). According to Vinogradov et al. (2001), it is also the winter dominant in the Yenisei Gulf. It was present in high numbers near Dickson Island in mid-March 2000 and adult females comprised one-third of all specimens found one month later (Vinogradov et al., 2001). *D. bungei* is endemic to the high Arctic. Its distributional range extends along the Siberian coast, from the western part of the Chukchi Sea (Stepanova, 1937 in Timofeev, 1998) to the Pechora Sea (Zelikman, 1961 in Timofeev, 1998). Relict populations were also found in two meromictic lakes and a couple of stratified fjords on Ellesmere Island, northern Canada (Bowman and Long, 1968; Van Hove et al., 2001).

Seasonal dynamics has been thoroughly studied in the Laptev Sea (Abramova, 1998), where *D. bungei* has at least two generations per year (Abramova, 1996). In Buorkhaya Bay over 70% of males and females were found to be mature in January-February. Nauplii first appeared in the plankton in February and reached abundance maxima in March-April and September. From February to October all developmental stages occurred in the plankton in variable proportions, but later in October-November CV and CVI, containing considerable fat inclusions, dominated (Abramova, 1998). In the Laptev Sea *D. bungei* appears to be more or less restricted to the shallow regions (Kosobokova et al., 1998). Though Timofeev (1998) suggests that its maximal abundance is related to salinities between 17-20 psu, the species is obviously well adapted to a much wider range (Table 18). Hanssen (1997) classified *D. bungei* as herbivorous. No indication for dormancy in this species was found in the literature and an immediate necessity of resting eggs is not discernable.

Calanus glacialis

Considered an inhabitant of the Arctic shelf (Jaschnov, 1970; Conover, 1988) *C. glacialis* displays a 2-year life-cycle (Tande et al., 1985; Kosobokova and Perzova, 1990; Conover and Sifred, 1993) that is well tuned to the strong seasonality of high latitude environments. In the White Sea spring spawned eggs developed to C4 and C5, the main overwintering stages, by the end of the first and the second season, respectively (Kosobokova and Perzova, 1990). A similar pattern had been suggested for the Barents Sea (Tande et al., 1985). Ontogenetic differences in lipid content (Table 16) hint at a major role of the copepodid stages 3 and 5 in dark season survival in this region. The species, which is primarily herbivorous (Conover and Siferd, 1993), accumulates large amounts of wax esters as a long-term energy reserve and the developmental arrest in late copepodids (Hirche, 1998) indicates dormancy.
C. glacialis has the capacity to survive extended periods of starvation and responds to sudden food exposure with rapid gonad development (Hirche, 1989). Nevertheless, a flexible strategy, which combines food-independent and food-dependent modes (Hirche and Kattner, 1993), allows *C. glacialis* to extend its reproductive period by spawning prior to the spring phytoplankton bloom using stored lipids (Smith, 1990; Hirche and Kattner, 1993), though egg production generally tends to track microalgal biomass (ice algae or phytoplankton) in the surface layer (Conover and Sifred, 1993; Madsen et al., 2001). This guarantees that first feeding nauplii occur after phytoplankton production has begun (Conover and Huntely, 1991; Ringuette et al., 2002). However, at least older stages are believed to be even capable of feeding on ice algae (Runge and Ingram, 1988).

Microcalanus pygmaeus

Unlike the 3 species discussed so far, *M. pygmaeus* is bipolar in distribution (Hopkins, 1985; Kurbjeweit, 1993; Auel and Hagen, 2002), while a relict population is known to exist in a Scottish sea loch (Marshall, 1949). At times

M. pygmaeus can be numerically dominant in both, Arctic (Auel and Hagen, 2002) and Antarctic (Schnack-Schiel and Mizdalski, 1994) waters. It lives on a variable diet (Voronina and Sukhanova, 1976) and correspondingly reproduction does not depend on phytoplankton abundance (Schnack-Schiel and Mizdalski, 1994). In fact the species' entire life cycle appears to be hardly affected by environmental variability. In the Weddell Sea, *M. pygmaeus* seems to remain active throughout the year (Pasternak and Schnack-Schiel, 2001). It grows all year round (Schnack-Schiel and Mizdalski, 1994), does not include diapause in its life cycle (Pasternak and Schnack-Schiel, 2001) and may even spawn irrespective of season, though two reproduction maxima are discernable, one in autumn and one in late winter (Kurbjeweit, 1993). *M. pygmaeus* is thought to complete its live cycle in one year (Zmijewska et al., 2000).

Pseudocalanus spp.

The remaining two calanoids found to be abundant in the Kara Sea plankton in autumn 1997, 1999 and 2000 (Deubel et al., 2003) are the congeners *P. major* and *P. acuspes*. Due to the lack of information from seasons other than autumn, little is known about their ecology in the study area.
However, a detailed description of the life cycle of *P. acuspes* is available from the Canadian Arctic (Conover and Siferd, 1993). Here, this species, which may be the most abundant and productive copepod in north polar latitudes (Conover and Huntley, 1991), can complete a generation in one year. It overwinters mainly as developmental stages C3-C5 and copepodids mature using sympagic production. Spawning of newly fertilized females begins in late spring and continues most of the summer, but its development rate is sufficiently rapid, so that both structural growth and enough lipid storage take place to permit overwintering of a range of developmental stages (Conover and Siferd, 1993).
Norrbin (1994, 1996) observed a similar pattern in populations from Northern Norway, where the older copepodite stages spend the winter in `active diapause´ (Elgmork, 1980), still feeding to some extent, but with considerably reduced metabolism. Wax esters accounted for 55-72% of total lipids in C4s and C5s (Norrbin et al., 1990) of this herbivore (Fortier et al., 2001). Interestingly, in Bedford Basin (Nova Scotia), where *P. acuspes* occurs as a relict form, most of the population rests through summer and autumn as C3-C5 and matures during the winter, ready to spawn around February (McLaren et al., 1989).
What is puzzling, is that Vinogradov et al. (2001) found nauplii of *P. acuspes* to occur near Dickson Island (Kara Sea) in February, although adult specimens were not detected.

Information on *P. major* originates largely from studies performed in the Laptev Sea, where it was among the 3 most common copepod species in the summer of 1993 and the autumn of 1995 (Kosobokova et al., 1998; Lischka et al., 2001). In late winter (March, April), it made up less than 0.5-2.0% of the total density of populations, but 9-42% of total biomass. At that time of the year the population consisted predominantly of females in copepodite stages 5 and 6 (Abramova, 1996). Though Timofeev (1998) concluded that its maximal abundance is linked

to salinities between 17-20 psu, Vinogradov et al. (1995) found *P. major* to be missing from samples from the Yenisei estuary only if surface salinity was less than 0.9 psu. The species was describes as herbivorous by Hanssen (1997), but it was also observed to feed on river detritus input in coastal waters of the Kara Sea (Vinogradov et al., 1995).

Less frequent species

Physiological abilities and nutritional requirements similar to those discussed above for the six most common calanoids in the Kara Sea are also observable in several of the less frequent copepod species (Tables 15-18). *Calanus finmarchicus*, *Calanus hyperboreus*, *Chiridius obtusifrons*, *Jaschnovia brevis*, *Metridia longa*, *Pareuchaeta glacialis* and *Pareuchaeta norvegica*, for example, store considerable amounts of lipids. Furthermore, numerous species are not exclusively herbivorous and some tolerate a large range of salinities. Finally, *Acartia longiremis*, *C. finmarchicus* and *C. hyperboreus* are well known to undergo diapause in the adult or in a late copepodid stage. Nevertheless, information on relevant autecological aspects is lacking for a number of species. How they cope with adverse environmental conditions during the winter, like reduced levels of primary production and shrinking areas of intermediate salinity, remains unclear.

Table 19: Duration of embryonic development at 0°C for some of the calanoid copepods that occur in the Kara Sea. Values were calculated using Belehrádek equations from the literature

Species	Equation	Embryonic development at 0°C in days	Reference
Calanus glacialis	$D=1067(T+12.97)^{-2.05}$	5.58	McLaren et al., 1988
Calanus finmarchicus	$D=691(T+10.6)^{-2.05}$	5.46	Corkett et al., 1986
Calanus hyperboreus	$D=1575(T+14.4)^{-2.05}$	6.65	Corkett et al., 1986
Metridia longa	$D=1099(T+15.1)^{-2.05}$	4.21	McLaren et al., 1969
Pseudocalanus acuspes	$D=1949(T+12.59)^{-2.05}$	10.83	McLaren et al., 1989

Although *Temora longicornis* and *Centropages hamatus* are known to produce resting eggs (Perzova, 1974; Marcus, 1989; Lindley, 1990; this study), none of the nauplii that hatched from the samples taken in the Kara Sea resembled their offspring. But the two species are not particularly abundant in the plankton and may even be restricted to coastal waters (Vinogradov et al., 1995; Fetzer et al., 2002), so that the eggs may have simply eluded sampling. Alternatively, the critical environmental challenges faced by *T. longicornis* and *C. hamatus* in polar waters might be fundamentally different from those faced by their congeners in temperate latitudes and thus the production of resting eggs does not necessarily have to be advantageous. But as the Kara Sea constitutes the north-eastern fringe of their respective areas of distribution (Halsband-Lenk et al., 2002), one would expect both species to depend on some sort of adaptation to environmental variability.

Unfortunately, data on instar duration of the early postembryonic stages is lacking for most of the Kara Sea calanoids. However, taking into account the low incubation temperature (0°C) and the period of time between successive screenings, the 10 nauplii found to hatch from the samples are assumed to be stage 1. As *Pareuchaeta glacialis* and *Pareuchaeta norvegica* are the only two among the 26 calanoids in the Kara Sea, which produce eggs large enough to house embryos that are 400 μm in length (Auel, 2004), 9 of 10 specimens are likely to belong to these two species. However, neither of them has ever been reported to produce resting eggs, and both usually carry their eggs attached to the genital opening rather than releasing them into the water column. On the other hand, Nicholls (1934) observed egg hatching in *P. norvegica*, even if they detached from the female. Whether the nauplii hatched from subitaneous rather than resting eggs is difficult to know. Embryonic development in some the major copepods from Arctic waters takes less than 3-5 weeks at 0°C (Table 19)(the time between collection of BP01-46 and hatching), but exact values for *Pareuchaeta* spp. are unknown.

CONCLUSIONS

The present study revealed profound differences between the two investigation areas. While calanoid copepod resting eggs were very abundant in the German Bight, they seemed to be entirely absent from the Kara Sea. Taking into account that alternative adaptations to extreme seasonality are widespread in copepod species from the Siberian Arctic, resting eggs are apparently either dispensable or inadequate as a safeguard against adverse environmental conditions in this region. Whether this holds true for polar waters in general, remains to be established.
In the German Bight, in contrast, nauplii hatched from sediment samples in large quantities indicating densities of more than one million viable eggs per square metre of seafloor. Only two species accounted for the vast majority of all specimens found. Based on the multitude of insights gained from the experiments performed and in consideration of the seasonality patterns of numerous biotic and abiotic parameters, it has been concluded that resting eggs play a crucial or even vital role in the life-cycle of these two species. In *Centropages hamatus*, which is absent from the plankton for several months in winter, they appear to guarantee year-to-year survival, whereas in the perennial *Temora longicornis* they may reduce mortality from predation in times when predators are abundant and improve the utilisation of the spring bloom. Thus, on the basis of the information currently available, resting eggs appear to be a safeguard against adverse environmental conditions in the German Bight.

But despite the fact that the present study yielded fundamental insights into calanoid copepod resting eggs in the German Bight, intensive research is still necessary to achieve a consolidated knowledge of the underlying mechanisms and true benefits. In the future it will be essential to

- determine whether the resting eggs produced by *T. longicornis* and *C. hamatus* are diapause or quiescent subitaneous eggs
- find out whether dormancy induction is governed by internal triggers (i.e. an internal clock) or environmental cues
- identify the cues that mediate or presage the deterioration of the environmental conditions and thus are responsible for the induction of resting egg production
- uncover environmental factors other than low food or high predator abundance that at times reach levels which may endanger the survival of the two species
- assess the seasonal cycle of hatching of resting eggs in the field
- specify the triggers and their respective threshold values responsible for the termination of dormancy

A comprehensive understanding of these issues will improve predictions on the effect of climate change on the population dynamics of *T. longicornis* and *C. hamatus* in the German Bight and may thereby facilitate the evaluation of the impact of global warming on plankton communities in this region. As resting eggs will have implications on plankton dynamics wherever they occur in the life-cycle of dominant calanoid copepod species, they should also be considered in plankton modelling.

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