

Contribution of walleye pollock eggs to the Gulf of Alaska food web in spring

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Comparison of eggs, larvae at hatch and zooplankton lengths in the Gulf of Alaska

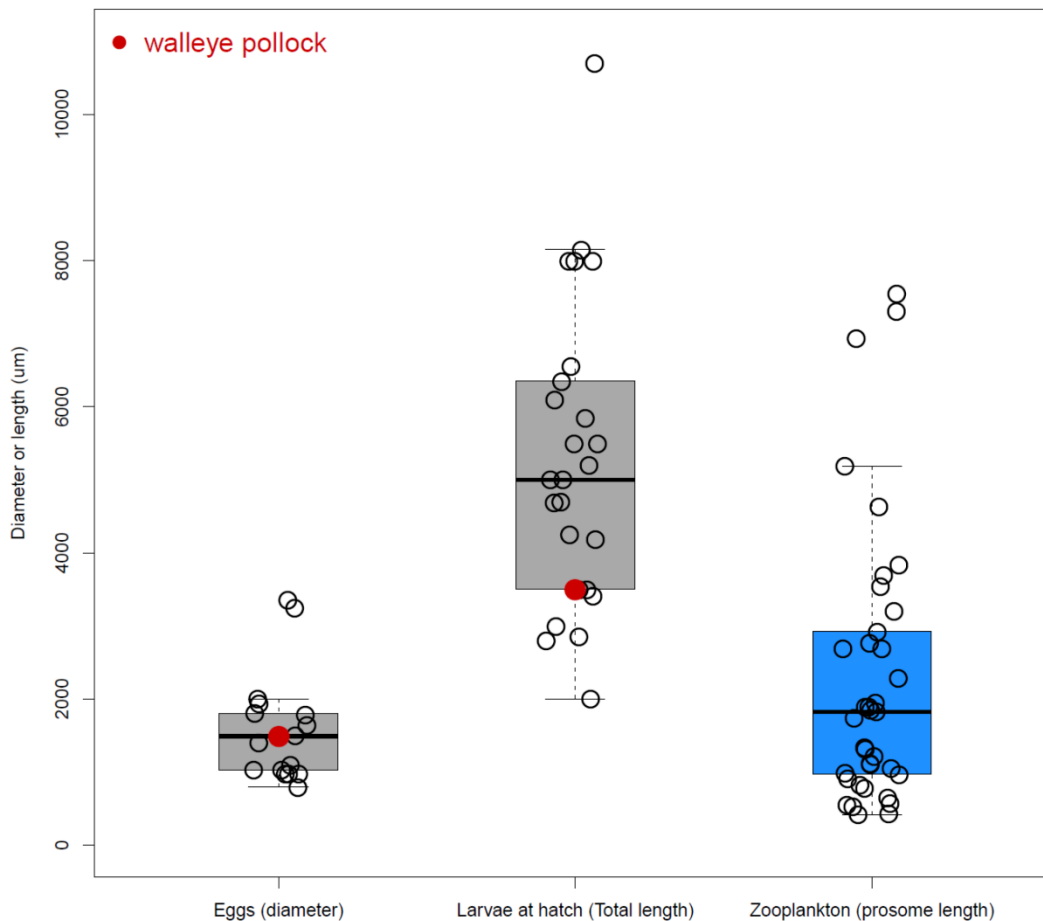


Fig. S1: Comparison of egg diameter and larval length at hatch of walleye pollock (red) and 26 common fish species in the Gulf of Alaska, and prosome lengths of the zooplankton species used in this study. Estimates for egg and larval length at hatch of the fish species were obtained from the Ichthyoplankton Information System [National Oceanic and Atmospheric Administration. (21 June 2019) [<http://access.afsc.noaa.gov/ichthyo/index.php>], and shown in Table S1. The data on zooplankton lengths are show in Table S3.

Table S1

Summary of mean and min-max ranges of egg diameter [μm] and larval hatch lengths from 26 common fish species in the Gulf of Alaska, used for Figure S1. Data was obtained from Ichthyoplankton Information System [National Oceanic and Atmospheric Administration. (21 June 2019) [<http://access.afsc.noaa.gov/ichthyo/index.php>]], and shown in Table S1, while the data on zooplankton lengths are show in Table S3.

Species	Egg diameter [μm]	Hatch size [μm]
<i>Gadus chalcogrammus</i>	1490 \pm 285	3500 \pm 500
<i>Hippoglossoides elassodon</i>	3250 \pm 500	6100 \pm 800
<i>Ammodytes personatus</i>	790 \pm 120	5500 \pm 1500
<i>Sebastes</i> spp.		4690 \pm 180
<i>Gadus macrocephalus</i>	1030 \pm 50	3500 \pm 500
<i>Lepidopsetta polyxystra</i>		4190 \pm 1240
<i>Platichthys stellatus</i>	1090 \pm 215	2000 \pm 100
<i>Lepidopsetta bilineata</i>	970 \pm 110	3500 \pm 500
<i>Atheresthes stomias</i>	1780 \pm 200	4250 \pm 550
<i>Isopsetta isolepis</i>	970 \pm 135	2800 \pm 100
<i>Anoplarchus</i> spp.	1400 \pm 105	6350 \pm 575
<i>Cryptacanthodes aleutensis</i>	1800 \pm 5	10700
<i>Anoplarchus insignis</i>		5200
<i>Leptoclinus maculatus</i>		8000
<i>Poroclinus rothrocki</i>		5500
<i>Liparis</i> spp.	1640 \pm 86	3410 \pm 63
<i>Hexagrammos decagrammus</i>		8000 \pm 1000
<i>Arteidius harringtoni</i>		3000
<i>Lumpenella longirostris</i>		8000
<i>Hippoglossus stenolepis</i>	3350 \pm 450	8150 \pm 350
<i>Liparis fucensis</i>	980	2850 \pm 50
<i>Glyptocephalus zachirus</i>	2000 \pm 205	5000
<i>Pleuronectes quadrituberculatus</i>	1940 \pm 275	5850
<i>Radulinus asprellus</i>		4700
<i>Mallotus villosus</i>	1030 \pm 135	5000 \pm 2000
<i>Clupea pallasii</i>	1500 \pm 205	6550 \pm 950

Model input data

Overview of the data resources used to model walleye pollock egg production. Furthermore, data ranges for each parameter are presented based on previous literature. The range of the literature values were used to assess the sensitivity of the egg production estimates (see Sensitivity analysis section).

The energy flux of a particular egg release is a function of the total number of eggs spawned, the proportion of eggs that do not survive the egg stage, and the energy content of an egg. Only non-surviving eggs are considered as those contain the energy made available to the ecosystem. The annual number of walleye pollock eggs spawned was calculated by combining female fecundity and female spawning stock biomass estimates from Shelikof Strait (Dorn et al. 2017, Table 1.10).

Fecundity

Fecundity data for walleye pollock measured in the Shelikof Strait were available from previous studies by Picquelle and Megrey (1993), Kim and Gunderson (1989) and Miller et al. (1986).

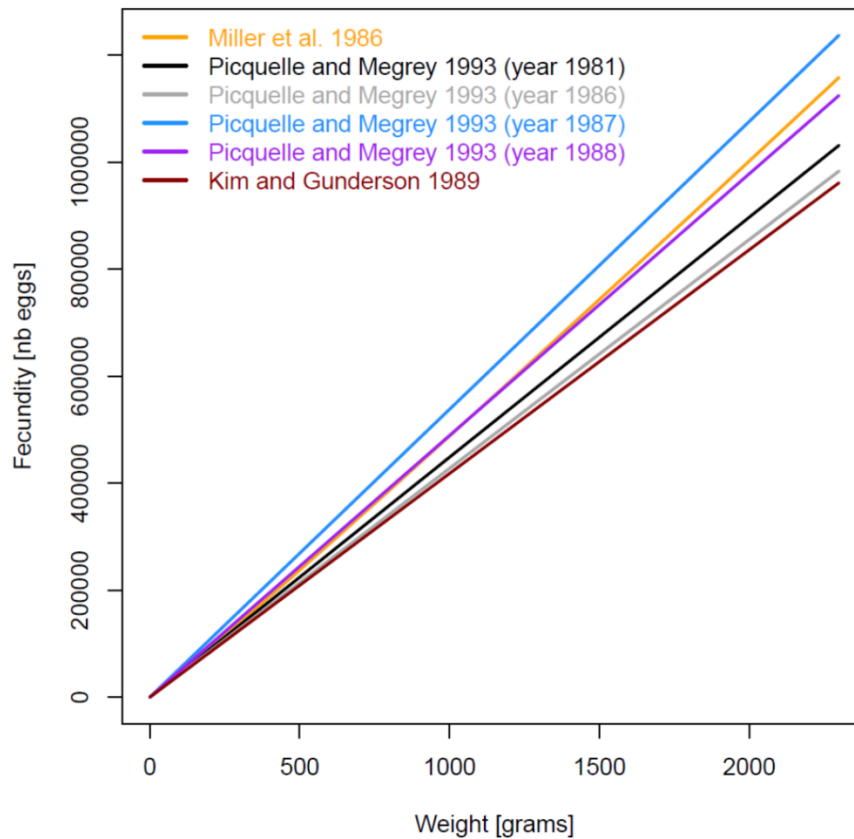


Fig. S2: Linear slopes from the empirical data on female weight and fecundity used to obtain the fecundity parameter in this study.

Estimates of female fecundity were 472.1 (range: 427.5-538.0) eggs/gram based on the previous empirical data (Table S2). The slope of the fecundity weight relationship for relevant years were used to get estimated number of eggs per gram female. The relationships by Picquelle and Megrey (1993) and Kim and Gunderson (1989) were both assumed linear in their analyses, while the best relationship in Miller et al. (1986), was best described as power relationship (Fig. S2). However, this relationship was only slightly non-linear and for estimates of fish less than 2000 grams (the case in our study), a linear regression fitted almost as well and provided essentially the same fecundity estimates.

Total number of eggs spawned

Annual female spawning stock biomass was estimated based on acoustic surveys in Shelikof Strait (1981 – 2017) taking into account the age structure of the population, proportion

mature-at-age, and assuming a 50% female to male ratio (Dorn et al. 2017, Stienessen et al. 2017). Our data on total egg numbers based on acoustic surveys compared well with previous estimates based on empirical egg data (Fig. S3, Kim & Gunderson 1989, Picquelle & Megrey 1993, Brodeur et al. 1996). In general our egg estimates were slightly lower than previous numbers of eggs released.

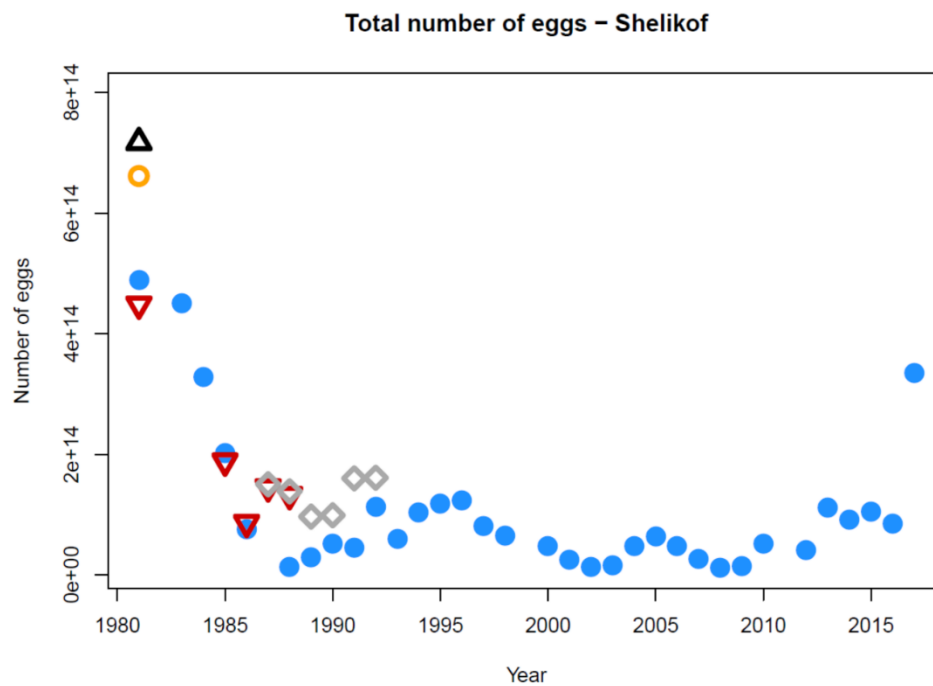


Fig. S3: Egg estimates of walleye pollock in the Shelikof Strait from Acoustic Surveys (blue) in the present study, compared to previous estimates by Picquelle & Megrey (red triangle, 1993), Brodeur et al. (grey diamond, 1996) and Kim and Gunderson (1989) from egg production (black triangle) and acoustic (orange circle) estimates.

Egg weights

Data on egg weights were available from Hinckley (1990) and Laurel et al. (2018). We used the mean value of 0.12 mg DW based on Hinckley (1990), who also provide the total range of egg weights as 0.097-0.139 mg DW based on estimates of 1319 walleye pollock eggs (Table S2). The values in Laurel et al. (2018), were similar with a mean 0.117 (0.101-0.125 mg DW) We did not include estimates of walleye pollock eggs from the Bering Sea as these

are consistently larger (~0.24 mgDW, Harris et al. 1986, Hinckley 1990) and would have resulted in overestimation of egg production. Egg size does not appear to change noticeably during development but is related to female size and condition (Harris et al. 1986).

Incubation time and mortalities

Incubation time was assumed to be 14 days though it can range from 12 to 16 days depending on temperature (Blood 1994). The area of Shelikof Strait was estimated as 17586 km² with an uncertainty of this estimate assumed to be ±5%. Mortality estimates vary from 0.06 to 0.30 (Picquelle & Megrey 1993, Brodeur et al. 1996). Similarly, Kim and Gunderson (1989) estimated within year mortalities of 0.1 to 0.4 for walleye pollock eggs.

Summary table of model inputs

Table S2: Summary of model input parameters (mean values) and ranges used for the sensitivity analyses. % range refer to the range of min max relative to the average value for each parameter

Parameter	Unit	Mean	Min	Max	% range	Reference
Fecundity	Eggs/gram female	472.1	427.5	537.9	91-114	Picquelle & Megrey 1993, Miller et al. 1986, Kim & Gunderson 1989
Egg weight	mg Dry weight	0.12	0.097	0.13	81-116	Hinckley et al. 1990, Laurel et al. 2018
Shelikof Area	km ²	17586	16707	18465	95-105	ArcGIS v.10.4.1 ^a
Egg incubation time	days	14	12	16	86-114	Blood et al. 1994
Daily egg mortality	day ⁻¹	0.2	0.06	0.3	30-150	Brodeur et al. 1996, Picquelle & Megrey 1993 ^b
Dry-weight : Carbon	% mgDW to C	35.3	29.2	39.6	83-112	Harris et al. 1986

^aArea range assumed ± 5%

^bKim & Gunderson 1989 Within year mortality vary from 0.1 to 0.4

Sensitivity analyses

Upscaling empirically measured processes to the ecosystem level is well known to carry substantial uncertainty. Based on the parameter ranges in Table S2 we assessed the sensitivity of our egg production calculations. In this simulation we used the mean egg number 1.06e+14 based on the mean female spawning stock biomass from the annual surveys, and the average fecundity, and systematically varied each parameter across the range of the empirically measured values (Fig. S4).

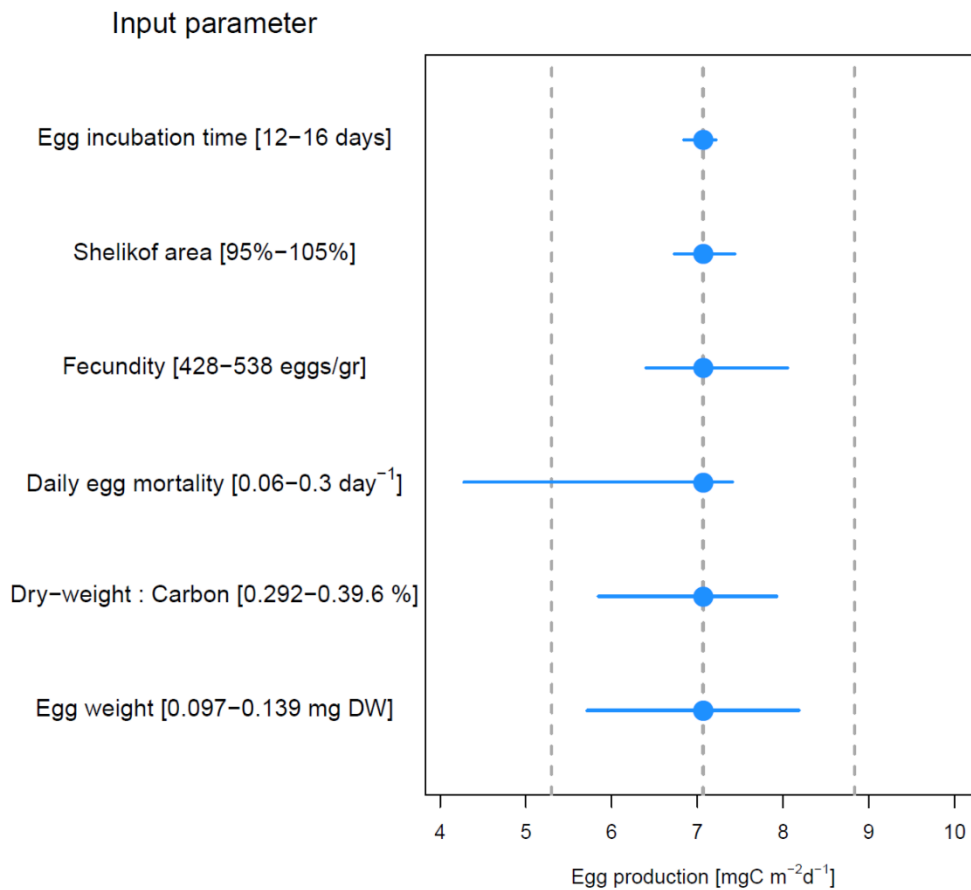


Fig. S4: Overview of sensitivity analysis with a fixed number of eggs released where each parameter was individually varied systematically over the range of that empirical data. Vertical grey dotted bars denote $\pm 25\%$ of the mean egg production estimate. Min-Max range denotes how much variation was present in the ranges of the empirical data.

Mortality variation was the biggest source of uncertainty. Note that the influence of mortality was skewed in that a low mortality rate, and thus higher survival to the larval phase, lowered egg production. However, an instantaneous daily mortality of 0.06 is unusually low and only occurred in a single year (Picquelle & Megrey 1993). Any mortality rate above 0.15 results in low survival and thus large energy contribution to the food web. For example, if the assumed daily mortality of 0.2 with an average incubation time of 14 days results in a total mortality of 93% of the spawned eggs. Overall, no individual parameter influenced total egg production by more than 25% of initial values except at the unusually low mortality rate (Fig. S4, grey bars denote $\pm 25\%$).

Zooplankton production

We calculated daily zooplankton production rates for each copepod taxon based on previously established relationships. Daily secondary production rates for each copepod taxon and stage were calculated as $P = NWg$, where P was production ($\text{mg C m}^{-3}\text{day}^{-1}$), N was the number of individuals (m^{-3}), W was the individual biomass (mg m^{-3}), and g was the growth rate (day^{-1}). Number of individuals (N) was measured using counts from net tows (see Kimmel et al. 2018 for net tow details) and has been measured annually between 1990-2011, and in 2013, 2015 and 2017 in the Shelikof Strait. Biomass (W) was estimated using literature values of dry weight for each taxon and stage (Supplementary Table S3). Biomass was converted to carbon (C) assuming 40% of Dry Weight (Båmstedt 1986). Growth rate (g) was estimated using equations from the literature (Table S4).

Table S3. Prosome length (μm), dry weight (μg) and egg mass ($\mu\text{g C}$) of copepod species. Prosome length and dry weight source is indicated. Egg masses are from Huntley and Lopez (1992).

Species	Stage	Prosome Length (μm)	Dry Weight (μg)	Source	Egg mass ($\mu\text{g C}$)
<i>Acartia</i> spp.	CVI	1110 ¹	11	Size: http://www.arcodiv.org/watercolumn/copepod/Oithona_similis.htm 1 Weight: (Peterson et al. 1991)	0.035
<i>Calanus marshallae</i>	CII	966 ± 22.56	4.27 ± 0.87	(Liu & Hopcroft 2007)	0.188
	CIII	1331 ± 60.67	10.19 ± 5.09		
	CIV	1824 ± 99.43	38.06 ± 12.84		
	CV	2684 ± 175.27	236.22 ± 97.70		
	CVI	2923 ± 83.30	248.85 ± 60.12		
<i>Calanus pacificus</i>	CV	1950 ± 120	71 ± 16	(Ueda et al. 2008)	0.25
	CVI ¹	2290 ± 90	118 ± 160		
<i>Eucalanus bungii</i>	CI	1220 ± 70	18 ± 6	(Ueda et al. 2008)	0.204
	CII	1890 ± 80	24 ± 4		
	CIII	2770 ± 130	35 ± 12		
	CIV ¹	3690 ± 200	68 ± 13		
	CV ¹	5190 ± 330	221 ± 71		

	CVI ¹	6940 ± 400	535 ± 143		
<i>Metridia pacifica</i>	CI	428 ± 16.26	0.92 ± 0.27	(Liu & Hopcroft 2006)	0.3
	CII	568 ± 19.27	2.25 ± 0.38		
	CIII	779 ± 36.22	5.37 ± 0.75		
	CIV	912 ± 126.71	9.02 ± 3.85		
	CV	1311 ± 134.52	35.76 ± 13.08		
	CVI	1851 ± 133.22	112.33 ± 30.00		
<i>Neocalanus cristatus</i>	CII	1740 ± 120	30 ± 7	(Ueda et al. 2008)	1.39
	CIII	3200 ± 200	79 ± 35		
	CIV	4630 ± 200	250 ± 138		
	CV	7310 ± 190	1983 ± 987		
	CVI ¹	7550 ± 290 ¹	4170 ± 1244		
<i>Neocalanus</i> spp.	CII ³	1120 ± 60	20 ± 6	(Ueda et al. 2008)	0.42
	CIII	1887 ± 159.29	42.57 ± 23.19		
	CIV	2685 ± 218.27	169.66 ± 72.70		
	CV	3540 ± 301.48	562.57 ± 319.16		
	CVI	3840 ± 130 ¹	791 ± 232 ²		
<i>Oithona</i> spp.	CVI	550 ¹	0.9	Size: http://www.arcodiv.org/watercolumn/copepod/Oithona_similis.htm ↓ Weight: (Vidal & Smith 1986)	0.002
<i>Pseudocalanus</i> spp.	CI	415 ± 44.60	0.70 ± 0.18	(Liu & Hopcroft 2008)	0.05
	CII	522 ± 37.7	1.39 ± 0.68		
	CIII	652 ± 76.47	2.36 ± 1.05		
	CIV	821 ± 110.28	5.69 ± 2.11		
	CV	981 ± 176.18	8.46 ± 3.68		
	CVI	1052 ± 137.90	10.21 ± 4.83		

¹ Only adult female size reported in the study

² Adult female *Neocalanus flemingeri*

³ *Neocalanus plumchrus*

Table S4. Growth rate equations and sources. T is temperature (°C) and BW (body weight, μg C individual⁻¹) (Hirst & Lampitt 1998).

Equation	Taxa
$\log_{10}(g) = -0.6516 - 0.5244(\log_{10}(BW))$	<i>Acartia</i> spp. CVI, <i>Calanus</i> spp. CVI, <i>C. pacificus</i> CVI, <i>E. bungii</i> CV, <i>M. pacifica</i> CVI, <i>N. cristatus</i> CVI, <i>Neocalanus</i> spp. CVI
$\log_{10}(g) = 0.0111T - 0.2917(\log_{10}(BW)) - 0.6447$	<i>Calanus</i> spp. CII-CV, <i>C. pacificus</i> CV, <i>E. bungii</i> CI-CV, <i>M. pacifica</i> CIV-CV, <i>N. cristatus</i> CII-CV, <i>Neocalanus</i> spp. CII-CV
$\log_{10}(g) = -1.7726 + 0.0385T$	<i>Oithona</i> spp., <i>Pseudocalanus</i> spp. CVI
$\log_{10}(g) = -1.4647 + 0.0358T$	<i>Pseudocalanus</i> CI-CV

Sensitivity analysis of temperature effect on zooplankton production

To assess the influence of temperature on copepod production rates we performed a sensitivity analysis for the production of each species over the range of temperatures experienced in the Shelikof Strait in April or May. We restricted the sensitivity analysis to temperature as a full analysis of copepod production models is beyond the scope of the current study and have been dealt with elsewhere (Huntley & Lopez 1992, Hirst & Sheader 1997, Hirst & Lampitt 1998, Hirst & Bunker 2003). The purpose of this analysis was to assess the influence of temperature on production rates of each copepod species or stage in the Gulf of Alaska. For each species and stage, we first calculated the long term mean in abundance for data collected in either April or May. Next we systematically varied temperature across realistic values observed in the Gulf of Alaska in spring. Specifically, the temperature variation in April across all years ranged for April 1.7°C to 6.9 °C with a mean of 4.3°C. Temperature for May varied from 3.6°C in the coldest year, to 7.0°C in the warmest, with a mean of 5.2°C. These values provided the boundaries for our sensitivity analysis. Copepod production rates were then calculated following the same equations used to calculate annual zooplankton production for April and May (Table S4), see section “Zooplankton production”. Overall the influence of temperature on production rates was low for all species (Fig. S5, Fig. S6). Only *Oithona* sp., and *pseudocalanus* sp. production estimates varied substantially with changing temperatures, however the biomass contribution of these copepods to overall production in the Gulf of Alaska was minimal. The modest influence from variation in temperature is in line with previous studies that showed that biomass is the primary driver of variation in copepod production rates and that growth rates have less variability at lower temperatures ranges (Huntley & Lopez 1992) such as the ranges experienced in spring in the Gulf of Alaska.

April zooplankton sensitivity

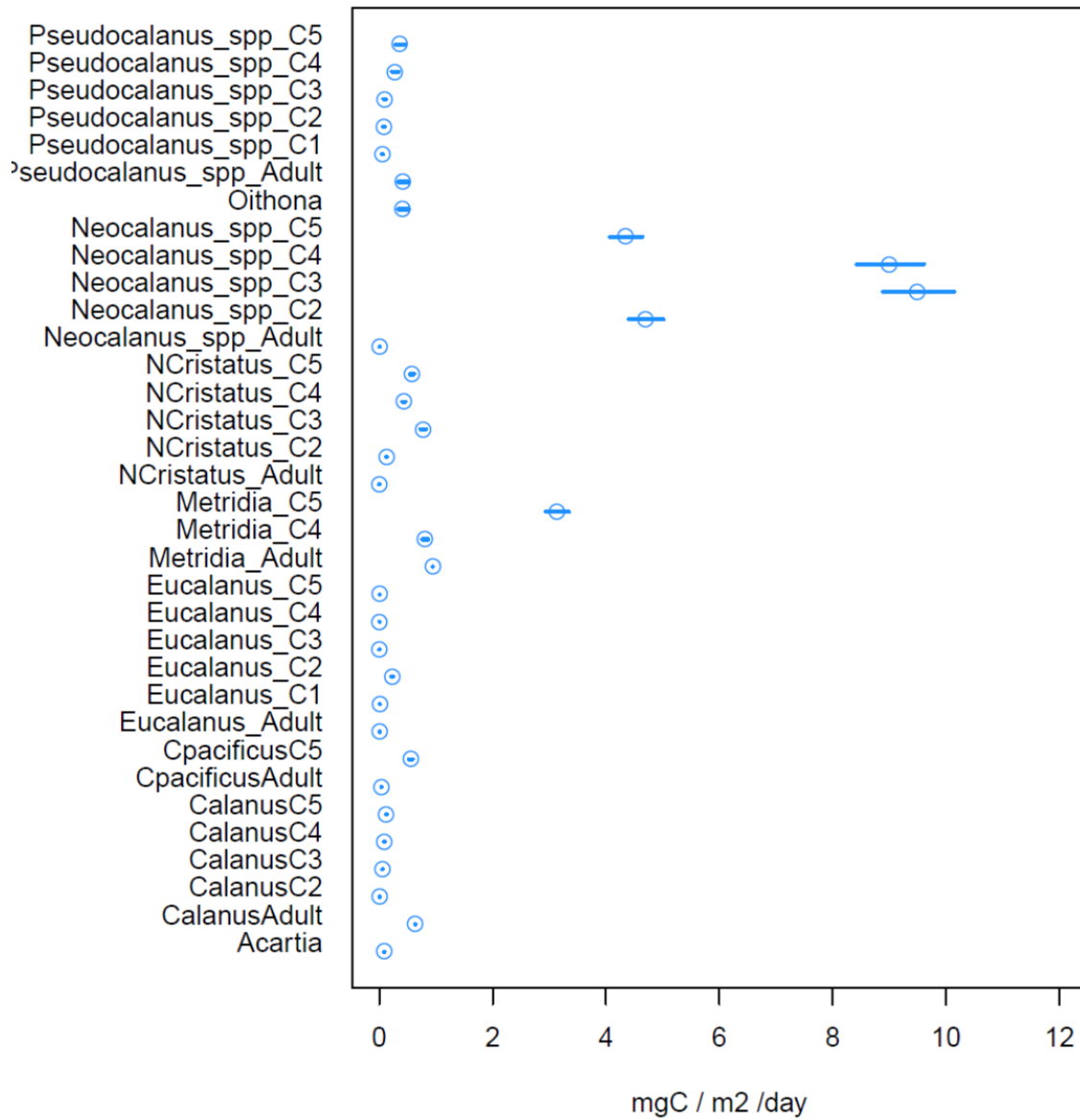


Fig. S5: Overview of the influence of temperature on zooplankton production rates in April. Circle denotes production estimate at mean temperature for each species. Error bar denotes production at minimum and maximum temperature for each species.

May zooplankton sensitivity

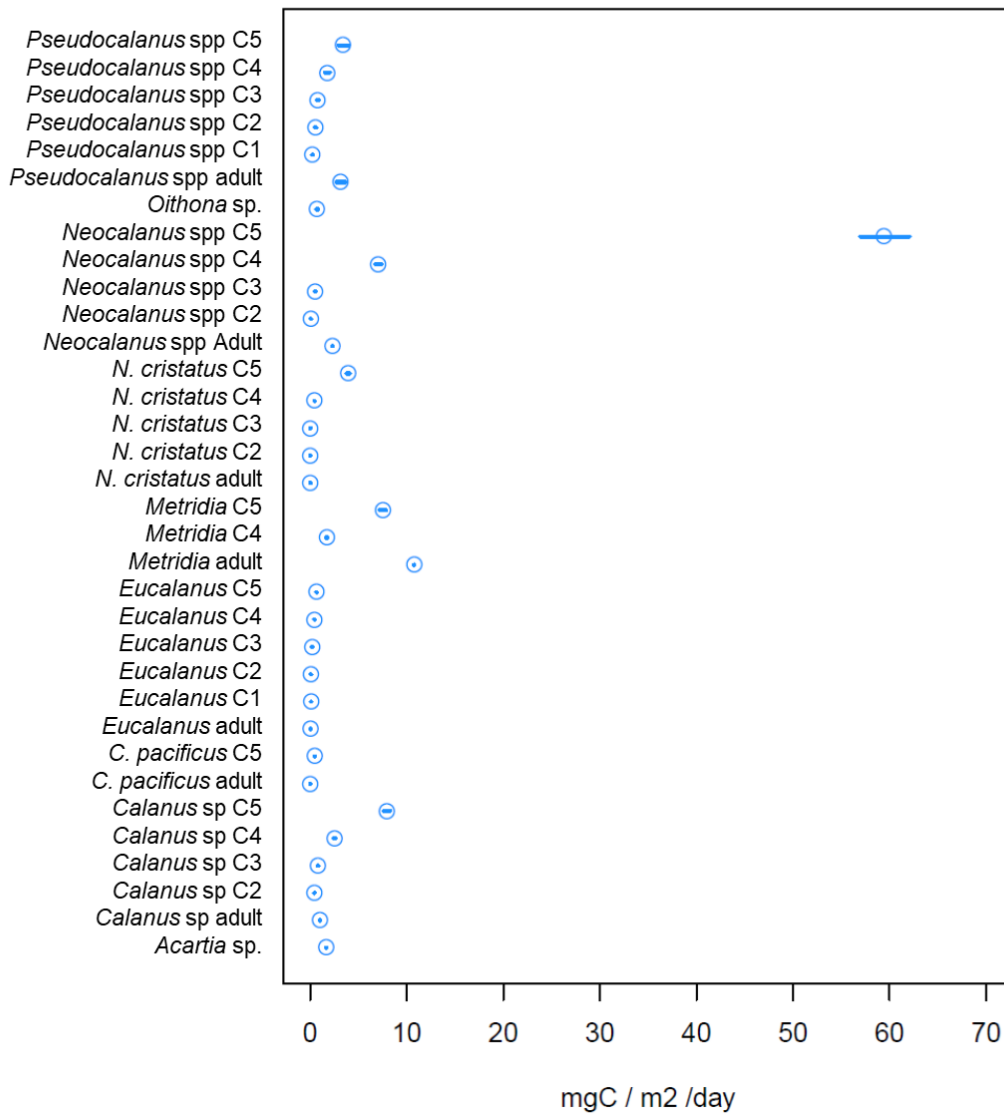


Fig. S6: Overview of the influence of temperature on zooplankton production rates in May. Circle denotes production estimate at mean temperature for each species. Error bar denotes production at minimum and maximum temperature for each species.

Zooplankton seasonal peak abundance *Neocalanus* CV stages

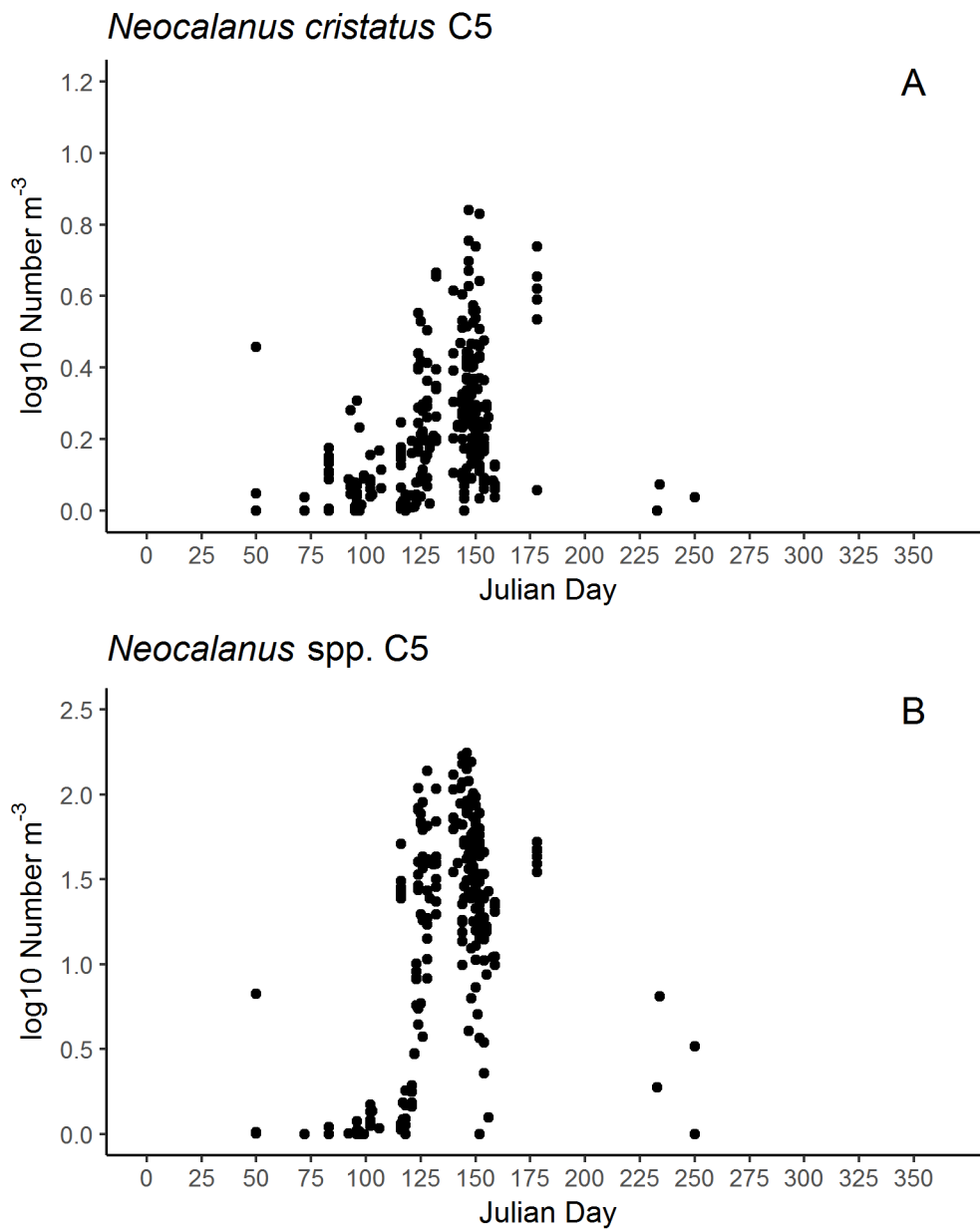


Fig. S7: Timing in Julian days of peak abundance (log₁₀ number m⁻³) of A) *Neocalanus cristatus* and B) *Neocalanus* spp. based on empirical long-term measurements in spring during the years 1990-2011, 2013, 2015 and 2017 from line 8 Shelikof Strait.

Phenology of Net Primary Production

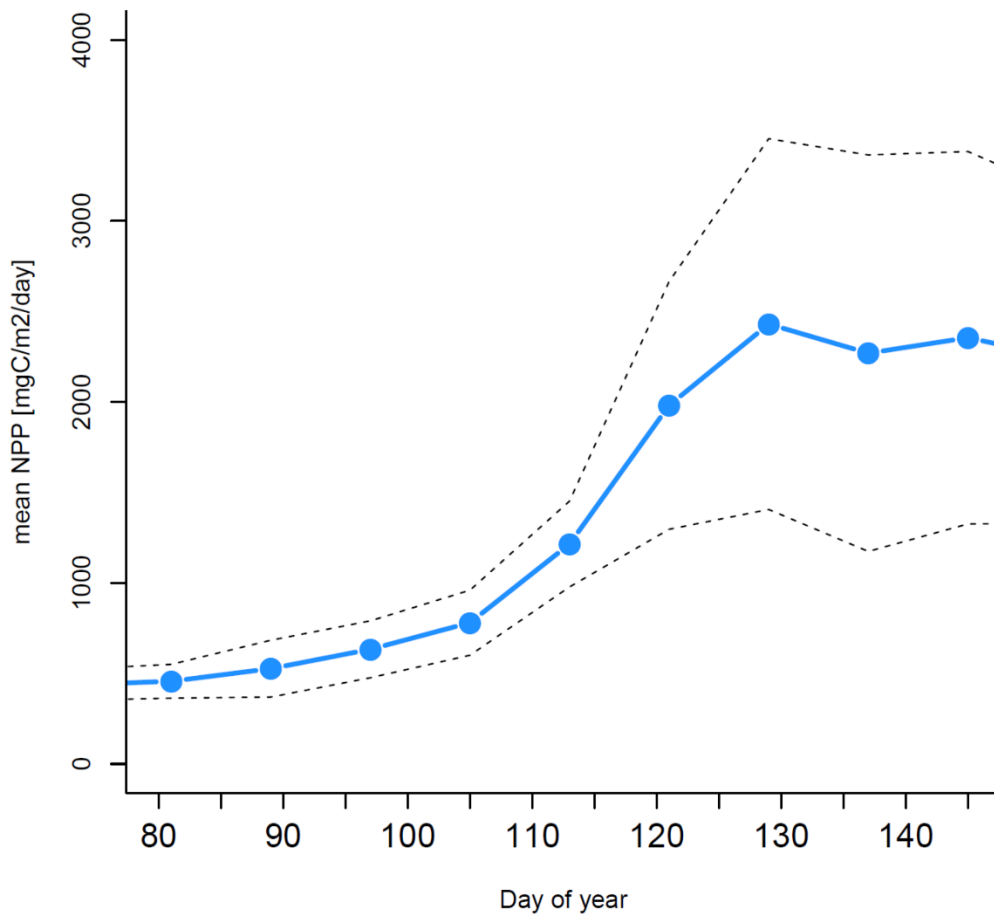


Fig. S8: Phenology of the mean (blue) and Standard deviation (black dotted lines) of primary production from the Shelikof Strait (area 55-60°N and 150-160°W) estimated from MODIS data and calculated following a Vertically Generalized Production Model, based on 8-day averaged MODIS surface chlorophyll concentrations, sea surface temperature and cloud-corrected PAR, and presented as $\text{mgC m}^{-2} \text{d}^{-1}$ (Behrenfeld & Falkowski 1997) for the years 2003-2017.

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