



FEATURE ARTICLE

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

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ABSTRACT: Pulsed resources are prevalent phenomena in nature that can have disproportionately large and long-lasting effects on ecosystem production. Many fishes aggregate and spawn at high densities and release large amounts of resources to the environment in the form of eggs. These spawning events can provide pulsed dietary resources for a range of consumers; however, this is still an understudied topic particularly in the Gulf of Alaska food web. Here we assessed the magnitude and timing of eggs from walleye pollock *Gadus chalcogrammus* and their energy contribution to a highly productive ecosystem in Shelikof Strait, Gulf of Alaska. Our results show that aggregate spawning events of walleye pollock contribute considerably to the resource fluxes of this coastal food web in spring. Walleye pollock egg resources constituted on average 18.9% of April and 5.8% of May copepod production in the Shelikof Strait marine food web. In addition, the resource contributions from eggs appear 1 to 3 wk earlier than the spring peak rates of zooplankton production and thus occur at a time when equivalent dietary resources are still limited for many consumers. Our analysis showed that spawning events of walleye pollock provide an important pulsed resource subsidy in the Gulf of Alaska ecosystem.

KEY WORDS: Egg boon · Trophic transfer · Gulf of Alaska · Ecosystem production · Fishes · Zooplankton · Walleye pollock · *Gadus chalcogrammus*



Walleye pollock, *Gadus chalcogrammus*, egg boons provide energy to the Gulf of Alaska food web.

Photo: Alison L. Deary, NOAA Fisheries

1. INTRODUCTION

Pulsed resources, i.e. intense but brief periods of high resource availability (Yang et al. 2008), are prevalent phenomena in nature (Jentsch & White 2019). Despite being punctuated events, resource pulses often have disproportionately large and long-lasting effects on ecosystem production (Holt 2008, Yang et al. 2008, Lewandowska et al. 2015). In mid-to high-latitude ecosystems, seasonality is a major

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forcing factor, and consequently, pulsed resource subsidies often vary tremendously in time and space (Yang & Naeem 2008) and quality and quantity (Richardson & Wipfli 2016). Yet, the timing and magnitude of resource pulses are sensitive to environmental fluctuations and are organism specific, something that in turn influences consumer growth, survival and reproduction (Chmura et al. 2019). In fact, differential shifts in consumer–resource phenologies are common (Kharouba et al. 2018) and can lead to greater consumer–resource synchrony or alternatively trophic mismatches (Cushing 1990, Neuheimer et al. 2018), which can have widespread impacts on food web dynamics and production (Holt 2008). The importance of a resource pulse ultimately depends on its magnitude and timing relative to the consumer, and to what extent it occurs when equivalent resources are limiting (Richardson & Wipfli 2016).

Many fish species aggregate and spawn at high densities, releasing large amounts of energy and nutrients to the environment (Barneche et al. 2018). In addition to primary- and secondary-derived production, pulsed resources released during spawning events, also referred to as egg boons (Fuiman et al. 2015), can provide important resource subsidies in marine food webs (Polis et al. 1997). For example, Atlantic cod *Gadus morhua* (Kjesbu et al. 1991), Pacific herring *Clupea pallasii* (Fox et al. 2014), Atlantic herring *C. harengus* (Varpe et al. 2005) and tropical reef fishes (Nemeth 2009) all aggregate in high numbers during spawning and contribute resources to marine food webs in the form of eggs. Similarly, salmon eggs and other nutritional components, such as milt and adult carcasses, provide important subsidies for both fishes and mammals in freshwater ecosystems (Armstrong et al. 2016 and references therein). For both salmon and Pacific herring, spawn timing varies across spatial gradients, and thus several successive resource pulses, i.e. resource waves (Armstrong et al. 2016), provide extended subsidies for consumers that migrate across the landscape or seascape (Lok et al. 2012).

Fish eggs have high energy content but are vulnerable to predation by a range of small to large predators due to their small sizes (Bunn et al. 2000). A range of consumers, including pelagic fishes, invertebrates, detritivores and decomposers (Brodeur & Merati 1993, Bunn et al. 2000, Kuribayashi et al. 2017) all forage on fish eggs, while higher trophic level consumers also prey on the adults during spawning aggregations (Nemeth 2009, van Deurs et al. 2016). Fish eggs, through maternal inputs, are rich in essential

long-chained polyunsaturated fatty acids (Laurel et al. 2010, Fuiman 2018), which can be a limiting resource in both freshwater (Brett & Muller Navarra 1997) and marine systems (Litzow et al. 2006). Despite their significance in terms of providing resource pulses for fueling ecosystem production (Erisman et al. 2017, Šmejkal et al. 2017), the importance of egg boons is still an understudied topic.

The Gulf of Alaska is a highly productive boreal ecosystem. Peaks in primary and secondary production commonly occur in early to mid-May (Waite & Mueter 2013) and provide resources to support large numbers of higher trophic level species (Adams et al. 2007). Due to their high abundance, walleye pollock *Gadus chalcogrammus* are a key trophic linkage in the Gulf of Alaska food web as both predators and prey (Springer 1992). Walleye pollock are a primary prey species for seabirds, marine mammals and other adult fishes (Adams et al. 2007), whereas this species in turn preys on many invertebrates, particularly euphausiids (Urban 2012), and adult and younger life stages of other fishes (Adams et al. 2007). Walleye pollock also support a large commercial fishery, and have experienced large annual to decadal scale oscillations in abundance (Dorn et al. 2017), with consequent impacts on spawning stock biomass and recruitment (Ciannelli et al. 2005). In the Gulf of Alaska, walleye pollock aggregate in a relatively restricted area and spawn at depth (150–250 m) at high densities in early spring (e.g. estimated female spawning stock biomass in 2017 was 3.5×10^5 t; Dorn et al. 2017), primarily in Shelikof Strait (Kendall et al. 1996). Walleye pollock eggs are primarily found at depths between 150 and 250 m but rise during development, while later in spring eggs also appear closer to the surface (Kendall 1994). As is common for marine fishes (Llopiz et al. 2014), mortality of walleye pollock eggs and larvae is high (Brodeur et al. 1996). Previous studies on walleye pollock egg and larval ecology have focused on survival in relation to recruitment dynamics; however, no study has assessed the fate of the majority of walleye pollock eggs that do not survive (commonly >95%, Brodeur et al. 1996). A range of other species, such as gammarid amphipods, euphausiids and fishes, forage on walleye pollock eggs and larvae (Bailey et al. 1993, Brodeur & Merati 1993). Therefore, walleye pollock eggs may provide an important resource subsidy to the Gulf of Alaska food web.

Here, we combine modeling with extensive empirical data on walleye pollock from Shelikof Strait, and for the first time assess the magnitude and timing of eggs as a resource in this productive coastal ecosys-

tem. We contrast the walleye pollock egg boons to zooplankton production based on the assumption that consumers that prey on zooplankton also forage on walleye pollock eggs and larvae which are of similar size (Brodeur et al. 1991, Fuiman et al. 2015; see Fig. S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m632p001_supp.pdf). Larval survival is critically dependent on the timing of available zooplankton resources during first feeding (Hjort 1914). Walleye pollock spawn in early to mid-April (Matarese et al. 2003) and have egg and endogenous larval phases of approximately 14 ± 2 d (Hinckley 1990) and 7 ± 2 d (Porter & Theilacker 1999), respectively, thus first feeding larvae require adequate resources around 3 wk after spawning. If spawning occurs so that larvae hatch when food availability is high (Platt et al. 2003, Burrow et al. 2011), the eggs will be spawned around 3 wk in advance, and potentially before the initiation of the main pulse of phytoplankton and zooplankton production. Accordingly, we hypothesized that: (1) Walleye pollock egg boons contribute significant resources to the Shelikof Strait ecosystem on the same order of magnitude as spring zooplankton production. (2) The timing of walleye pollock egg boons precedes the rapid increase in zooplankton production in spring, providing a resource subsidy for consumers during a time period when equivalent resources such as zooplankton prey are still limited.

2. MATERIALS AND METHODS

2.1. Approach

We used data from long-term monitoring efforts by the Alaska Fisheries Science Center Ecosystems and Fisheries-Oceanography Coordinated Investigations program (EcoFOCI; Kendall et al. 1996) and previously published empirical values to evaluate the magnitude and timing of walleye pollock egg boons in Shelikof Strait, Gulf of Alaska (Fig. 1). To evaluate our Hypothesis 1, first we calculated the total and average daily energetic contribution of eggs to the marine food web in spring. Second, we estimated primary and zooplankton production rates during the same period. Third, we modeled annual changes in egg boon phenology by coupling our egg production calculations with previous estimates of walleye pollock spawn timing (Rogers & Dougherty 2019). To assess the timing hypothesis, we contrasted egg boon phenology to zooplankton development times of *Neocalanus* copepodite Stage V (CV) stages, which are the species that

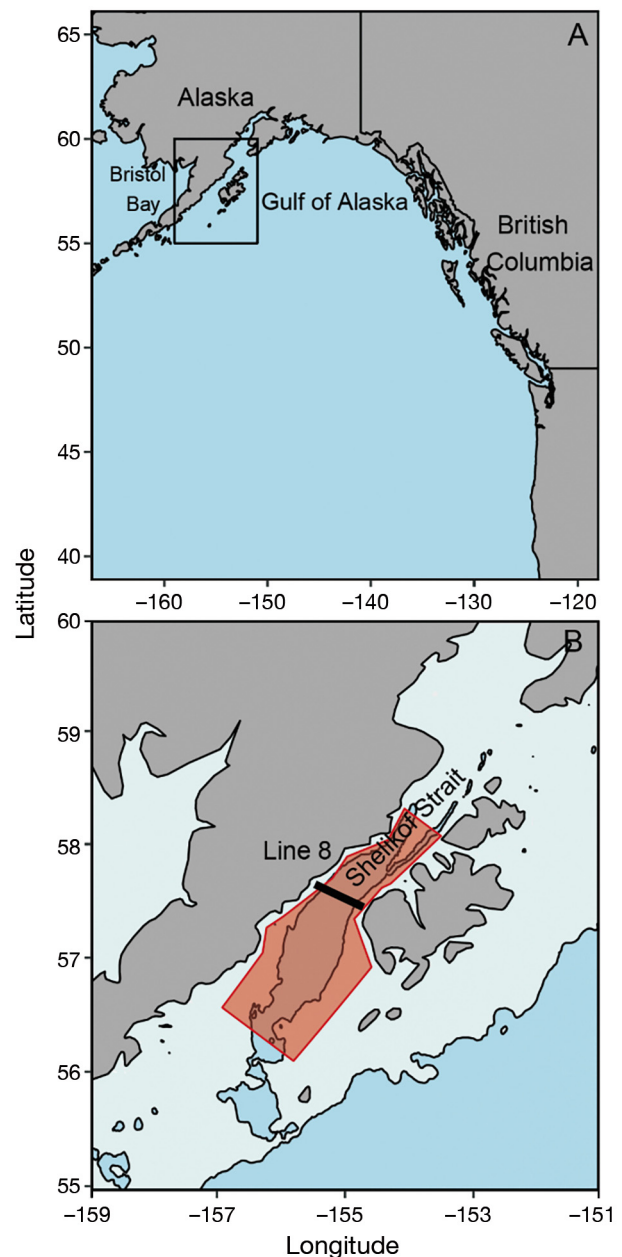


Fig. 1. Overview of (A) the Gulf of Alaska area and (B) Shelikof Strait, showing the area used for the egg boon estimates (red shaded area) and Line 8 (solid line), the collection area of the zooplankton data. Bathymetry line in (B) denotes the 200 m depth contour

have the highest biomass and represent the majority of zooplankton production in spring. All egg and plankton estimates were calculated as rates of production in $\text{mgC m}^{-2} \text{d}^{-1}$. Production estimates were considered informative, as they provide the rate of energy (often expressed in carbon units) generated over time, while biomass estimates give a static measure of the current standing stock (Jenkins 2015).

2.2. Calculation of egg resources in Shelikof Strait

Total egg production from spawning was calculated based on (1) the total number of eggs spawned, (2) the proportion of eggs that do not survive the egg stage, which is a function of egg mortality and incubation time, and (3) the energy content of an egg. Only non-surviving eggs were considered, as those are the resources made available to the ecosystem.

The annual number of walleye pollock eggs spawned was calculated by combining female spawning stock biomass estimates (Dorn et al. 2017) and female fecundity from the Shelikof Strait. 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, the proportion mature-at-age, and assuming a 50% female-to-male ratio (Stienessen et al. 2017). An average value of female fecundity of 472.1 eggs g^{-1} body weight (range: 427.5–538.0) was used based on previous studies by Picquelle & Megrey (1993), Kim & Gunderson (1989) and Miller et al. (1986) (Table S2, Fig. S2).

Based on the total number of eggs spawned (N_{eggs}), the total number of non-surviving eggs was calculated as:

$$\text{Non-surviving eggs} = N_{\text{eggs}} \times (1 - e^{-M \times IT}) \quad (1)$$

where M is the daily mortality rate and IT is the incubation time. Daily egg mortality estimates vary from 0.06 to 0.30 d^{-1} (Picquelle & Megrey 1993, Brodeur et al. 1996); we used a value of 0.2 (Table S2). Incubation time was on average 14 d, although it can range from 12 to 16 d depending on temperature (Blood 1994).

Based on the number of non-surviving eggs, average daily egg production ($\text{mgC m}^{-2} \text{d}^{-1}$) during the spawning season in the Shelikof Strait was calculated as:

$$\text{Egg production} = \sum \frac{\text{Non surviving eggs} \times W_{\text{egg}} \times C_{\text{conv}}}{A \times SD} \quad (2)$$

where W_{egg} is the egg dry weight (DW, in mg). For the egg weight, we used a mean value of 0.12 mg DW based on Hinckley (1990), who also provided the total range of egg weights as 0.097–0.139 mg DW based on estimates from 1319 walleye pollock eggs (Table S2). Similar values with a mean of 0.117 (0.101–0.125 mg DW) were estimated by Laurel et al. (2018). C_{conv} is the DW to carbon ratio of 35.3% (range 29.2–39.6%; Harris et al. 1986). A is the area of the Shelikof Strait, which was estimated as 17 586 km^2 , using ArcGIS v.10.4.1 (Fig. 1). SD is the spawn duration, here assumed to be 34 d based on the

median duration of the spawning season previously estimated for the walleye pollock population (Rogers & Dougherty 2019). A median spawn time duration of 34 d was used to allow for comparison between the total spring egg production estimates and the April and May zooplankton production rates where we did not have specific data on biomass peaks and phenology. Egg production estimates were calculated for each year for the time period 1981–2017 (excluding the years 1982, 1987, 1999 and 2011 when data were not available). Additional information about the input data and associated references are available in the Supplement. For the primary egg production model described above, we used average literature values for each input parameter, while the ranges of each parameter were used to assess uncertainties of our estimates (Table S2). 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 1.06×10^{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 empirically measured values. A similar sensitivity analysis was performed for zooplankton production as it relates to temperature (Figs. S5 & S6). All analyses were conducted using R (R Core Team 2018).

2.3. Phytoplankton and zooplankton production estimates

To compare the relative importance of the egg boons in terms of magnitude and timing, net primary production and April and May zooplankton production were estimated. Net primary production for the Shelikof Strait (areas 55–60°N and 150–160°W) was estimated from MODIS data (www.science.oregonstate.edu/ocean.productivity/standard.product.php) and calculated following a vertically generalized production model, based on 8 d averaged MODIS surface chlorophyll concentrations, sea surface temperature and cloud-corrected photosynthetically active radiation, and presented as $\text{mgC m}^{-2} \text{d}^{-1}$ (Behrenfeld & Falkowski 1997).

We calculated daily production rates for each copepod taxon and stage as $P = NWg$, where P is production ($\mu\text{gC m}^{-3} \text{d}^{-1}$), N is the number of individuals (m^{-3}), W is the individual biomass (μg), and g is the growth rate (d^{-1}). The number of individuals (N) was measured using counts from net tows (see Kimmel et al. 2018 for net tow details) conducted annually between 1990 and 2011 and biennially thereafter.

Biomass (W) was estimated using literature values of dry weight for each taxon and stage (Table S3). Biomass was converted to carbon assuming 40% of DW is comprised of carbon (Bamstedt 1986). Growth rate (g) was estimated using equations from the literature (Table S4). Temperature values for the growth rates were calculated using water temperature at 50 m depth obtained from the University of Alaska Fairbanks oceanographic station GAK1, located at 59° 50.7' N, 149° 28.0' W (<http://research.cfos.uaf.edu/gak1/>). Average temperature data for April or May were used for the production estimates of that specific month. For the years 1990, 1997 and 2009, the May temperatures were not measured. Instead, for 1997 and 2009 we used EcoFOCI SeaCAT data at 50 m to calculate the production estimates, while for 1990 we used the long-term May average from the GAK1 line. Production estimates were summed across all species and life-history stages and integrated over a depth of 120 m to yield estimates in terms of $\text{mgC m}^{-2} \text{d}^{-1}$. A depth of 120 m was used since the mixed layer depth averages ~ 120 m at GAK1 in spring (Sarkar et al. 2005), and because previous studies have shown that the majority of the zooplankton production occurs above this depth (Napp et al. 1996, Coyle & Pinchuk 2005).

2.4. Phenology of egg production and plankton

Annual estimates of daily egg production phenology were modeled based on previous walleye pollock spawn timing estimates (Rogers & Dougherty 2019). Spawning of the walleye pollock population in Shelikof Strait commonly follows a normal distribution with a median peak timing in early April, but it can shift annually up to 24 d, and the spawn duration also varies among years, from 16 to 57 d (Rogers & Dougherty 2019). Daily egg releases for each year were modeled, as the total spawned eggs normally distributed over time (Eq. 1) from start to end of spawning. We then modeled the daily energy contributions of non-surviving eggs in terms of carbon production (Eq. 2) for each year for the time period 1981–2017 (excluding the years 1982, 1984, 1987, 1999 and 2011, 2014, 2016 and 2017, when data were not available for either spawn timing or female spawning stock biomass).

We compared the egg phenology estimates to development times of the CV stage of the copepods *Neocalanus cristatus* and *Neocalanus flemingeri/plumchrus* (hereafter *Neocalanus* spp.) because they are the dominant contributors to zooplankton biomass

during the spring peak in the Gulf of Alaska (Coyle & Pinchuk 2003, Sousa et al. 2016). The life cycle of both *N. cristatus* and the congeners labelled as *Neocalanus* spp. are similar in the Gulf of Alaska region. *N. cristatus* reproduces at depth, primarily in November, emerges in spring, develops to the CV stage by May/June and enters diapause in June/July (Miller et al. 1984, Kobari & Ikeda 1999). *Neocalanus* spp. reproduce in January and February at depth, emerge in spring, develop to CV stage and enter diapause in June (Liu & Hopcroft 2006). We designated the egg release date for *N. cristatus* as 15 November and for *Neocalanus* spp. as 1 January to match the months of peak reproduction (Miller et al. 1984). Developmental times for the CV stages were estimated using the equation:

$$\kappa = \ln\left(\frac{CW}{EW}\right)/g \quad (3)$$

where κ is the developmental time in days, CW is the carbon mass of stage CV, and EW is the copepod egg mass, both in $\mu\text{g C}$, and g is the growth rate, assumed to be constant over time (Kjørboe & Hirst 2008). We estimated copepod egg mass and CV stage mass from the literature (Table S3). We used the mean temperature from Station GAK1 for the period January–May as an estimate for the temperature regime experienced by developing copepods.

3. RESULTS

On average, walleye pollock egg production was $7.1 \text{ mgC m}^{-2} \text{d}^{-1}$ (Fig. 2A). Production varied by over an order of magnitude depending on the year, with the lowest production in 2008 ($0.8 \text{ mgC m}^{-2} \text{d}^{-1}$), and the highest production in 1981 ($32.6 \text{ mgC m}^{-2} \text{d}^{-1}$; Fig. 2B). The uncertainty of these single annual estimates modeled from annual egg numbers and the mean empirical input parameters was assessed with a sensitivity analysis (Table S2, Fig. S4). This analysis showed that the influence of each parameter altered estimates of egg production by no more than 25%, with mortality, female fecundity and egg weight the most influential parameters (Fig. S4). Our total egg estimates also generally matched well with previous results based on repeated empirical measurements of eggs at different development stages that were done for some years in the Shelikof area (Fig. S3, Kim & Gunderson 1989, Picquelle & Megrey 1993, Brodeur et al. 1996). The sensitivity analysis and comparison with previous data indicated that our egg calculations should be indicative of the magnitude of the

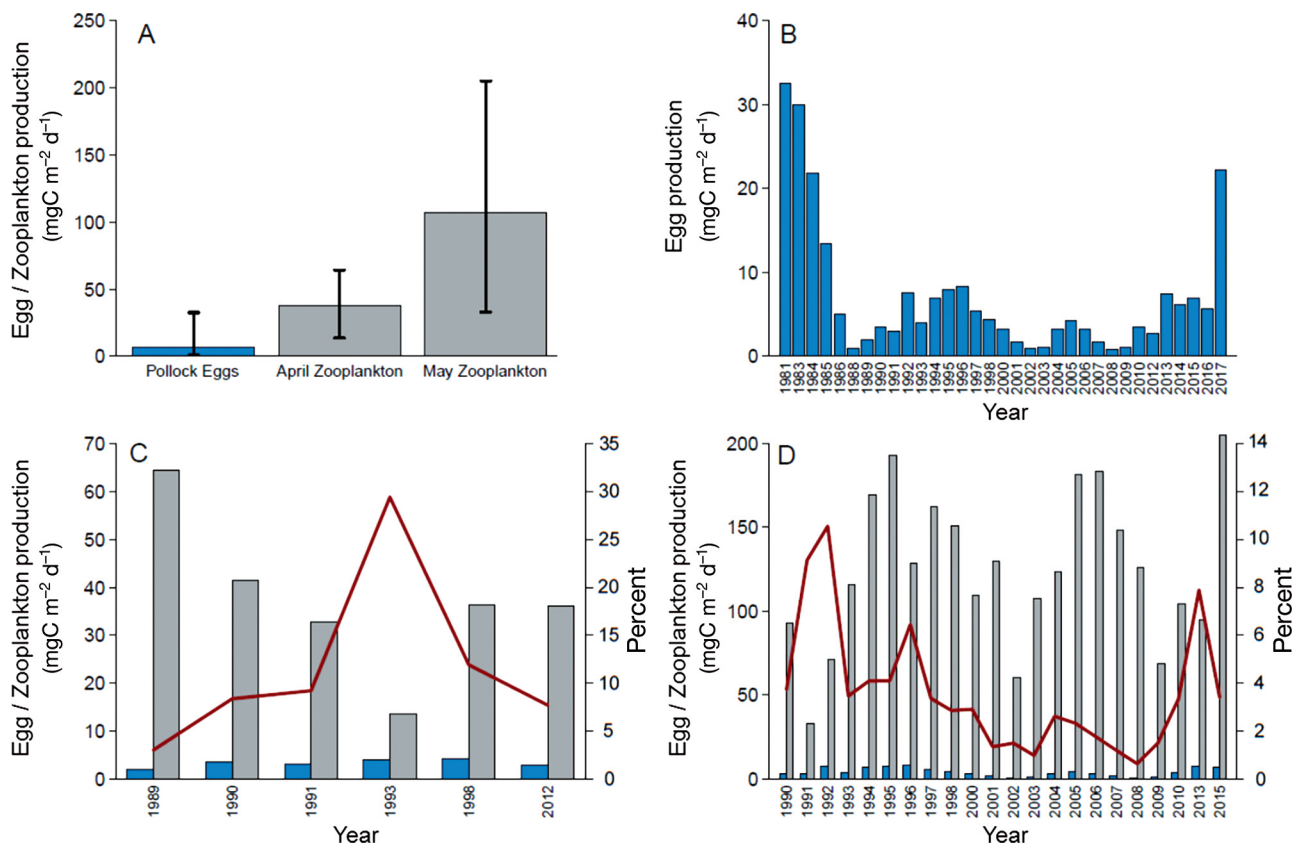


Fig. 2. Overview of egg and zooplankton production estimates. (A) Average production ($\text{mgC m}^{-2} \text{d}^{-1}$) of walleye pollock eggs, and April and May zooplankton for all years. (B) Annual walleye pollock egg production. (C,D) Comparisons of annual walleye pollock egg production (blue) with (C) April zooplankton (grey) and (D) May zooplankton (grey) production. Red lines in C and D denote the relative proportion of walleye pollock egg production to total zooplankton production

annual egg boon in the Gulf of Alaska, even if such estimates carry uncertainties.

Next, we compared the relative importance of fish egg production estimates to spring copepod production, as this was considered an equivalent resource for potential predators due to the similarity in sizes between eggs and zooplankton (Fig. S1). April zooplankton production averaged $37.5 \text{ mgC m}^{-2} \text{d}^{-1}$ (range: $13.7\text{--}64.4$), while average May zooplankton production was $121.0 \text{ mgC m}^{-2} \text{d}^{-1}$ (range: $33.1\text{--}205.3$, Fig. 2A). The influence of variable temperature on copepod production rates was overall low; instead, variation in copepod biomass was the main driver of annual production estimates (Figs. S5 & S6). Only *Oithona* sp. and *Pseudocalanus* sp. production estimates varied substantially with changing temperatures, although the biomass contribution of these copepods to overall production was minimal.

On average, walleye pollock egg production was 18.9% compared to April and 5.8% compared to May average zooplankton production. A total of 6 years

allowed for year-specific comparisons between April zooplankton and egg production (1989–1991, 1993, 1998 and 2012; Fig. 2C), while comparisons with May zooplankton production were possible for 24 years during the time period 1990–2015 (Fig. 2D). The annual walleye pollock egg production ranged between 3.0 and 29.4% of April zooplankton production depending on the year (Fig. 2C). Egg production was between 0.6 and 10.6% of May zooplankton production (Fig. 2D). However, no direct annual comparisons were possible when fish egg production was at peak values ($>20 \text{ mgC m}^{-2} \text{d}^{-1}$; e.g. 1981, 1983, 1984 and 2017).

The phenology of an early (1996), average (2013) and late spawn year (2009) was modeled based on previous spawn timing estimates from Rogers & Dougherty (2019). Overall differences in peak egg production were 25 d among years (Fig. 3A,C). For the earliest spawning year (1996), egg production peaked on day of year (DOY) 100 at $21.3 \text{ mgC m}^{-2} \text{d}^{-1}$ (Fig. 3A), while for the average year (2013) produc-

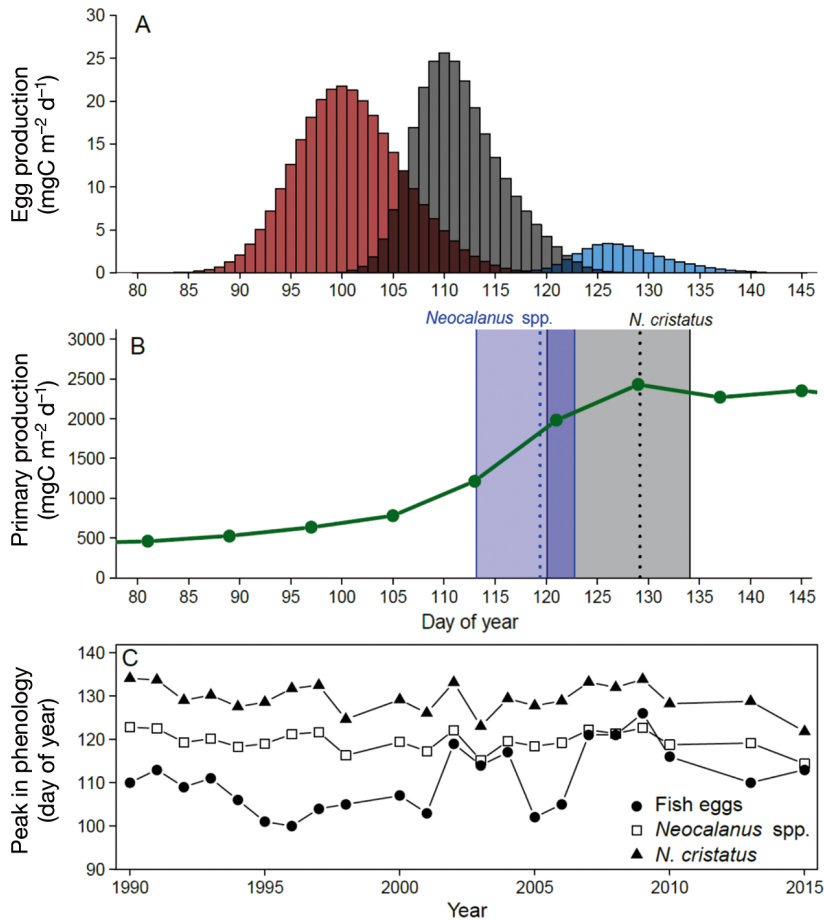


Fig. 3. Daily egg production for (A) an early (1996, red), average (2013, grey) and late (2009, blue) year of walleye pollock spawning. (B) Phenology of primary production (green) and the range (shaded areas) and mean (dotted lines) of *Neocalanus cristatus* copepodite stage V (CV) (black) and *Neocalanus spp.* CV (blue), and (C) annual peak timing for fish eggs (circles), *Neocalanus spp.* CV (open squares) and *N. cristatus* CV (triangles) production. Phenology of egg production for each year was modeled based on spawn timing estimates from Rogers & Dougherty (2019). Average net phytoplankton production in spring was modeled based on MODIS data (Behrenfeld & Falkowski 1997), while *Neocalanus* CV development times were estimated based on measurements and equations provided in Tables S3 & S4

tion of non-surviving eggs peaked on DOY 110, with a peak of 25.5 mgC m⁻² d⁻¹. Peak egg production for the late year (2009) occurred on DOY 126, with a low peak production of 3.5 mgC m⁻² d⁻¹.

Data for zooplankton development time to the CV stage for the 2 taxa (*N. cristatus* and *Neocalanus spp.*) were used as a proxy for estimating the timing of spring zooplankton production. Annual development time for *N. cristatus* to reach stage CV occurred, on average, on DOY 129 (range: 120–134; Fig. 3B), while for *Neocalanus spp.*, average time to reach stage CV occurred on DOY 120 (range: 113–123). Long-term empirical zooplankton biomass data from the Shelikof

Strait supported the development time calculations and showed that the general peak of stage CV *N. cristatus* and *Neocalanus spp.* occurred, on average, between DOY 125 and 150 for both species (Fig. S7). Phytoplankton production onset was fairly consistent for almost all years and occurred, on average, around DOY 110 (Fig. 3B); however, since the MODIS chl a data are based on 8 d averages, there is an inherent uncertainty of ± 4 d for those estimates. While the timing of phytoplankton production onset was consistent, the magnitude varied substantially among years (Fig. S8).

On average, peak walleye pollock egg production occurred about 19 d earlier than peak CV abundance of *N. cristatus* and 9 d earlier than peak CV abundance of *Neocalanus spp.* (Fig. 3C). The biggest difference occurred in 1996, when walleye pollock peak egg production was 32 and 21 d earlier than *N. cristatus* and *Neocalanus spp.*, respectively. Only in 1 year (2009) did peak egg production occur after the peak CV abundance of *Neocalanus spp.*. The consistently earlier occurrence of the egg boons indicates that this resource is commonly available to other consumers before the increase in zooplankton production in spring.

4. DISCUSSION

4.1. Egg energy contribution in spring

Aggregate spawning events of walleye pollock contributed considerably to the energy and nutritional fluxes of the Shelikof Strait marine food web through the introduction of eggs into the ecosystem, supporting our first hypothesis. The annual contribution of walleye pollock egg production was, on average, 18.9% of April, and 5.8% of May zooplankton production. Spawning is a contracted occurrence both in space and time, and thus while walleye pollock egg boons may contribute little to total annual ecosystem production, it appears to provide an important resource subsidy for predators during the weeks of peak spawning. In the Gulf of Alaska, walleye pollock eggs are consumed by a range of predators, including adult walleye pollock,

other fishes, decapods, amphipods, euphausiids and jellyfish (Bailey et al. 1993, Brodeur & Merati 1993, Brodeur et al. 1996). Previous estimates of egg consumption show that particularly euphausiids and gammarid amphipods can consume up to 20–30% of eggs in the water column while cannibalism can also be substantial (Bailey et al. 1993, Brodeur & Merati 1993). How much the eggs contribute quantitatively to the energy budgets of these consumers is unknown. In other systems, pelagic fish egg consumption by planktivorous fishes and gelatinous predators can be as much as 30–70% of the natural egg mortality (Hunter 1980, Ellis & Nash 1997) and contribute up to 90% of gelatinous predator diets (Purcell 1985). It is assumed that the majority of eggs are actively predated in the Gulf of Alaska (Kim & Gunderson 1989), yet some fraction of eggs likely die of natural mortality and are incorporated into microbial pathways or sink and become available to benthic consumers. How these resource pathways are partitioned should be a future avenue of research, as this is not well resolved and likely varies spatially and temporally.

In the Gulf of Alaska, walleye pollock eggs are spawned at depth (Napp et al. 1996), and their vertical distribution differs from zooplankton that are primarily abundant in the upper 50 to 100 m (Napp et al. 1996). As a dietary resource, eggs may be particularly important for predators that forage in deeper waters (Bailey et al. 1993, Brodeur & Merati 1993), either permanently or during vertical migrations. The deeper vertical distribution of eggs also suggests that benthic consumption may be important, and egg resources may represent an important component to benthic–pelagic coupling in Shelikof Strait. In other ecosystems, invertebrate predation of fish eggs has been shown for a range of marine and freshwater species (Polis et al. 1997, Schindler et al. 2003, Taylor & Dunn 2017), while larger predators, including teleosts, sharks, and whales are known to forage efficiently during spawning aggregations (Varpe et al. 2005, Nemeth 2009). Our analyses on walleye pollock concur with these general findings that egg boons can provide an important, but alternative, resource pathway to bottom-up derived production (Fuiman et al. 2015), which is likely used by a range of decomposers and predators in marine food webs.

4.2. Phenology of egg boons

In marine ecosystems, the timing of resource availability is of primary importance for the survival,

reproduction and growth of animals (Neuheimer et al. 2018). The spawning phenology of walleye pollock varies inter-annually by up to 3 wk (Rogers & Dougherty 2019). Walleye pollock spawn just before the initiation of the spring bloom, resulting in optimal feeding conditions when the surviving larvae start feeding after approximately 3 wk (Porter & Theilacker 1999, Laurel et al. 2010). The timing of the peak abundance of the CV stages of *N. cristatus* and *Neocalanus* spp. served as a proxy for zooplankton phenology and occurred several weeks after the initiation of the spring bloom. Despite the uncertainty in the exact timing of peak abundance of the CV stages, our estimates are in good agreement with other studies showing that peak biomass in spring is dominated by these 2 congeners (Coyle & Pinchuk 2003, Sousa et al. 2016). Furthermore, an examination of our empirical data on CV abundance for these 2 taxa shows a window for the timing of peak CV abundance (Fig. S7) that is similar to the model estimates. Average peak production of fish eggs commonly occurred 10–20 d before the increase in zooplankton production. Years with early egg production, in particular, preceded zooplankton development, and were also characterized by higher total egg production. Consequently, in most years, the timing of peak egg production precedes the increase in zooplankton production, suggesting that walleye pollock eggs appear at a crucial time when planktivorous consumers may be otherwise resource limited.

4.3. Uncertainties in production estimates

The purpose of our study was to evaluate the potential importance of the resource contribution of eggs to the marine food web. Upscaling empirically measured processes to the ecosystem level carries noticeable uncertainty. The sensitivity analysis showed that female fecundity and egg weights were the most influential parameters; however, no single parameter altered estimates of egg production by more than 25% (Fig. S4). Lower egg mortalities would have influenced our estimates, but it is unlikely that we consistently underestimated egg mortalities since we used a relatively modest value of 0.2 d^{-1} , which is well within the range of previous estimates for walleye pollock (Kim & Gunderson 1989). In addition, we did not model the contribution of endogenously feeding larvae, although this would be a likely additional resource contribution to the food web, since mortality rates of fish larvae at hatch are also commonly high

(Peck et al. 2012). Our estimates of egg numbers based on acoustic survey data (Dorn et al. 2017) were similar to previous empirical estimates of total egg numbers for walleye pollock (Fig. S3, Picquelle & Megrey 1993) and comparable to a range of other teleosts (Fuiman et al. 2015).

Zooplankton production rates are difficult to estimate empirically (Poulet et al. 1995). Using the equations of Hirst & Lampitt (1998), Coyle & Pinchuk (2003) estimated that copepod production along the Alaska shelf in April was $31 \text{ mgC m}^{-2} \text{ d}^{-1}$ which compares well to our average estimates of $37.5 \text{ mgC m}^{-2} \text{ d}^{-1}$. Our May production estimates based on coastal data were higher, on average at $121.0 \text{ mgC m}^{-2} \text{ d}^{-1}$, compared to their estimate of $35 \text{ mgC m}^{-2} \text{ d}^{-1}$ (Coyle & Pinchuk 2003), which included both coastal and deeper stations. It should be noted that our production estimates represent only the copepod fraction of the zooplankton production, excluding organisms such as euphausiids, amphipods, appendicularians, pteropods and other decapods. Overall, fish egg and zooplankton production estimates are unlikely to have been consistently biased, and thus should provide good approximations for evaluating the relative magnitudes of egg and zooplankton production in the Shelikof Strait ecosystem in spring.

Obtaining robust measures of egg production phenology and zooplankton CV development times involves uncertainty. Spawn timing was estimated from larval walleye pollock captured in late May to early June, and while the larval fish surveys generally covered the period of peak larval abundance (Matarese et al. 2003), the earliest and latest-spawned larvae may have been under-sampled, resulting in an underestimate of the spawning duration (Rogers & Dougherty 2019). However, any bias is likely to be small, and inter-annual variation in the timing of spawning generally agrees with other data sources (Rogers & Dougherty 2019 and references therein). The development times calculated for *N. cristatus* (165–180 d after their release date of 15 November) appear to match well with other studies. Tsuda et al. (2004) reported that *N. cristatus* went from the egg stage to C1 in about 40 d at 2°C and Kobari & Ikeda (1999) reported that development from CI to CV took 120 d. The temperatures observed by Kobari & Ikeda (1999) ranged from 2–3°C throughout the water column until April, when surface temperatures began to rise and about 1 mo prior to the local peak in CV abundance. This gives a total development time from egg to CV of approximately 160 d, which with an egg release time of mid-November results in development to CV occurring around DOY 125–135, similar

to our estimates and previous work (Miller et al. 1984). For *Neocalanus* spp., our range of 113–122 d matches well with 120 d reported by Miller & Nielsen (1988) and 119–123 d reported by Liu & Hopcroft (2006). Moreover, these estimates were well supported by the long-term empirical data, which showed peak abundance of both CV *Neocalanus* stages occurring in mid-May (DOY 125–150; Fig. S7), consistently later than our estimates of peak walleye pollock egg production.

4.4. Importance of egg boons for ecosystem dynamics

Fish spawning aggregations create important nutritional subsidies in marine systems (Polis et al. 1997, Varpe et al. 2005, Fuiman et al. 2015), as shown here for walleye pollock, and in freshwater systems (Schindler et al. 2003). Spawning events also increase nitrogen and phosphorus fluxes (Post & Walters 2009) and can thus fuel primary production (Archer et al. 2015). We estimated egg production in terms of carbon production; however, eggs are rich in long-chained polyunsaturated fatty acids (PUFAs) (Laurel et al. 2010). Fuiman et al. (2015) highlighted that fish eggs are 10, 5 and 70 times richer in the essential long-chained PUFAs docosahexaenoic acid (22:6 3), eicosapentaenoic acid (20:5 3) and arachidonic acid (20:4 6), respectively, compared to zooplankton species, mostly from temperate regions. However, many boreal zooplankton species contain and store substantial amounts of lipids (Lee et al. 2006), thus the differences between the amount of essential long-chained PUFAs in eggs and zooplankton are likely smaller in the Gulf of Alaska and other higher-latitude ecosystems. Nonetheless, walleye pollock eggs likely provide an important lipid subsidy, including essential long-chained PUFAs, which is an important but at times limited resource in the Gulf of Alaska food web (Litzow et al. 2006).

Different fish populations have unique life histories and spawning modes, and their energetic inputs vary substantially in time and space. For example, in the Gulf of Alaska a proportion of walleye pollock spawns considerably earlier near the Shumagin Islands compared to the rest of the population (Dougherty et al. 2007). It should be noted that the spawning biomass of walleye pollock is high relative to other fish species, and thus variations in walleye pollock spawning biomass may have large impacts on seasonal egg energy input to the system, a phenomenon that is likely common across ecosystems that are dominated

by selected species (e.g. sardines and anchovies in upwelling regions). Nonetheless, in the Gulf of Alaska, other abundant species such as Pacific halibut *Hippoglossus stenolepis*, arrowtooth flounder *Atheresthes stomias* and Pacific cod *Gadus macrocephalus* have very high fecundities (3–4 million eggs per female) and thus large energetic capacities for supporting ecosystem production. Furthermore, Pacific halibut eggs contain significant amounts of energy due to their large size (diameter of 2.9–3.8 mm), and along with arrowtooth flounder, spawn from December to March (Matarese et al. 2003), well before the spring bloom, at a time period when other nutritional resources are scarce. Combined, the egg resource pulses from species which differ in their respective time of spawning could provide an extended wave of pulsed egg resources to the Gulf of Alaska food web, similar to what has been observed for salmon and Pacific herring in other ecosystems (Armstrong et al. 2016). Likewise, in other ecosystems, aggregate spawners such as Atlantic herring (Van Damme et al. 2009), Pacific herring (Fox et al. 2014, 2018) and Atlantic cod (Kjesbu et al. 1991) all deposit large energy subsidies to their respective environments. If transient energy pulses from different species provide considerable resource contributions to the ecosystem, it also implies that maintaining a diverse fish community and protecting spawning locations (Erisman et al. 2017) are essential for preserving high production levels in marine food webs. Furthermore, exploitation of individuals from the adult population not only impacts recruitment potential of the particular target species, it also diminishes or in severe cases removes (Hutchings & Myers 1994) eggs as resource subsidies for other consumers. A reduction of the egg resource flux even at sustainable harvesting rates due to removal of spawning capacity will alter the flow of nutrients in the food web and should be an additional consideration for ecosystem-based fisheries management.

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