

Pollock and “the Blob”: Impacts of a marine heatwave on walleye pollock early life stages

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Abstract

The North Pacific marine heatwave of 2014–2016 (nicknamed “The Blob”) impacted marine ecosystems from California to Alaska, USA, with cascading effects on fisheries and fishing communities. We investigated the effects of this anomalous ocean warming on early life stages of walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska. In spring of 2015, pollock larvae were caught at record low levels relative to a 30-year time series. Survival rates were low during the summer, and by late summer, numbers were further reduced, with very low abundances of juvenile (age-0) pollock. Our analyses suggested multiple mechanisms for this decline: (a) Low-saline conditions may have impacted egg buoyancy and survival; (b) population densities of zooplankton nauplii may have been too low to support first-feeding larvae; (c) body condition of age-0 pollock was poor and a bioenergetics model indicated that reduced quality of zooplankton prey, coupled with warmer temperatures, increased the ration required for positive growth by up to 19%, at a time when prey abundance was likely reduced. Thus, walleye pollock experienced a cascade of poor conditions for growth and survival through early life stages, resulting in the near disappearance of the 2015 year class in the population by the end of their first year. These impacts differ from previous warm years and emphasize the importance of looking beyond simple temperature–abundance relationships when predicting species responses to climate warming.

KEYWORDS

bioenergetics, body condition, early life history, *Gadus chalcogrammus*, Gulf of Alaska, ichthyoplankton, recruitment

1 | INTRODUCTION

Starting in the winter of 2013/2014, anomalous atmospheric conditions over the northeast Pacific Ocean led to the largest marine heatwave on record (Bond et al., 2015; Di Lorenzo & Mantua, 2016). The heatwave, nicknamed “The Blob” (Bond et al., 2015), persisted through 2015 and into 2016, with sea surface temperatures up to three standard deviations above average

(Di Lorenzo & Mantua, 2016). The anomalously warm waters in the northeast Pacific corresponded to abnormal ecological observations spanning multiple trophic levels. In the California Current System, phytoplankton production and biomass were low (Gómez-Ocampo et al., 2018), gelatinous zooplankton proliferated (Brodeur et al., 2019), a toxic algal bloom related to warm conditions spanned the North American west coast with major fisheries-related economic repercussions (McCabe et al., 2016), Columbia River

Chinook salmon *Oncorhynchus tshawytscha* were in poor condition (Daly et al., 2017), and a series of mass mortality events and strandings of marine mammals and seabirds were observed (summarized in Cavole et al., 2016; Piatt et al., 2020). Farther north, persistent warming was observed throughout the Gulf of Alaska (GOA) that extended from the surface down to 300 m (Walsh et al., 2018). Species of fish and zooplankton were noted far north of their typical ranges (Bond et al., 2015), seabird die-offs occurred (Piatt et al., 2020), and Pacific cod *Gadus macrocephalus* experienced a population decline leading to a severe reduction in catch limits (Barbeaux et al., 2020). By studying ecological responses to the warm anomaly, we can improve our understanding of how climate conditions alter ecosystem processes and functioning, as well as the impact on species of commercial interest.

Walleye pollock (*Gadus chalcogrammus*) is a widely distributed gadid found on the continental shelves of the North Pacific Ocean. In the Gulf of Alaska, walleye pollock (hereafter “pollock”) are one of the dominant fishes by biomass in the ecosystem (Gaichas et al., 2011) and play a nodal role as both predator and prey (Gaichas & Francis, 2008; Springer, 1992). Pollock are also the target of a \$100M fishing industry in the Gulf of Alaska (first wholesale value; Dorn et al., 2018). Shifts in pollock abundance can therefore alter the structure of the ecosystem and have significant impacts on commercial fisheries and fishing communities in Alaska. Pollock recruitment is highly variable and, as for most marine fishes, sensitive to conditions experienced during the first year of life (Duffy-Anderson et al., 2016). Understanding the direct and indirect effects of a warm ocean environment on the ecology of pollock early life stages can help provide an understanding of the processes regulating recruitment in this species.

The first year of life of walleye pollock is characterized by high mortality, where eggs, larvae, and young-of-year (age-0) juveniles

must survive a series of transitions between habitats and life stages (Duffy-Anderson et al., 2016). Shelikof Strait (Figure 1) is the primary spawning ground for the Gulf of Alaska stock, and mature individuals aggregate there in March and April to spawn. Eggs incubate at depths of >150 m for about two weeks before hatching and rising to the upper 50 m of the water column as larvae (Kendall et al., 1994). Larvae hatch into a highly advective environment, subjected to the rapid drift of the Alaska Coastal Current to the southwest along the Alaska Peninsula. Larvae begin feeding about 5–6 days after hatching, their diet consisting primarily of copepod eggs and nauplii. During this first-feeding period, larvae may be subject to food-limited growth, and subsequent increased predation mortality (Canino et al., 1991). Post-larval juveniles occupy mid-water habitats from the nearshore to the shelf edge, with high densities in the Semidi Bank area downstream of the Shelikof spawning area. From mid- to late summer (August–September), juveniles shift from a diet consisting primarily of copepods (especially *Calanus marshallae*) to one dominated by euphausiids (Wilson et al., 2011, 2013). Euphausiids are an especially energy-rich prey (Mazur et al., 2007) that have been associated with improved late summer body condition in age-0 pollock (Wilson et al., 2013). In the adjacent Bering Sea, high energy storage (i.e., lipid content) prior to winter has historically led to increased overwinter survival and stronger year classes (Heintz et al., 2013; Siddon et al., 2013). Overwinter mortality is high in general, as young pollock are subject to predation from abundant piscivorous groundfishes (Bailey, 2000).

Previous studies of the effects of changes in temperature on pollock recruitment have found mixed results. Early studies found a positive relationship between springtime temperatures and larval pollock survival, with cold years corresponding to higher rates of larval mortality, especially during the first week post-hatch (Bailey et al., 1996). This was hypothesized to be related to the

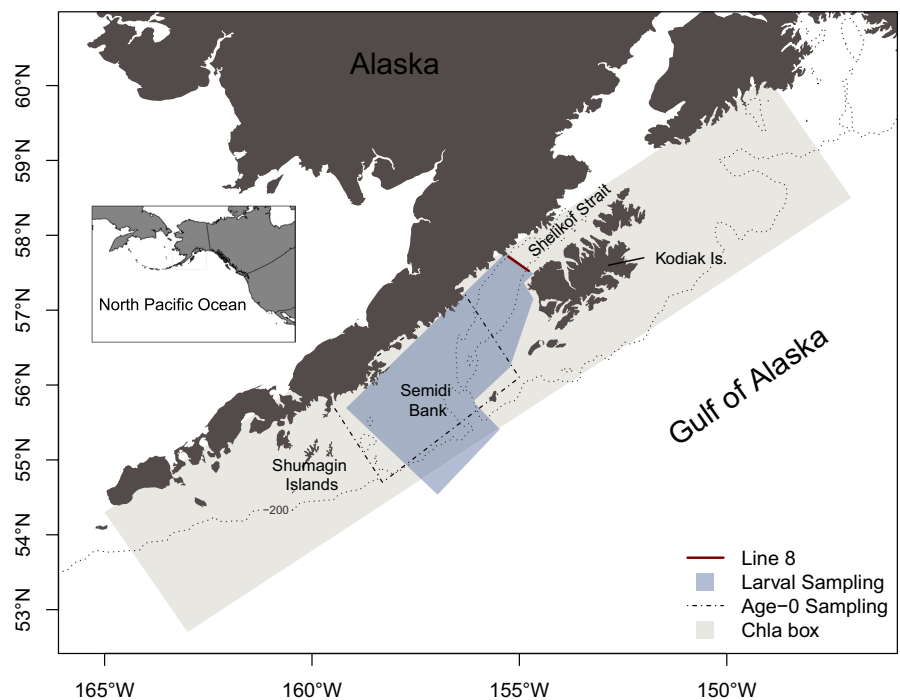


FIGURE 1 Study area in the western Gulf of Alaska, indicating locations of long-term sampling of larval (blue shaded polygon) and age-0 (dashed line) pollock. Spring physical oceanographic and zooplankton monitoring occurs at Line 8 (solid red line) between Kodiak Island and the Alaska Peninsula. A time series of primary productivity was derived from MODIS data over the area indicated by the light gray box [Colour figure can be viewed at wileyonlinelibrary.com]

timing of microzooplankton production, particularly of copepod nauplii, which are a primary prey item of first-feeding larvae (Bailey et al., 1995). A time series analysis found no apparent effect of spring temperatures on larval abundance (Doyle et al., 2009), while statistical models provided evidence that recruitment (as estimated in an age-structured assessment model) was negatively related to springtime temperatures (A'mar et al., 2009). These studies on their own give little indication of what to expect in an anomalously warm year. One possible explanation for these inconsistent findings is that temperature is only one of many factors that often interact to regulate survival and recruitment in this species (e.g., Ciannelli et al., 2004). Indeed, previous studies have suggested that wind mixing, transport, eddy formation, and prey and predator abundance may impact year-class strength of pollock in the GOA (Bailey, 2000; Bailey & Macklin, 1994; Megrey et al., 1996), with the importance of different mechanisms changing over time (i.e., relationships are nonstationary; Bailey, 2000; Ciannelli et al., 2004).

Here, we investigate the effects of the marine heatwave on the ecology of walleye pollock through their first year of life. Our objective was to examine empirical and model-based data on multiple life stages and ecosystem components to evaluate support for hypothesized mechanisms explaining the pollock recruitment failure coincident with the heatwave. We specifically focus on three early life stages: eggs in early spring, larvae in late spring, and age-0 juveniles in late summer. First, we evaluate the hypothesis that hydrographic conditions affected the vertical position of eggs in the water column and increased mortality. Second, we investigate the timing of primary production and the availability of zooplankton prey to test the hypothesis that larvae were food-limited. Finally, we use a bioenergetics model to investigate the hypothesis that warmer temperatures and reduced prey quality lowered the body condition and increased the consumption demands of juvenile fish prior to their first winter. Support for additional potential mechanisms is evaluated in the discussion. While the heatwave persisted through 2016,

we focus only on the 2015 year class because of a lack of survey coverage in recent even-numbered years.

2 | METHODS

2.1 | Environmental data

A time series of monthly sea surface temperatures was derived from NOAA NCEP Reanalysis data (Kalnay et al., 1996), averaged over a box defined by 54.3°N–56.2°N and 151.9°W–157.5°W. Anomalies were calculated relative to the monthly mean temperatures from 1948 to 2019. Water column profiles of temperature and salinity from the late larval period were derived from hydrographic casts (Sea-Bird SBE-49) along Line 8, a routinely sampled transect between Kodiak Island and the Alaska Peninsula (Figure 1), during the period May 25–June 8. Profiles from four deep (>200 m) stations were averaged for each year with available data (2000, 2003–2011, 2013, 2015, 2017). (See Figure 2 for an overview of the time series and models included in this study.)

2.2 | Phytoplankton

Satellite-derived estimates of near-surface chlorophyll *a* concentrations were used to characterize the seasonal timing and magnitude of phytoplankton biomass on the shelf from 2002 to 2015. Composite 8-day average chlorophyll *a* estimates from the MODIS (Moderate-resolution Imaging Spectroradiometer) instrument onboard the AQUA satellite (Hu et al., 2012) were downloaded on April 20, 2017, from <https://coastwatch.pfeg.noaa.gov/>. A time series for the western Gulf of Alaska shelf was developed by averaging the remotely sensed chlorophyll *a* concentrations over an area defined by the box shown in Figure 1 for each 8-day period from February 15 to October 15 in each year. There are known limitations to using

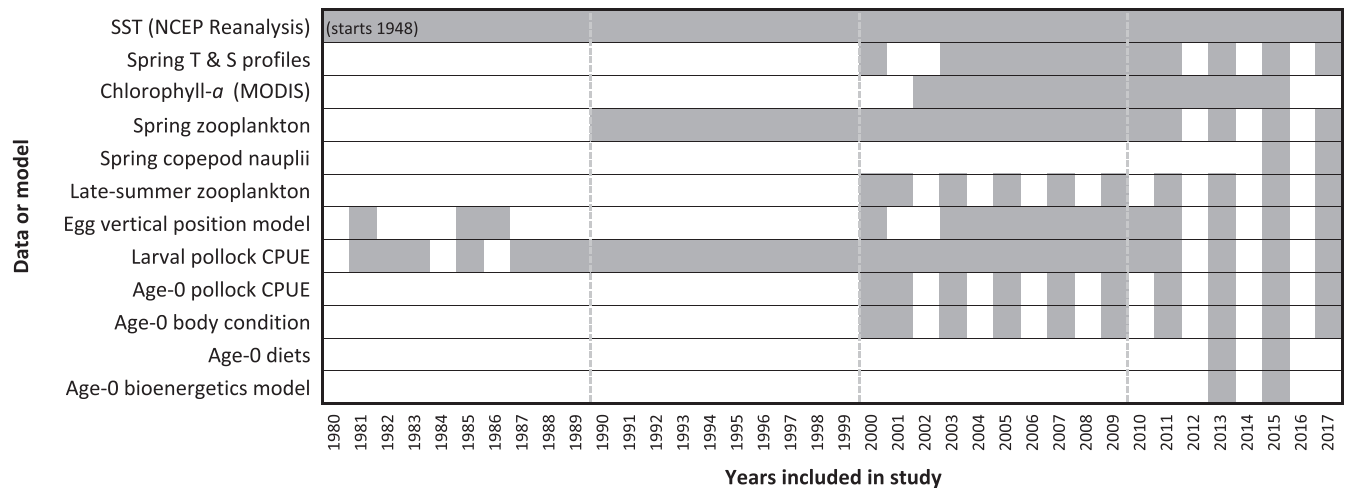


FIGURE 2 Time series data and models used in this study, with gray shading indicating years included

satellite-derived estimates of chlorophyll *a* in glacially influenced coastal regions with suspended sediments (Waite & Mueter, 2013); however, we use the satellite data to describe seasonal patterns and relative trends, not to calculate absolute concentrations.

2.3 | Zooplankton

Zooplankton were collected along Line 8 during late May and early June and again in late summer (August–September) in the core Semidi age-0 sampling region (Figure 1). Zooplankton were collected using oblique tows of paired bongo nets (20-cm frame, 153- μ m mesh, and 60-cm frame, 333- or 505- μ m mesh) (Incze et al., 1997; Napp et al., 1996). The tows were within 5–10 m of the bottom depending on sea state. Smaller zooplankton, including copepod nauplii that are the primary prey of larval pollock (Incze & Ainaire, 1994), were sampled using a 25-cm frame, 53- μ m mesh CalVET (California Cooperative Oceanic Fisheries Investigations Vertical Egg Tow). Two CalVET nets were towed vertically from near bottom to the surface at a total of 25 stations in both 2015 and 2017. Volume filtered was estimated using a General Oceanics flowmeter mounted inside the mouth of each net. All samples were preserved in 5% buffered formalin/seawater. Zooplankton were identified to the lowest taxonomic level and stage possible at the Plankton Sorting and Identification Center in Szczecin, Poland, and verified at the AFSC, Seattle, Washington, USA. Starting in 2012, the 60-cm frame net had its mesh changed to 505 μ m. The majority of taxa were not affected by this change; however, the potential for some differences to arise were noted. In order to minimize the effect of this change, we selected life history stages that were unlikely to be affected by the mesh size based on prior analyses of mesh retention (Incze et al., 1997; Kimmel & Duffy-Anderson, 2020; Siefert & Incze, 1989). Zooplankton densities are reported in No. m^{-3} .

We selected several zooplankton taxa for assessment based on their relevance to larval and juvenile walleye pollock. For samples collected in May/June along Line 8 (Figure 1), we reported the abundance of nauplii > 150 μ m as they comprise the greatest fraction of nauplii in the water column and were found to make up 98% of walleye pollock diets (Incze & Ainaire, 1994). The CalVET nets have only been used within the larval sampling area since 2015, so we reported data from 2015 and 2017 (due to biennial sampling schedule). In addition, we calculated the standardized abundance anomalies of two copepod taxa that are the primary sources of nauplii: *Pseudocalanus* spp. (75%) and *Metridia pacifica* (18%) adults (Incze & Ainaire, 1994). The *Pseudocalanus* spp. grouping includes up to three species: *P. newmani*, *P. minutus*, and *P. mimus*, with the latter being the dominant species on the shelf in spring and summer (Napp et al., 2005). For data collected in late summer/early autumn in the age-0 sampling area (Figure 1), we reported the standardized abundance anomalies of the primary prey of juvenile walleye pollock, *C. marshallae* stage C5, and euphausiids (Wilson et al., 2006, 2009, 2011). Copepods > 2 mm prosome length are the primary prey of juveniles < 50 mm SL (Wilson et al., 2009) and the large copepod most prevalent in summer in neritic waters is *C. marshallae* C5 stage

(Coyle & Pinchuk, 2005). The primary prey for juveniles between 50 and 140 mm are adult and juvenile euphausiids (Wilson et al., 2009). The 60-cm bongo net likely underestimates juvenile and adult euphausiid abundance (Hunt et al., 2016; Sameoto et al., 1993) as smaller plankton nets will underestimate large euphausiids, while larger plankton nets will underestimate small euphausiids (Eriksen et al., 2016). Here, we report the furcilia abundance as a proxy for the overall abundance of the dominant euphausiids in the region: *Thysanoessa longipes* and *Euphausia pacifica*, *T. inermis*, and *T. spinifera*, with the latter two species most prevalent in the sampling area (Coyle & Pinchuk, 2005). Standardized abundance anomalies were calculated as follows: For each year within the sampling region, the mean, $\log_{10} + 1$ -transformed abundance was calculated for each taxa (X). Using this yearly time series of transformed abundance, the long-term, annual mean (\bar{X}), and standard deviation (\bar{S}) were calculated. The standardized anomaly (SA) for each year was then computed as $SA = \frac{X - \bar{X}}{\bar{S}}$.

2.4 | Egg vertical position model

Stage-specific vertical position of walleye pollock eggs spawned in Shelikof Strait was modeled using hydrographic profiles of temperature ($^{\circ}$ C), salinity, and density ($\sigma_t = \text{kg/m}^3 - 1,000$) (Sea-Bird Scientific, 2017) that were measured on Line 8 during May 26, 2015. The model was based on Kendall and Kim (1989) assuming the stage-dependent specific gravity for type II eggs, which is the most common class of eggs and has heavier early development stages than the type I class (Hinckley et al., 1996). Following Kendall and Kim (1989), Stokes' law was used to estimate the vertical velocity (cm/s) of eggs in the water column. Spawning was assumed to occur at 290 m over a seafloor depth of 300 m based on observations from egg and spawner surveys (Kendall et al., 1994; Kim & Nunnallee, 1990). We used the updated temperature–egg development relationships from Blood et al. (1994), rather than from Bates (1987), and allowed the kinematic viscosity of water (cm^2/s) to change within the water column based on temperature and salinity (Ramsing & Gundersen, 1994); these changes to the model had little effect on the predicted egg vertical trajectory. We divided each of the 21 egg development substages, which were nested within 6 stages, into 100 steps to allow subdaily resolution of stage-specific development time and outputted the predicted vertical position after each step. For comparison, we computed the vertical trajectories of eggs for other years with hydrographic profile data from Line 8 during May 20–June 8 depending on year (2000, 2003–2011, 2013, 2017) or from Kendall and Kim (1989) (1977, 1981, 1985, 1986).

2.5 | Larval data

The Alaska Fisheries Science Center's (AFSC) Ecosystems and Fisheries-Oceanography Coordinated Investigations Program (EcoFOCI) has been sampling ichthyoplankton in the Gulf of Alaska since the 1970s.

The primary gear was a 60-cm paired bongo frame equipped with either 333- or 505- μm mesh nets and flowmeters and towed obliquely at evenly spaced, predetermined sites to 100 m depth or 10 m off bottom in shallower water. Previous work has shown that catches of walleye pollock larvae do not differ between the two mesh sizes (Shima & Bailey, 1994). Samples were preserved in 5% formalin and larval pollock were sorted, counted, and measured for standard length (SL) to the nearest millimeter at the Plankton Sorting and Identification Center in Szczecin, Poland. We used samples collected during a consistently sampled time period (the late larval period; May 18–June 7) and spatial area (from the Shelikof Strait and Sea Valley to east of the Shumagin Islands; Figure 1). Counts of larvae were standardized to No. m^{-2} sea surface area as a measure of catch per unit effort (CPUE). A time series index of abundance was developed for 1981–2017 by calculating an area-weighted mean CPUE (Doyle et al., 2009). The late larval period was not surveyed in 1984, 1986, 2012, 2014, or 2016.

2.6 | Juvenile data

Age-0 pollock were sampled in late summer (primarily August–September) by the EcoFOCI Program in 2000, and odd years from 2001 to 2017. A sampling grid on the Semidi Bank was occupied in all years, and a second grid near Kodiak Island was sampled since 2005. A small-mesh mid-water trawl was used to sample the upper 200 m or from 5 m off bottom. Pollock were enumerated and measured for standard length. Age-0 pollock were distinguished from older age groups by length (age-0 < 140 mm SL). Age-0 pollock catch m^{-2} was calculated by dividing total age-0 pollock counts by volume filtered by the trawl and multiplying by the maximum depth fished by the net following Wilson et al. (2009). A time series of age-0 abundance was developed for the consistently sampled Semidi region (Figure 1) by calculating an area-weighted mean catch m^{-2} in each year, using the same methodology as for the larval index.

A random sample of individuals was frozen at sea and later processed in the laboratory for body weight and food habits (see Wilson et al., 2009, 2013 for details). Samples were thawed and up to 20 individuals were selected to represent the range of sizes collected. Each fish was blotted dry, measured to the nearest 1 mm SL, and weighed to the nearest 1 mg. Stomachs were excised between the esophagus and pylorus and preserved in a sodium borate-buffered 10% formalin solution. For each stomach, contents were extracted, blotted dry, weighed to the nearest 0.01 mg, and sorted by digestion state and by the lowest practical taxonomic level. Well-digested prey fragments were separated from intact (>75% whole) individuals. Additionally, copepods and euphausiids were each sorted into size groups: 1) small copepods (≤ 2 mm prosome length, PL), large copepods (>2 mm PL), 3) euphausiid furcillae (ca. ≤ 5 mm length), and euphausiid juveniles and adults. All individuals in each digestion taxonomic were enumerated, blotted dry, and collectively weighed to the nearest 0.01 mg.

A body condition index was calculated as the residuals from a regression of $\ln(\text{body weight})$ on $\ln(\text{length})$ using data from all

surveys combined (Le Cren, 1951). Residual body weight was available for the extent of survey time series and Buchheister et al. (2006) showed that it correlated with bomb calorimetry-determined whole-body energy content for juvenile pollock. Day of year was included as a covariate in the regression to account for seasonal changes in body condition (Buchheister et al., 2006), and a generalized additive model was used to allow for non-linearity in the day-of-year effect. An annual index was calculated for the core Semidi area by weighting individual condition values by station-specific CPUE.

2.7 | Pollock productivity and mortality rates

Early life stage processes may be captured as the number of surviving larvae produced per unit of spawning stock biomass. This productivity metric captures variation in fecundity as well as survival through egg and early larval stages and is measured as the log-transformed ratio of mean larval CPUE (calculated above) to female spawning stock biomass (SSB, estimated from the stock assessment for walleye pollock (Dorn et al., 2018)). Because larval abundance is measured as an index (mean CPUE) and is not absolute abundance, we present a standardized (z-score) productivity index.

An instantaneous mortality rate was calculated for the late larval stage to age-0 juvenile stage (approximately May–September) for each year the larval and age-0 surveys were executed. The rate was calculated as $M = -\ln(\text{CPUE}_{\text{Juv}_y} / \text{CPUE}_{\text{Larv}_y}) / d_y$, where d_y is the number of days between the yearly mean survey date for the two surveys and varies from 96 to 124 days. CPUE_{Juv} and $\text{CPUE}_{\text{Larv}}$ are the mean catches of age-0 juveniles and larvae, respectively, in No. m^{-2} . Because the entire populations of larvae and age-0 are not surveyed in a given year, the mortality is expressed as a ratio of average densities within the standard survey areas and may include factors other than mortality, such as dispersal.

Confidence intervals were calculated by bootstrapping: For each year and time series, a sample was drawn from a distribution given by the mean and standard error of the estimate, and the mortality rate was calculated. The error distribution was assumed to be normal for the larval and age-0 abundance indices, and lognormal for SSB, reflecting the methodology for estimating those quantities. This was repeated 1,000 times and 95% confidence intervals were calculated from the resulting distributions for each year.

Linear regressions were used to test for relationships between thermal conditions and pollock abundance, productivity, and mortality indices. Specifically, spawner productivity and $\ln(\text{larval CPUE})$ were regressed against mean March–May SST, and M and $\ln(\text{age-0 CPUE})$ were regressed against mean June–August SST.

2.8 | Bioenergetics model

In order to assess the growth conditions for juvenile pollock in 2015 compared to previous years, we used a bioenergetics

modeling approach. This approach synthesizes the combined effects of changes in thermal conditions, prey quality, and prey quantity on walleye pollock growth. The Wisconsin bioenergetics model, version 4.0 (Deslauriers et al., 2017), uses a balanced energy budget where energy for growth is total energy consumed minus energy for activity, respiration, and waste. It operates on a daily time step incorporating mass- and temperature-dependent functions for metabolism and maximum consumption. Parameter values for juvenile walleye pollock were based on Ciannelli et al. (1998). Inputs to the model were pollock diets (prey items by %Wt), taxon-specific prey energy densities (J/g), predator (pollock) energy density (J/g), water temperature, pollock body weight (g), and daily ration (% of body weight). We fit the model to observations from the core Semidi area in 2013 and 2015. The year 2013 was chosen as it was a relatively average year in terms of temperature and age-0 body condition, but the survey extent and timing closely matched 2015. Temperature was measured as the mean temperature of the upper 50 m across all stations within the core Semidi area. Annual mean diet composition was characterized as the mean percent by weight of the 11 most prevalent prey groups, adjusted to sum to 100%. Diets and mean weights were characterized for three length classes of fish that were well represented in each of the years: 45–54 mm, 55–64 mm, and 65–74 mm. Prey energy density values were taken from the literature (Table S1; Mazur et al., 2007; Wilson et al., 2013). Because daily ration size is unknown and uncertain to estimate, we ran the model for a range of ration sizes ($0.03\text{--}0.065\text{ g g}^{-1}\text{ day}^{-1}$) for each year (2013, 2015) and size class (50 mm, 60 mm, 70 mm) in order to determine the difference in ration size needed to maintain positive growth given thermal conditions and prey quality in 2015 versus 2013. To assess the relative contribution of differences in temperature, diet composition, and body weight to required ration sizes, we ran three simulations. In each, we used observed values for 2013 and set either temperature, diet composition, or body weight equal to the observed 2015 values, thus allowing us to compare the relative contribution of each variable in isolation.

3 | RESULTS

3.1 | Temperature and salinity

Sea surface temperatures in the Gulf of Alaska were above average starting in January 2014, with high temperatures persisting through all of 2014, 2015, and 2016. This is the longest period of continuous warm monthly sea surface temperature anomalies in the data record (since 1948; Figure 3a); the strongest monthly warm anomaly was in September 2016. Other warm periods included 1983–1984 and 2004–2005. The period 2007–2012 comprised an extended cold phase in the Gulf of Alaska. Temperature measurements from a transect of Line 8 near Kodiak Island indicated that the warming in spring of 2015 was most notable at depth, and extended to

200 m (Figure 3b). Temperatures at 200 m were $>6^{\circ}\text{C}$, compared to an average (2000–2013) of 4.8°C . Salinity measurements indicated unusually fresh conditions throughout the top 200 m, similar to only 2003 and 2004 (Figure 3c).

3.2 | Phytoplankton

MODIS-derived estimates of chlorophyll *a* concentrations suggest that phytoplankton biomass in the western Gulf of Alaska was not anomalous in terms of magnitude or timing in 2015 (Figure S1), although chlorophyll *a* estimates were not available for the 8-day period around May 21, 2015, due to persistent cloud cover. The average annual pattern of chlorophyll *a* includes a rapid increase starting in late April, an annual maximum in May, lower sustained concentrations through the summer, and a smaller peak in late summer to early fall. In 2015, chlorophyll *a* concentrations followed this same pattern (Figure S1).

3.3 | Zooplankton

The mean copepod naupliar ($>150\text{ }\mu\text{m}$) abundance was 11 L^{-1} in both 2015 and 2017 during the spring survey. Across all sampled stations, the overall range of nauplii differed slightly as evidenced by differences in the 25th and 75th percentiles, which were $6\text{--}12.7\text{ L}^{-1}$ and $6\text{--}16.5\text{ L}^{-1}$ in 2015 and 2017, respectively (Figure 4). There was no significant difference in the mean abundance between the years ($t = 0.01, p = .99$); however, in 2015, 75% of the nauplii abundance estimates observed were less than 13 L^{-1} , a density below which 25% of pollock guts have been observed to be empty (Theilacker et al., 1996). The primary nauplii producers had differing patterns in 2015: abundances of *Pseudocalanus* spp. adults were above average, whereas *M. pacifica* adults had a large, negative anomaly in 2015 (Figure S2). During late summer, abundance of *C. marshallae* C5 was above average in 2015, whereas abundance of euphausiid furcilia was low (Figure S2).

3.4 | Egg vertical position model

In 2015, the vertical trajectory of the most common class of walleye pollock eggs in Shelikof Strait (Type II) was predicted to have been lower in the water column and shorter in duration than the trajectories for all other years in our comparison. As expected from the egg stage-dependent schedule of specific gravity (Kendall & Kim, 1989), all trajectories ascended during early stages to a mid-stage plateau and then descended to the seafloor (Figure 5). The trajectory for 2015 was unique among all years compared in that it plateaued early, never ascended above 270 m, reached the seafloor only 5 days after fertilization, and terminated (i.e., hatched) earlier than all other years.

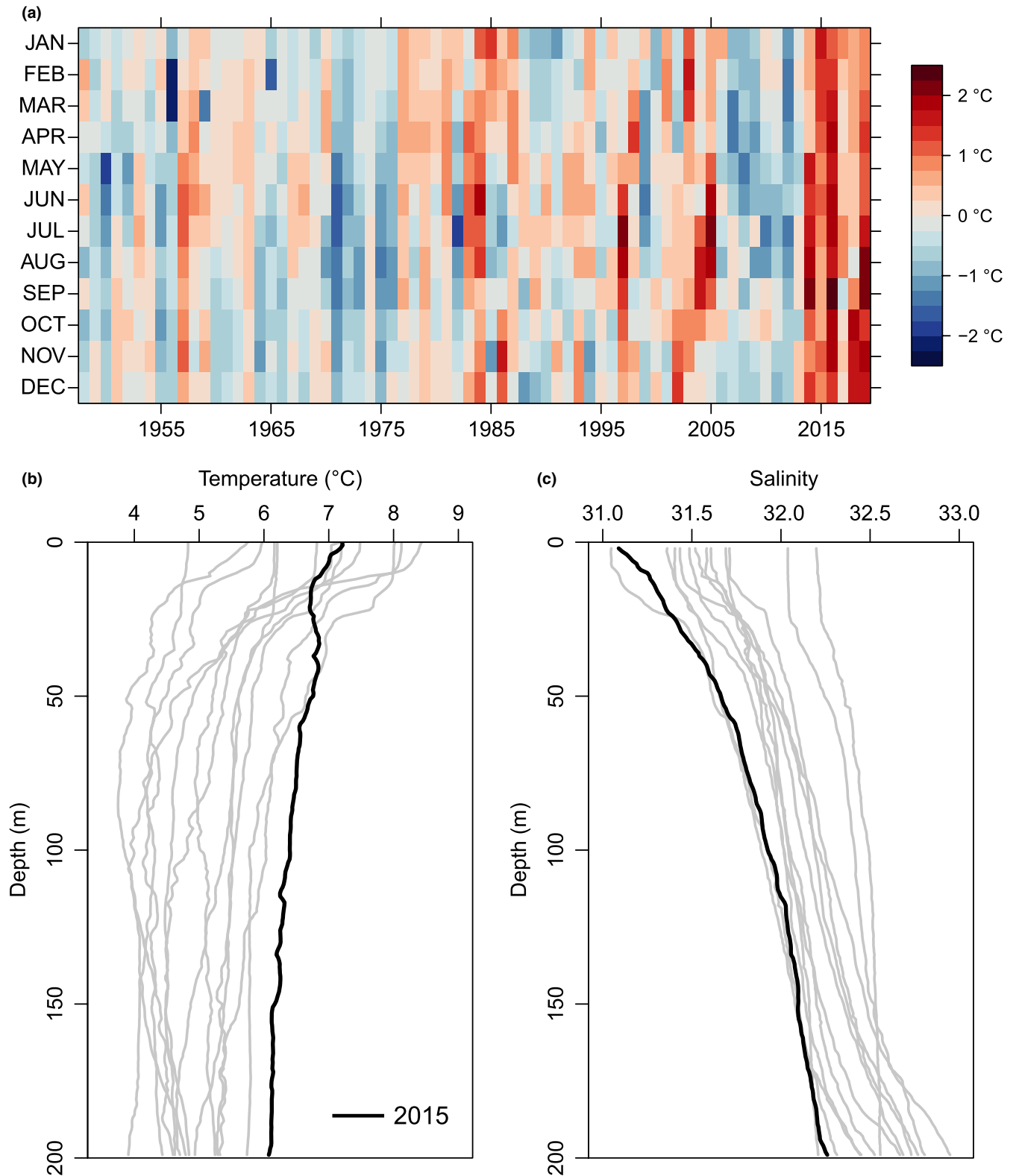


FIGURE 3 Physical characteristics of the Gulf of Alaska before and during the heatwave. (a) Sea surface temperature anomalies in the Gulf of Alaska derived from NCEP Reanalysis data. Data extend through 2019. (b) Average temperature and (c) salinity profiles from Line 8, from 2000 to 2017, sampled between 5/25 and 6/8. No data were available for 2001, 2002, 2012, 2014, or 2016. Values from 2015 are shown in black

3.5 | Abundance and survival of walleye pollock

In 2015, the mean No. m^{-2} of larval pollock in late May to early June was 1.6 larvae, the lowest in the time series 1981–2017 (Figure 6), and 2.5 SDs below the historical mean (ln-scale). The previous survey, in 2013, captured 163 larvae m^{-2} . Prior years with low abundance were 2004 (1.8 m^{-2}), 1985 (4.6 m^{-2}), and 1991 (5.5 m^{-2}). Low estimated abundance of larval pollock in 2015 was followed by low catches of age-0 pollock in late summer (mean 2015 CPUE = 0.001 m^{-2}), approximately 1/50th of the next lowest catch (0.06 m^{-2} in 2003), and 5 SDs below the historical mean (ln-scale). The estimated instantaneous mortality rate (M) from late May until early September 2015 was the highest observed in our time series (Figure 6). The estimated number of larvae produced in 2015 per unit spawning stock biomass ("spawner productivity") was also the lowest during the period for which data exist (Figure 6).

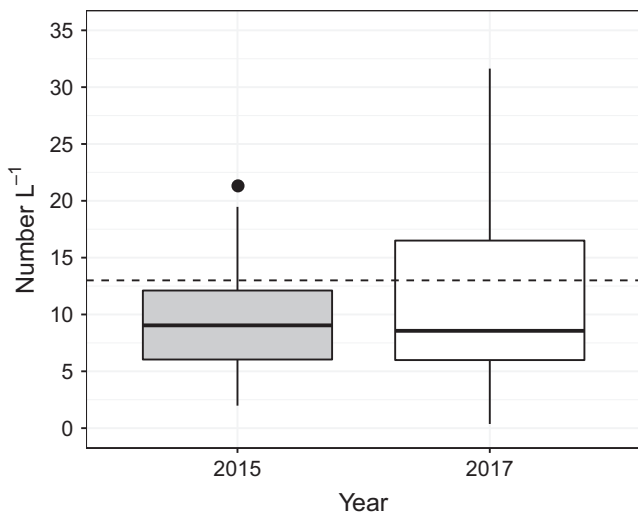
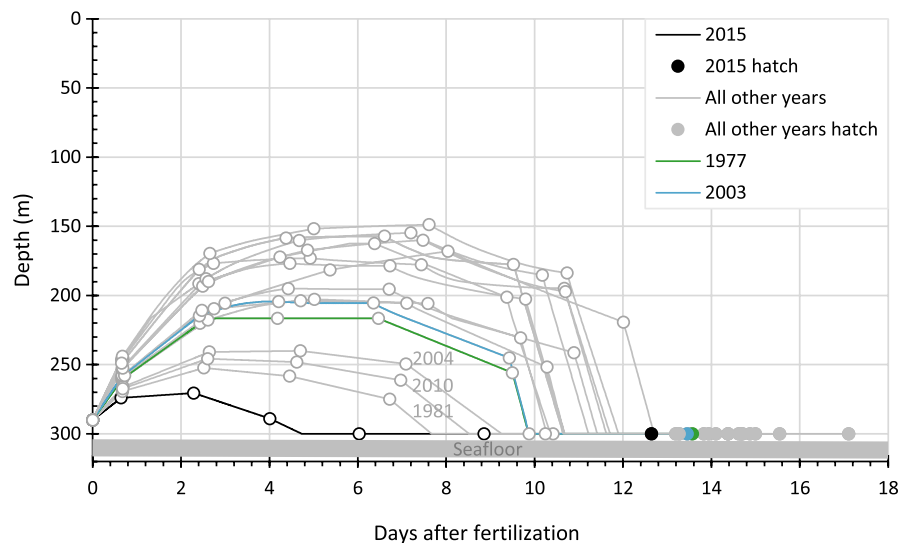


FIGURE 4 Density of copepod nauplii > 150 μm in 2015 and 2017 from 25 stations within the larval sampling area (Figure 1). Horizontal line shows the estimated density (13 L^{-1}) below which 25% of larval pollock have empty guts (Theilacker et al., 1996)

FIGURE 5 Predicted trajectories of the vertical position of Type II walleye pollock eggs in Shelikof Strait by year class (1977, 1981, 1985, 1986, 2000, 2003–2011, 2013, 2017). Trajectories start (0 d) at the assumed spawning depth (290 m). Subsequent symbols indicate the endpoint of each of six egg development stages. All trajectories reached the seafloor (300 m) prior to the end of the embryonic period (i.e., hatch), which is indicated by filled symbols. The 2015 year class and some notable others (see text) are distinguished by color or labels



While 2015 was anomalous in terms of temperature as well as abundance and survival of early life stages, there was no historical relationship between thermal conditions and $\ln(\text{larval CPUE})$ ($n = 32$, $p > .10$), $\ln(\text{age-0 CPUE})$ ($n = 10$, $p > .10$), M ($n = 10$, $p > .10$), or spawner productivity ($n = 32$, $p > .10$; Figure S3). The year 2005, which had warmer mean summer temperatures than 2015, saw the highest age-0 abundance and lowest mortality rate in the time series (Figure S3), in stark contrast to the 2015 observations.

3.6 | Condition, diets, and growth potential in late summer

Body condition of juvenile pollock was poor in 2015, as indicated by low weight at length in late summer, and was second lowest in the time series after 2005 (Figure 7). For a given length, individuals weighed 6% less in 2015 compared to 2013, which was a relatively average year in terms of body condition. The three years with lowest mean condition were the three warmest years as measured by mean summer SST. However, the summer of 2003 was only slightly cooler than 2015, yet age-0 pollock had the highest condition in the time series.

A comparison of pollock stomach contents suggests that prey resources differed for juvenile pollock in 2013 compared to 2015 (Figure 8). Considering fish in the 50-mm size range, the primary prey items by weight in 2013 were juvenile and adult euphausiids (65%) and large (>2.5 mm total length) copepods (25%). In 2015, juvenile and adult euphausiids comprised less than 3% of the diets of 50-mm pollock, and large copepods comprised 64%. For all size classes, euphausiids were relatively less prevalent in 2015 compared to 2013 in terms of percent contribution by weight (Figure 8). For 50-mm and 60-mm fish, a smaller proportion of individuals had euphausiids present in their diets in 2015 compared to 2013 ($\chi^2 = 31.8$, $p < .01$ for 50-mm; $\chi^2 = 8.7$, $p < .01$ for 60-mm). For the larger size class (70-mm), the proportion of fish with euphausiids in their diets did not differ significantly between 2013 and 2015.

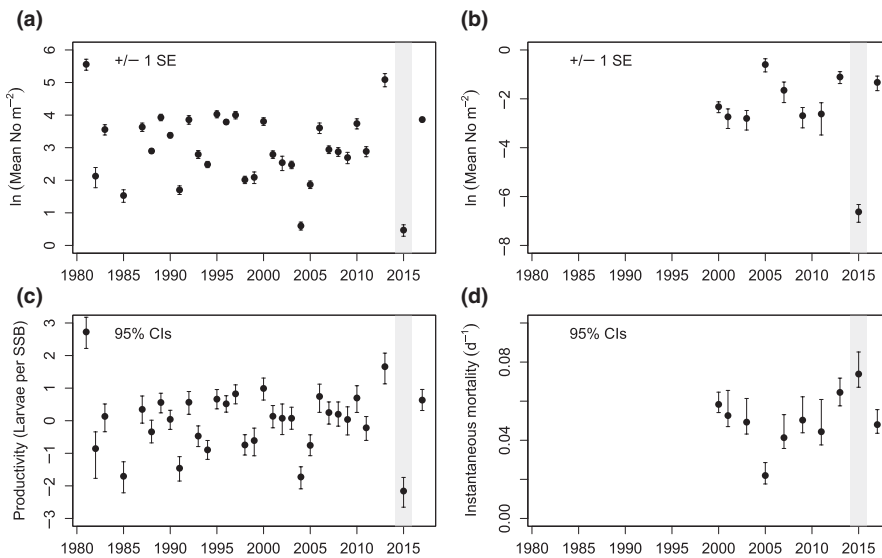


FIGURE 6 Time series of (a) mean CPUE of larval walleye pollock in late May sampling period within a standard survey area, (b) mean CPUE of age-0 walleye pollock sampled in late summer, (c) productivity measured as the standardized ln ratio of larvae per unit of SSB, and (d) estimated instantaneous mortality rate from the late larval to early juvenile stage. Gray shading indicates data for 2015. CPUE, catch per unit effort; SSB, spawning stock biomass

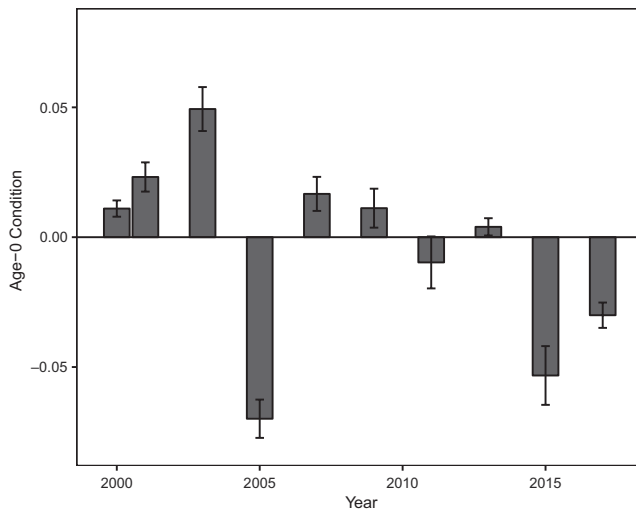


FIGURE 7 CPUE-weighted and day-corrected average body condition (± 1 SE) of age-0 pollock captured in late summer ($N_{\text{total}} = 4,656$, $N_{2015} = 115$). CPUE, catch per unit effort

Using a bioenergetics model, we estimated the amount of consumption of prey required for a fish to achieve positive growth given the observed temperatures and diets. In 2013, a 60-mm fish would need to consume at least 4.3% of its body weight per day to maintain positive growth. In 2015, the same-sized fish would need to consume at least 4.9% of its body weight per day, an increase of 14%. For a 50-mm fish, consumption would need to increase by 19%, and for a 70-mm fish, consumption would need to increase by 10%. The warmer temperatures in 2015 were responsible for approximately half of the increase in required consumption (Figure 9). Changes in the prey composition (as measured by taxon percent weight in stomach contents) contributed a majority of the remaining differences in required ration sizes. The stomach contents of age-0 pollock were comprised of prey with lower energy densities for all three size classes in 2015 relative to 2013. This difference was particularly notable for the smallest size class fish, which had an average prey energy density in 2015 of 5,099 J/g ($SD = 336$) compared to 5,611 J/g

($SD = 400$) in 2013, a significant difference ($t = 5.9$, $p < .01$) due in large part to the near absence of energy-dense euphausiids in stomachs of 50-mm pollock in 2015.

4 | DISCUSSION

For pollock in the Gulf of Alaska, the marine heatwave of 2014–2016 corresponded to the lowest abundance and survival rates of early life stages in the data record and, as a result, the near-total loss of a year class (2015) in the population. Estimates of the abundance of the 2015 year class at age 1 from an age-structured stock assessment model are 0.1% of the long-term mean (Dorn et al., 2018). In the first few weeks and months of life, where daily mortality rates are high, changes in mortality can have a drastic effect on ultimate year class size. The expectation for GOA pollock is that most of the variability in mortality occurs between feeding larval and juvenile stages (Megrey et al., 1996). In 2015, the cohort had been impacted by high mortality before the feeding larval stage, as indicated by an extremely low productivity index. Poor survival persisted over summer in association with poor body condition attributable to temperature-related increases in metabolic demand and lower availability of preferred prey. Our analyses suggest pollock experienced a combination of direct physiological effects of physical conditions (temperature, seawater density) on early life stages, as well as indirect bottom-up effects via changes in zooplankton prey.

4.1 | Egg buoyancy and vertical position

One hypothesis for low survivorship is that unprecedented hydrographic conditions contributed to increased egg mortality via effects on egg vertical position. The relative warmth and freshening of the lower water column increased the egg development rate and lowered seawater specific gravity, resulting in a unique vertical

FIGURE 8 Percent diet composition by weight for age-0 pollock collected in the core Semidi area in 2013 and 2015. Abbreviations for euphausiids indicate larval stages calyptopsis and furcilia (c + f) or juveniles and adults (j + a)

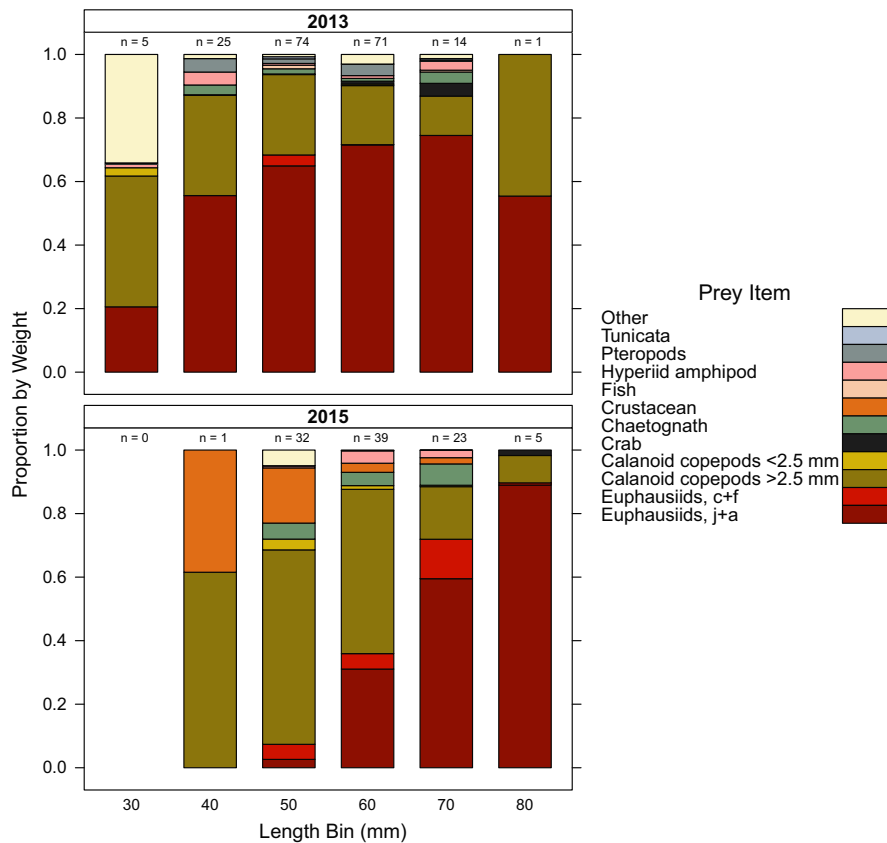
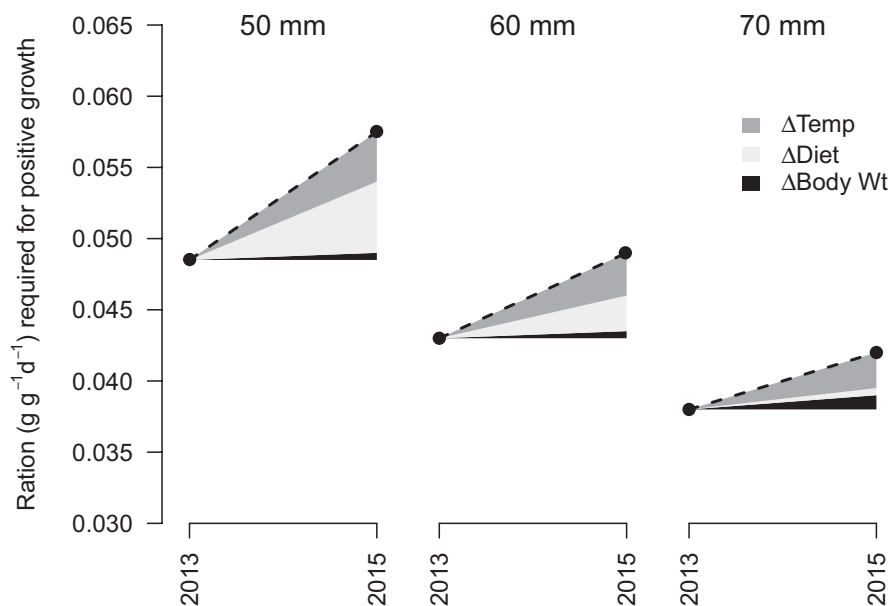


FIGURE 9 Bioenergetics model results showing the daily ration required to obtain positive growth rates in 2013 versus 2015 for three size classes of juvenile pollock. Shaded triangles show the relative contribution of changes in temperature, diet composition, or body weight to the increase in required consumption in 2015 relative to 2013



position trajectory predicted for walleye pollock eggs in 2015. Observations of low salinity in spring of 2015 were consistent with records from the Seward Line in the Central Gulf of Alaska (Batten et al., 2018). Our salinity profiles from May were the closest available following peak spawning (late March–April) in Shelikof Strait. We deemed them suitable for modeling egg vertical position given the apparent negligible change in surface and near-bottom temperature and salinity from March through May (Stabeno et al., 2004).

Egg-specific gravity of marine fishes is an adaptive response to the vertical structure of temperature and salinity in spawning areas because it affects egg dispersal and transport, which in turn affect survival (Sundby & Kristiansen, 2015). We hypothesize three mechanisms by which a deeper distribution of the typically pelagic eggs may have increased mortality. First, the lower position of eggs in the water column might have increased their vulnerability to predation by adult pollock (Schabetsberger et al., 1999)

and invertebrates (e.g., euphausiids; Brodeur et al., 1996). Second, horizontal dispersal of eggs may have been reduced, which is relevant to advection trajectory and density-dependent mechanisms; density-dependent mortality of larvae was high during 1981 (Duffy-Anderson et al., 2002) another year when the egg vertical position trajectory was low. Finally, a deeper distribution would increase the ascent distance larvae must traverse to reach prey-rich feeding areas upon hatching, which tend to be the upper 30 m (Napp et al., 1996). While temperatures were warm at depth ($>6^{\circ}\text{C}$), it is unlikely that thermal effects reduced egg survival, as pollock eggs successfully hatch at temperatures exceeding 10°C (Laurel et al., 2018). It is noteworthy that the unique trajectory for the 2015 year class corresponds with the lowest age-1 abundance on record as indicated by the stock assessment model (Dorn et al., 2018). Among the years in our comparison, however, mid-stage egg depth was not generally indicative of subsequent age-1 abundance (Figure 5). For example, year classes with the second lowest (2003) and the highest (1977) age-1 abundance estimates had similar vertical position trajectories, and three trajectories with low plateaus were for year classes with relatively low (2004), medium (2010), and high (1981) age-1 abundance. Considerable variation exists in the vertical position of walleye pollock eggs (Kendall, 2001; Kendall & Kim, 1989) and interannual variation has not been well studied.

4.2 | Feeding conditions for larval pollock

Temporal mismatch of first-feeding larvae with production of their prey has long been hypothesized to affect recruitment in marine fishes (Cushing, 1990) and depends on temperature-dependent processes. In seasonal environments, the spawn timing of fishes has evolved so that offspring arrive as prey production rapidly increases in spring. For pollock that primarily feed on copepod nauplii as first-feeding larvae, changes in the timing of spawning and speed of development relative to production of nauplii could result in a mismatch. Spawn timing of many fishes, including pollock, is temperature-dependent (Rogers & Dougherty, 2019). Earlier spawning and faster egg development in warmer years can advance the first-feeding larval period by over a week (Rogers & Dougherty, 2019). However, despite warm temperatures in 2015, spawn timing was approximately average, a likely consequence of a spawning population dominated by young fish that spawn later on average (Rogers & Dougherty, 2019).

The timing and magnitude of production of copepod nauplii as prey for larval fishes is also temperature-dependent. Warmer temperatures typically decrease copepod development times and increase growth rate and production (Hirst & Lampitt, 1998; Huntley & Lopez, 1992), so the warm temperatures in 2015 should have resulted in higher abundances of nauplii in the water column in May, assuming no food limitation. However, the opposite was observed; abundances of nauplii were low relative to requirements of larval pollock. Thermally mediated reduced clutch sizes of *Pseudocalanus*

spp. (Hirst & Lampitt, 1998; Napp et al., 2005) could partially explain these observations. Furthermore, the large, negative anomaly in *M. pacifica* abundance would suggest a significant drop in the contribution of nauplii of that species to the zooplankton community. Egg production rates for *M. pacifica* typically peak in May (Hopcroft et al., 2005); therefore, the timing of this drop in nauplii produced would be significant for larval pollock. Surface chlorophyll data from satellites suggest that primary production was not anomalous in terms of magnitude or timing in 2015; however, these estimates are based on ocean color observations and do not reflect potential changes in phytoplankton community composition (e.g., a higher fraction of the total primary production occurring in the smallest size fractions; Peter & Sommer, 2012) that may affect food quality for zooplankton (Galloway & Winder, 2015; Nejstgaard et al., 2001). Regardless, naupliar estimates from 2015 were low, lending credence to the idea that food limitation contributed to poor larval pollock survivorship.

4.3 | Age-0 bioenergetics

Conditions in late summer were also not conducive for growth and survival of age-0 pollock. Our bioenergetics modeling suggests a bottom-up mechanism whereby warmer temperatures, combined with reduced availability of preferred prey items (Wilson et al., 2006), contributed to poor body condition of age-0 pollock in 2015. Age-0 pollock in 2015 had to consume 10%–19% more prey to maintain the same level of growth as in 2013, a result of accelerated metabolic rates due to warm temperatures, and consumption of reduced-quality prey types. Most notable was the low abundance of euphausiids in pollock diets in 2015 compared to 2013, especially among fish < 70 mm in length. While the diet data suggest euphausiids were relatively less prevalent in 2015 compared to 2013, sampling of the prey field did not show notable differences in euphausiid abundances between those years. However, the zooplankton data that we present here are for early stage euphausiids because adult euphausiids are poorly sampled by bongo nets. Acoustic-trawl sampling of adult-stage euphausiids suggests slightly reduced euphausiid abundance in 2015 relative to 2013, although not as low as in some years (Ressler, 2017). The positive anomaly of *C. marshallae* in 2015 would benefit smaller juvenile pollock (< 50 mm); however, in a typical year, larger pollock preferentially switch to diets dominated by euphausiids (Wilson et al., 2009). Thus, age-0 pollock likely faced multiple compounding factors in 2015: high metabolic demands due to increased temperatures, and reduced availability of high-quality euphausiid prey for larger juveniles.

Poor body condition at end of summer may have negative implications for pollock survival through their first winter (Sogard & Olla, 2000). As prey densities decrease in winter, young pollock depend on energy stores to subsist, seeking out cooler waters to lower their metabolic demands when prey are scarce (Bailey, 1989). Warm winter temperatures can thus further exacerbate the impacts

of low energy stores, as behavioral thermoregulation becomes insufficient to balance metabolic demands. In the Bering Sea, energy storage prior to winter is a predictor of recruitment to age-1 (Heintz et al., 2013; Siddon et al., 2013), although this relationship has not been evaluated for pollock in the GOA.

Our bioenergetics model necessitated some simplifying assumptions, including static predator and prey energy densities based on published values. Previous work in the eastern Bering Sea suggests that taxon-specific energy densities are likely to be lower in warm years; for example, *Calanus* spp. percent lipid was 27% lower in a warm year compared to a cold year (Heintz et al., 2013). This decrease in energy density would exacerbate the differences in growth potential and consumption demands predicted by our model. More generally, a reduction in quality of zooplankton prey would be consistent with zooplankton abundance patterns during warming that suggest a reduction in body size and an increase in the proportion of smaller-sized zooplankton. In Alaska waters, increases in smaller zooplankton and more southern species have been observed in the Bering Sea (Kimmel et al., 2018), Prince William Sound (McKinstry & Campbell, 2018), and the Gulf of Alaska (Batten & Walne, 2011; Kimmel & Duffy-Anderson, 2020). Smaller zooplankton often have less lipid, thus decreasing the quality of prey available to predators such as age-0 pollock.

4.4 | Reproductive output

Low abundance of larvae in spring of 2015 might be linked to reduced reproductive output of the spawning stock that winter; however, the limited available data do not support this hypothesis. Spawning stock biomass was only slightly below average (Dorn et al., 2018), and an acoustic-trawl survey of spawners in Shelikof Strait found spawning females in average condition, with a mean gonado-somatic index approximately equal to the long-term mean (McCarthy et al., 2016). This is in contrast to the following year (2016), when spawners were in markedly poor condition as indicated by low weight at length and a below-average gonado-somatic index (Stienessen et al., 2017). Poor body condition has been linked to reduced fecundity and atresia in other gadids (Kjesbu et al., 1991). Thus, while poor condition of spawning females may have affected reproductive output as the heatwave persisted into 2016, existing evidence does not point to this as a problem in 2015. Detailed histological work is ongoing to determine whether ovarian development, maturation, and fecundity were atypical during heatwave years.

4.5 | Advection of larvae

The Alaska Coastal Current (ACC) carries eggs and larvae from spawning locations in Shelikof Strait to nursery grounds in the regions of the Semidi Bank and Shumagin Islands (Hinckley et al., 1991). Variation

in the ACC has been linked to unusual larval distributions in May, for instance, a reversal of flow in Shelikof Strait in 1996 displaced larvae to the northeast of their typical distribution (Bailey et al., 1999). Strong off-shelf flow could potentially advect larvae away from nursery grounds and into the strong Alaskan Stream, where they would be effectively lost to the system (Hinckley et al., 1991; Incze et al., 1989). Direct current measurements do not exist for 2015 in the study area; however, a satellite-tracked drifter drogued at 40 m (the depth of maximum larval abundance) and released May 25, 2015, in Shelikof Strait became entrained in an eddy near the exit of Shelikof Strait for over a month (Figure S4, data from https://www.ecofoci.noaa.gov/drifters/efoci_drifterData.shtml), suggesting conditions conducive to larval retention (Bograd et al., 1994; Stabeno et al., 1996). Modeled May–June transport speed though Shelikof based on the Hybrid Coordinate Ocean Model (HYCOM) indicated slow current speeds in 2015 relative to other years 1991–2017 (Kimmel & Duffy-Anderson, 2020), again suggesting retention as opposed to advection. Retention of larvae is consistent with observed surface winds, which lacked a strong southward component, and the buildup of low salinity water in 2015 (Wilson & Laman, 2020). Timing and location of spawning may affect the ultimate drift trajectory of eggs and larvae (Hinckley et al., 2001), but neither was anomalous in 2015 (McCarthy et al., 2016; Rogers & Dougherty, 2019). Thus, while detailed observations of currents on the Gulf of Alaska shelf are lacking for 2015, available data and models do not support a hypothesis of off-shelf larval advection.

4.6 | Predation and competition

The Blob has been implicated as the cause of additional atypical ecological occurrences in the Gulf of Alaska. Changes in groundfish spatial distribution (Yang et al., 2019) and groundfish weight at length (Barbeaux et al., 2020; Dorn et al., 2018), seabird die-offs and breeding failures (Piatt et al., 2020), and unusual mortality events for fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeanglia*) (Savage, 2017) were recorded. A sharp decline in Pacific cod biomass led to a federally declared fishery disaster (Barbeaux et al., 2020). Some of these observations may be the result of top-down forcing acting in concert with bottom-up processes to influence the marine ecosystem. Specifically, Piatt et al. (2020) hypothesized that warm temperatures through the water column in 2015 would have increased consumption demands of ectotherms, particularly Pacific cod, adult pollock, and arrowtooth flounder (Holsman & Aydin, 2015), leading to more rapid depletion of available forage fishes (including age-0 pollock) and zooplankton prey. Indeed, along with the age-0 pollock results reported here, forage fish abundances (e.g., capelin *Mallotus catervarius*; McGowan et al., 2020) and energy content (e.g., Pacific sand lance *Ammodytes personatus*; Von Biela et al., 2019) were low in 2015, which is consistent with the theory that predators with thermally elevated metabolic rates may have grazed down a forage base with lower nutritional value and energy content. Ultimately, the forage fish and euphausiid prey base may

have been insufficient to provision upper trophic level predators, leading to the mass die-offs observed (Piatt et al., 2020). For age-0 pollock, predation mortality likely increased during the Blob years, as did competition for energy-rich zooplankton prey. The 2012 year class of pollock was extraordinarily abundant and would have exacerbated these effects, either through direct predation on pollock eggs, larvae, or juveniles (i.e., cannibalism; Dwyer et al., 1987), or by competing for euphausiids, which remain a key prey item for pollock of all ages (Urban, 2012).

4.7 | The Blob and future warming

The 2014–2016 marine heatwave provides us with an example of anomalous and prolonged warm conditions in the Gulf of Alaska. While pollock early life stage data are not available for 2014 or 2016, the response in 2015 was not necessarily what would have been expected based on past warm years. For instance, 1997 and 2005, both warm years according to SST anomalies, resulted in average or above-average abundance of pollock early life stages. Lower trophic level responses to the heatwave also differed from previous warm years (Batten et al., 2018): the abundance of diatoms, which had previously been positively related to temperature, was greatly reduced in 2015, and zooplankton biomass became decoupled from diatom abundance (Batten et al., 2018). Oceanographic and ecosystem conditions beyond temperature contributed to these dynamics. Specifically, in 2015, low salinity water and a deep mixed layer depth were associated with delayed and reduced diatom production (Batten et al., 2018), and we have shown here the probable effect of low salinity waters on buoyancy of pollock eggs. Our results thus emphasize that temperature alone is not sufficient to characterize conditions for pollock survival or condition and additional oceanographic and ecosystem conditions must be considered. Temperature increases the potential for juvenile pollock growth, but also energetic demands; thus, the impact of warmer temperatures on juvenile pollock will depend on how prey resources are affected, which will in turn be determined by energetic demands of competitors in the ecosystem. These results highlight the importance of considering the dynamics of other ecosystem components when evaluating climate change impacts on individual species.

While it was underway, the 2014–2016 marine heatwave was a unique event in the NE Pacific Ocean, notable for its intensity, duration, and geographic scale (Di Lorenzo & Mantua, 2016). However, ocean conditions in 2019 were similarly warm, including at depth, and preliminary data show similar ecosystem responses, including low zooplankton and larval fish production, and particularly low abundances of juvenile gadids, including pollock (Zador et al., 2019). Heatwaves are predicted to increase in frequency under global warming (Frölicher et al., 2018), suggesting that rather than being an isolated event, the 2014–2016 heatwave may provide critical lessons for fisheries science and management through recurring warm conditions in the GOA. Ecosystem monitoring, including the early life stages of fishes, can give early

warning of ecosystem shifts that may have economic impacts both immediately and in years to come.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

L.A.R., M.T.W., and J.T.D.-A. designed the study; L.A.R. conducted analyses, with contributions from M.T.W. (egg vertical position model) and D.G.K. (zooplankton); J.F.L. processed age-0 pollock diets and prepared data files; L.A.R. drafted the manuscript with contributions from M.T.W. and D.G.K.; all authors contributed to manuscript revisions and final edits.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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