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Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Influence of environment on walleye pollock eggs, larvae, and juveniles in the southeastern Bering Sea

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ARTICLE INFO

Available online 21 February 2012

Keywords:

Walleye pollock
Early life stages
Environmental conditions
Generalized additive models
Theragra chalcogramma
Bering Sea

ABSTRACT

We examined the influence of environmental conditions on walleye pollock (*Theragra chalcogramma*) early life history in discrete stages at two ecological scales using a 17-year time series from the southeastern Bering Sea. Generalized additive models (GAMs) were used to quantify relationships between walleye pollock stages (eggs, yolk sac larvae, preflexion larvae, late larvae, and juveniles), the fine-resolution environment (temperature, wind speed, salinity, and copepod concentration), and the broad-resolution environment (annual spawning stock biomass, temperature, zooplankton biomass, and wind mixing). Early stages (eggs, yolk sac larvae, and preflexion larvae) were associated with high spawning stock biomass, while late stages (late larvae and juveniles) were not associated with spawning stock biomass. The influence of temperature increased with ontogeny: high egg abundance was associated with temperatures from -2 to 7 °C and negative annual temperature anomalies and high juvenile abundance was associated with temperatures from 4 to 12 °C and positive temperature anomalies. Winds enhanced the transport of early stages from spawning locations to shallower sampling depths, but did not affect feeding stages (preflexion larvae, late larvae, and juveniles) in a manner consistent with the encounter-turbulence hypothesis. Feeding stages were positively associated with localized copepod concentrations but not zooplankton biomass anomaly, suggesting that the localized measurements of potential prey is a better indicator compared to broad-scale conditions measured in areas where these stages do not necessarily occur. Broad-resolution covariates, however, explained a greater portion of the overall variation than did fine-resolution models. Of the environmental conditions examined, temperature explained more variation in abundance of walleye pollock early life stages than any other covariate. Temperature is likely a major driving force structuring variability in populations of walleye pollock in their first year of life, acting directly upon them and indirectly upon their physical habitat and prey community.

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1. Introduction

The southeastern Bering Sea (SEBS) is part of a productive, high-latitude ecosystem that provides critical spawning and larval habitat for demersal fish species. In particular, the SEBS serves as important spawning, nursery, and forage habitat for walleye pollock (*Theragra chalcogramma*, hereafter referred to as pollock), a target species for one of the world's largest commercial fisheries (FAO, 2007). Pollock account for about 60% of the total

landings of groundfish in Alaskan waters (Ianelli et al., 2009). Pollock also serve a key role in the Bering Sea food web, acting as prey for marine mammals and seabirds, piscivores, and zooplanktivores (Aydin et al., 2002). For Bering Sea pollock, female spawning biomass has fluctuated over the last four decades from 0.85 to 4.1 million metric tons and recruitment variability in the species is high, similar to other gadids (Ianelli et al., 2009). In the Gulf of Alaska (GOA) spawning biomass changes the initial production of eggs and availability of hatched larvae (Bacheler et al., 2009). Climate and hydrography influence the extent of transport from spawning grounds (Ciannelli et al., 2005; Wilson, 2009) and the survival and growth of larvae and juveniles (Porter et al., 2005; Logerwell et al., 2010).

Environmental conditions may act on growth and survival of pollock early life stages (ELS) either singly or in combination. For

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example, pollock egg development, time to hatch, and use of yolk reserves are controlled by temperature (Blood, 2002). Early larvae are more successful under both moderate wind-driven mixing and good prey conditions (Walline, 1985; Bailey and Macklin, 1994; Mueter et al., 2006). Olla et al. (1996) suggested that mixing and temperature interact to determine larval pollock feeding success, subsequent growth, and survival. Prey availability and temperature also interact to determine prey capture rates and survival of larvae, particularly when prey are scarce (Fukuchi, 1976). Adult pollock biomass, temperature, and wind conditions influence early juvenile and age-1 abundances in the Bering Sea (Wespestad et al., 2000; Duffy-Anderson et al., 2005; Mueter et al., 2006).

For Bering Sea pollock, there has been no comprehensive examination of all ELS and the relative importance of environmental conditions at each stage. Recently, Ciannelli et al. (2004) used a stage-specific approach to determine the density-dependent structure of pollock survival in the GOA. Bacheler et al. (2010) used a stage-specific approach to define the temporal distributions of pollock eggs and early stage larvae over the SEBS shelf. Bacheler et al. (2010) identified three unique spawning areas with distinct egg and early larval phenologies, but did not examine interannual or seasonal changes in the physical environment experienced by eggs, larvae, or juveniles. Objectives of the current study were to identify key factors that affect pollock ELS abundances in the Bering Sea, and to quantify the influence these factors have on abundances during the first year of development. We quantified the effects of temperature, salinity, zooplankton availability, winds, and adult spawning.

2. Methods

2.1. Ichthyoplankton sampling

Depth-integrated abundance (number collected per 10 m² sampled) of pollock ELS were measured during ichthyoplankton surveys conducted by NOAA's Alaska Fisheries Science Center (AFSC, see Matarese et al., 2003). Surveys targeted pollock spawning grounds, areas adjacent to spawning grounds, and areas of downstream transport. Data were selected to include only samples south of 60°N latitude and east of the Aleutian Basin as samples were collected rarely outside of this area (Fig. 1). Data also were limited temporally to those between February and October due to limited sampling outside of this window, and alignment with the spawning season (Bacheler et al., 2010). Surveys within the target area and dates occurred in 17 years within the time series (1988, 1991, 1992, 1994–2000, and 2002–2008, Table 1). It should be noted that Bacheler et al. (2010) identified three unique pollock spawning areas within our geographic range, but we opted to integrate the data to: (1) provide a synoptic look at factors influencing pollock ELS in the SEBS and (2) provide sufficient geographic coverage to ensure that all ELS were represented.

Abundances were divided by developmental stage to determine if stage-specific responses to environmental conditions existed. Separate analyses were conducted for eggs, yolk sac larvae (≤ 4.4 mm SL), preflexion larvae (4.5–9.9 mm SL), late larvae (10.0–24.9 mm SL), and juveniles (25.0–65.0 mm SL). Larval categories were based on standard length (SL) and key developmental attributes (Matarese et al., 1989). Juveniles > 65 mm were not considered because they were not effectively captured by our sampling nets. Sampling for eggs through preflexion larvae was conducted using obliquely towed bongo nets (333 or 505 μ m mesh). The number of tows containing late larvae and juveniles was rare relative to the other three stages. To increase the available sample size for these stages, we also examined catch records from the 1 m² MOCNESS (333 or 505 μ m mesh) and the 1 m² Tucker trawl (333 or 505 μ m mesh). Differences

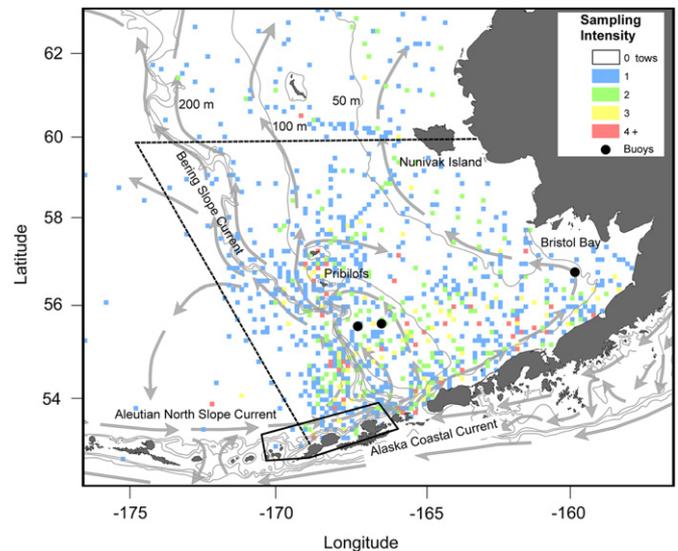


Fig. 1. The southeastern Bering Sea showing depth contours, major currents, locations of wind buoys, and ichthyoplankton sampling intensity (tows per 10 × 10 km grid cell). The box outlined by the broken lines indicates samples included in the current analyses and the box outlined by the solid lines represents locations of maturity surveys in the eastern Aleutian Islands.

Table 1

Summary of *Theragra chalcogramma* early life stage surveys in the southeastern Bering Sea. Number of cruises, gear types used, number of tows (*n*), and sampling date ranges. Tows examined were limited to bongo nets (BON), MOCNESS (MOC), and Tucker trawls (TUCK).

Year	Cruises	Gear	<i>n</i>	Dates
1988	2	BON	100	03/17–04/25
		TUCK	4	
1991	2	BON	71	03/11–05/08
1992	2	BON	35	04/16–07/14
		MOC	7	
1994	4	BON	101	04/16–09/21
		TUCK	8	
		MOC	9	
1995	5	BON	256	02/22–09/24
		TUCK	46	
		MOC	5	
1996	5	BON	16	03/06–09/15
		TUCK	9	
		MOC	19	
1997	4	BON	125	04/16–09/17
		TUCK	22	
		MOC	2	
1998	2	BON	17	04/07–09/14
1999	4	BON	108	04/14–09/14
		MOC	6	
2000	5	BON	40	02/17–09/22
2002	5	BON	35	05/13–10/06
		TUCK	3	
2003	4	BON	125	03/04–09/27
		MOC	9	
2004	5	BON	54	07/29–10/02
2005	7	BON	121	03/04–10/06
		MOC	20	
2006	4	BON	189	05/09–09/22
		MOC	12	
2007	7	BON	161	04/11–10/08
2008	6	BON	116	02/18–09/26
		MOC	13	

in selectivity between bongo, MOCNESS, and Tucker gears have been shown to be minor for all stages examined (Wiebe et al., 1976; Shima and Bailey, 1994). Volume filtered by each gear type was determined using calibrated flow meters. Table 1 lists the number of tows conducted with each sampling gear.

2.2. Adult maturity

To address the potential for variation in onset of spawning to impact abundance estimates from field surveys, gonad maturity data was collected by AFSC's Midwater Assessment and Conservation Engineering (MACE) program. Gonad maturity stage was assessed macroscopically by readers on the NOAA ships *Miller Freeman* and *Oscar Dyson* each winter using samples from trawls fished over pollock spawning grounds. Maturity data collected during pollock surveys from 1992 to 1996 were based on a 5-stage categorical scale developed specifically for walleye pollock (Williams, 2007). From 1996 to the present this scale was expanded to an 8-stage scale based on Maier's (1908) general teleost maturity classification (in Williams, 2007). Data from 1996 to 2007 were converted back to the 5-stage scale, where immature gonad was represented by stage 1 up to spent gonad represented by stage 5 (Stahl and Kruse, 2008). Since we were most interested in the possibility of delayed spawning related to sea ice or temperature conditions, we limited our examination to females larger than the presumed spawning length (35 cm fork length, FL; Stahl and Kruse, 2008) captured between March 1 and 10. These dates were sampled most consistently across years. Samples were restricted to hauls occurring in the eastern Aleutian Islands outlined in Fig. 1 to account for differences in spawning time across areas (Bacheler et al., 2010). We compared the stage of gonad maturity across temperature anomalies ($^{\circ}\text{C}$) based on net-mounted temperature sensor data collected during each tow. Maturity stages were compared using multiple linear regression with fork length and gear temperature anomaly as independent variables.

2.3. Environmental conditions: fine- and broad-resolution

Environmental conditions were examined at fine- and corresponding broad-resolutions when possible (Table 2). Broad-resolution indices have the advantage of larger sample sizes, while fine-resolution measurements address the immediate environmental conditions, which are more relevant to growth and survival of an early stage pollock. Fine-resolution analyses utilized point-source data from net tows, either measured at the same location and time or within one day of the tow. Fine-resolution variables examined included water temperature, salinity, wind speed, copepod concentration, day of year (DOY), location (an interactive term consisting of latitude and longitude), and year (as a factor). Temperature ($^{\circ}\text{C}$) and salinity data were derived from vertical CTD (Sea Bird 25, Sea-Bird Electronics, Bellevue, Washington, USA) profiles collected concurrently with ichthyoplankton samples from 2002 to 2008. Prior to 2002, vertical profiles matching ichthyoplankton tows in space and time were obtained from the EPIC data archive maintained by the Pacific Marine Environmental Laboratory (www.epic.noaa.gov/epic/). Wind speeds (m s^{-1}) on each day

of sampling were obtained from the National Data Buoy Center (www.ndbc.noaa.gov) for buoys (46021, 46782, and 46020) on the SEBS shelf (Fig. 1). Measurements of wind speeds were not always available for each day; therefore, weekly averages were used in these cases ($n=336$ tows). Concentration (number m^{-3}) of small-sized zooplankton (2–15 mm) were estimated from copepods collected in zooplankton tows made concurrently with ichthyoplankton sampling using a 20 cm bongo net with 153 μm mesh and equipped with a flow meter. Copepod concentrations were included only in the models for feeding stages (preflexion larvae, late larvae, and juveniles).

Broad-resolution analyses utilized published long-term anomalies and indices of environmental conditions derived from monthly or annual averages over large spatial areas. Indices included temperature anomaly, wind mixing, zooplankton biomass anomaly, and a female spawning stock biomass anomaly. Spring sea surface temperature anomaly (SSTa, $^{\circ}\text{C}$), summer bottom temperature anomaly (BTa, $^{\circ}\text{C}$), and spring and summer wind mixing indices (m s^{-1}) were obtained from the NCEP/NCAR Reanalysis project (Kalnay et al., 1996, <http://www.esrl.noaa.gov/psd/data/reanalysis/>). Indices for the month of May (spring) were used to examine effects on early stages (eggs, yolk sac, and preflexion larvae), while indices for June–July (summer) were used to examine effects on late larvae and juveniles. Zooplankton biomass anomalies (mg m^{-3}) were derived from a time series of summer zooplankton over the SEBS middle shelf collected by the Hokkaido University (Hunt et al., 2002, 2008; A. Yamaguchi (Hokkaido University) and J. Napp, unpublished data). Size of the spawning population was represented by annual female spawning stock biomass anomalies (SSB, tons). SSB values were derived from a statistical age-structured population abundance model for the eastern Bering Sea stock based on acoustic and bottom trawl surveys conducted by AFSC (Ianelli et al., 2009).

We used generalized additive models (GAMs) to quantify the influence of environmental factors on the abundance of pollock ELS (Hastie and Tibshirani, 1993; Wood, 2006). GAMs were chosen over linear models because preliminary inspection of the data suggested that non-linear relationships were common between stages and environmental factors. Also, surveys varied in spatial coverage, temporal coverage, and in the number of tows conducted in each year, which can be included in GAM model structure. Two types of models were used for each life history stage: fine-resolution and broad-resolution. Zero abundance was common in all data sets, particularly in later stages, requiring the use of the over-dispersed Poisson error distribution (Wood, 2006).

Fine- and broad-resolution covariates included in initial models for each response variable and each stage are shown in Table 2. Final model selection involved the choice of covariates and the level of smoothness for each covariate. For both model types, the cubic spline smoother s was used (Hamming, 1973). The level of smoothing was minimized to fewer than four knots to assure interpretability of results and to minimize effects of spatial autocorrelation in fine-resolution models (Stige et al., 2006; Heinenan et al., 2008). A final set of significant covariates was selected by backward stepwise elimination when p -values > 0.05 (Burnham and Anderson, 1998; Johnson and Omland, 2004). Interactions between covariates were also tested for significance and improving model fit. The final model was determined based on the lowest generalized cross validation (GCV) score. Akaike's Information Criterion (AIC) scores also were compared for each model and were in agreement with selection based on GCV. Final-selection models were checked for temporal autocorrelation (autocorrelation function, $\text{ACF} < 0.4$). All models were coded and analyzed using the *mgcv* library (version 1.4-1; Wood, 2008) in R version 2.7.2 (R Development Team, 2008).

Table 2

Variables considered for inclusion in generalized additive models. Fine-resolution covariates were measured in association with ichthyoplankton tows and broad-resolution covariates were monthly or annual counterparts to the fine-resolution measurements integrated over the eastern Bering Sea.

Fine-resolution	Broad-resolution
Year	–
Location	–
Day of year	–
Surface water temperature	Water temperature anomaly
Wind speed	Wind mixing
Zooplankton concentration	Zooplankton biomass anomaly
Salinity	–
Spawning stock biomass anomaly	–

3. Results

3.1. Ichthyoplankton

Eggs and larvae were collected in all years. Juveniles were rare in the time-series and absent in 1988, 1991, 2006, and 2008. Over 1 million eggs, 40,000 larvae, and nearly 5000 juveniles were collected over the course of this study. Eggs occurred in 63% of bongo tows, yolk sac larvae in 27%, and preflexion larvae in 60%. Late larvae occurred in 20% and juveniles in 4% of tows of all gear types. Most pollock ELS were collected over the continental shelf at depths less than 200 m. Eggs, yolk sac larvae, and preflexion larvae were collected in three distinct areas: Bering Canyon, Unimak Island and the Alaska Peninsula, and the Pribilof Islands (Fig. 2A–C). Late larvae were collected in two areas: Unimak Island and the Alaska Peninsula and the Pribilof Islands (Fig. 2D). Juveniles were collected in the Pribilof Islands, primarily, and across the middle and inner domains (Fig. 2E).

3.2. Adult maturity

Gonad maturity stage of female fish > 35 cm FL from cruises conducted from March 1 to 10, 1992 until 2007, was compared to fork length and gear temperature anomaly using multiple linear regression. Maturity stage was not related to gear temperature anomaly or fork length (Fig. 3, model $r^2=0.255$, $p > 0.05$).

3.3. Environmental conditions

Environmental factors were included in 66–100% of the final models. Fine-resolution models explained more deviance in the

abundance of each stage than did broad-resolution models (Tables 2 and 3). This difference was attributed to the inclusion of year, location, and DOY in the fine-resolution models, rather than the contribution of environmental covariates. Broad-resolution covariates explained a greater portion of the deviance for all stages than did the fine-resolution environmental covariates (Table 4).

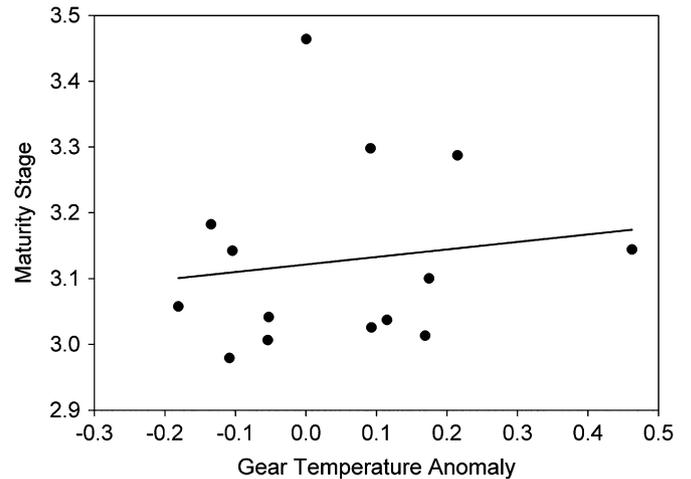


Fig. 3. Walleye pollock gonad maturity. Mean maturity stage and gear temperature anomaly in each year (1992–2007) from March 1 to 10 around Bogoslof Island and the eastern Aleutian Islands area outlined in Fig. 1.

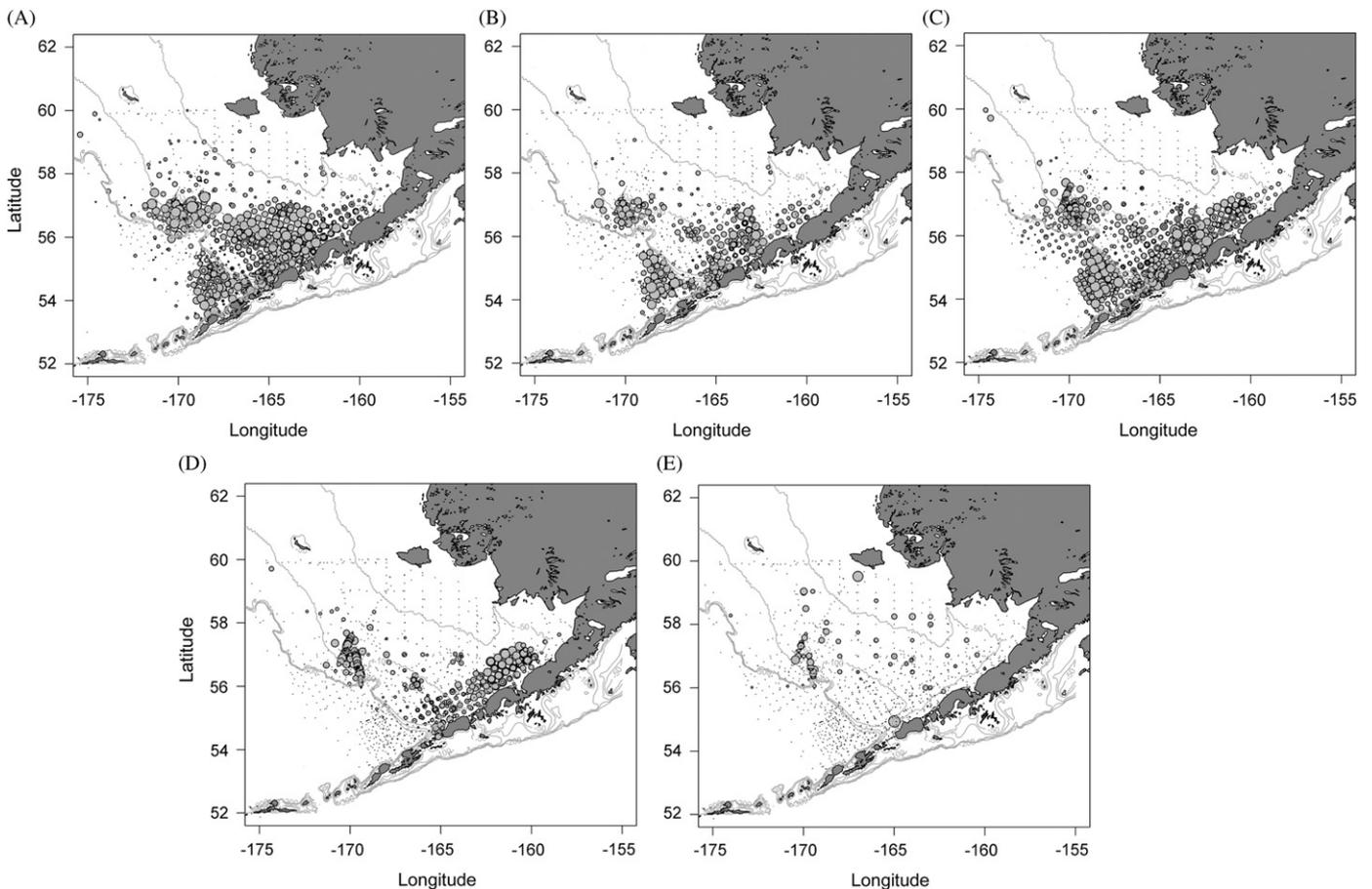


Fig. 2. Walleye pollock early life stages in the southeastern Bering Sea. Relative abundances of (A) eggs, (B) yolk sac larvae, (C) preflexion larvae, (D) late larvae, and (E) juveniles. The size of the bubbles is scaled to the largest catch within each stage.

Table 3

Generalized additive model results for fine-resolution (ichthyoplankton-associated) covariates. Percent of the total model deviance explained attributable to each covariate included for each stage and final model output. Deviance attributed to individual covariates was determined from comparison of full- and reduced-models. Covariates that were not considered in a given model are noted by *n/a* and those that were not significant in the final model are noted by *n. sig.*

	Egg	Yolksac	Preflexion	Late	Juvenile
Year	3.4	5.0	7.4	10.0	9.2
Location	2.5	1.3	1.1	1.4	3.2
Day of year	4.9	5.1	4.8	7.9	0.7
Temperature	0.6	0.9	1.9	1.7	1.1
Wind speed	1.0	1.0	<i>n. sig.</i>	0.9	<i>n. sig.</i>
Zooplankton	<i>n/a</i>	<i>n/a</i>	0.8	0.2	0.2
Salinity	1.3	<i>n. sig.</i>	<i>n. sig.</i>	<i>n. sig.</i>	<i>n. sig.</i>
r^2	0.543	0.229	0.403	0.551	0.154
% Deviance	51.2	28.8	44.8	59.3	41.3
# Tows	1393	1393	1393	1479	1479

Table 4

Generalized additive model results for broad-resolution (annual and monthly) covariates, spawning stock biomass (SSB), spring or summer temperature, wind mixing index, and zooplankton biomass. Percent of the total model deviance explained attributable to each covariate included for each stage and final model output. Deviance attributed to individual covariates was determined from comparison of full- and reduced-models. Covariates that were not considered in a given model are noted by *n/a* and those that were not significant in the final model are noted by *n. sig.*

	Egg	Yolksac	Preflexion	Late	Juvenile
SSB	7.1	5.0	0.7	<i>n. sig.</i>	<i>n. sig.</i>
Temperature	0.9	2.8	8.2	16.0	0.8
Mixing	2.6	0.4	<i>n. sig.</i>	5.4	8.8
Zooplankton	<i>n/a</i>	<i>n/a</i>	4.9	3.3	3.8
r^2	0.226	0.149	0.213	0.272	0.081
% Deviance	16.3	14.5	17.3	29.8	19.0
# Tows	1671	1671	1671	1902	1902
# Years	17	17	17	17	17

3.3.1. Fine-resolution

Fine-resolution models explained between 28.8% and 59.3% of the deviance for all stages of pollock development (Table 3). Interactions between fine-resolution covariates were not significant ($p > 0.05$). Salinity did not significantly contribute to the explanation of deviance for any stage. The influence of fine-resolution covariates on ELS was related to ontogeny, with either stage-specific changes, or different responses by early stages compared to late stages. The partial effect of location was dependent on stage and area examined. The spatial effect on egg abundance was highest in the north and lowest along the shelf break. The spatial effect on yolksac larval abundance was highest in the inner domain and lowest in the outer domain. The spatial effect of location on reflexion larval abundance was highest in the outer domain and lowest in the northeast. The spatial effect on late larval abundance was highest in the inner domain and lowest along the shelf break. The spatial effect on juvenile abundance was highest in the north and along the peninsula. Temporal distribution varied across stages, consistent with the temporal evolution of a cohort (Fig. 5). Positive effects of time on abundance were seen in eggs from DOY 100–150 (April–June), in yolksac larvae from DOY 100–175 (April–June), in reflexion larvae from DOY 100–200 (May–July), in late larvae from DOY 125–225 (May–August), and in juveniles from DOY 140–240 (May–Sept). A common trait for early stages was a low abundance of samples and high catch variability at the end of the summer, and high variability and few positive catches in the spring for juveniles.

Fine-resolution environmental covariates generally explained a smaller portion of the model variation than location or DOY. Temperatures associated with positive effects on abundance increased with ontogenetic stage (Fig. 6). The partial effect of temperature on egg abundance was positive at low temperatures (-2 to 7 °C) with most positive samples collected between 1 and 6 °C, and catch variability highest above this range. The temperature

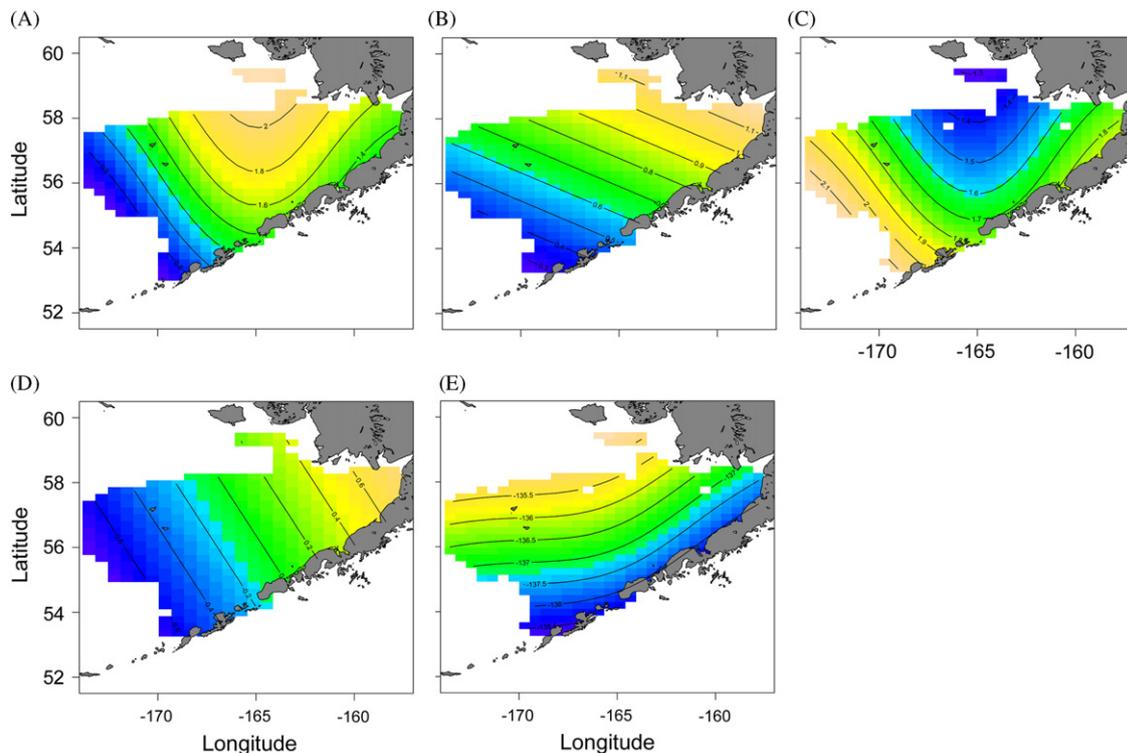


Fig. 4. Partial effect of spatial location. Warm colors indicate predicted increases and cool colors indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolksac larvae, (C) reflexion larvae, and (D) late larvae and in presence of (E) juveniles. Contours and numbers represent amplitude and direction of location effect strength, positive or negative.

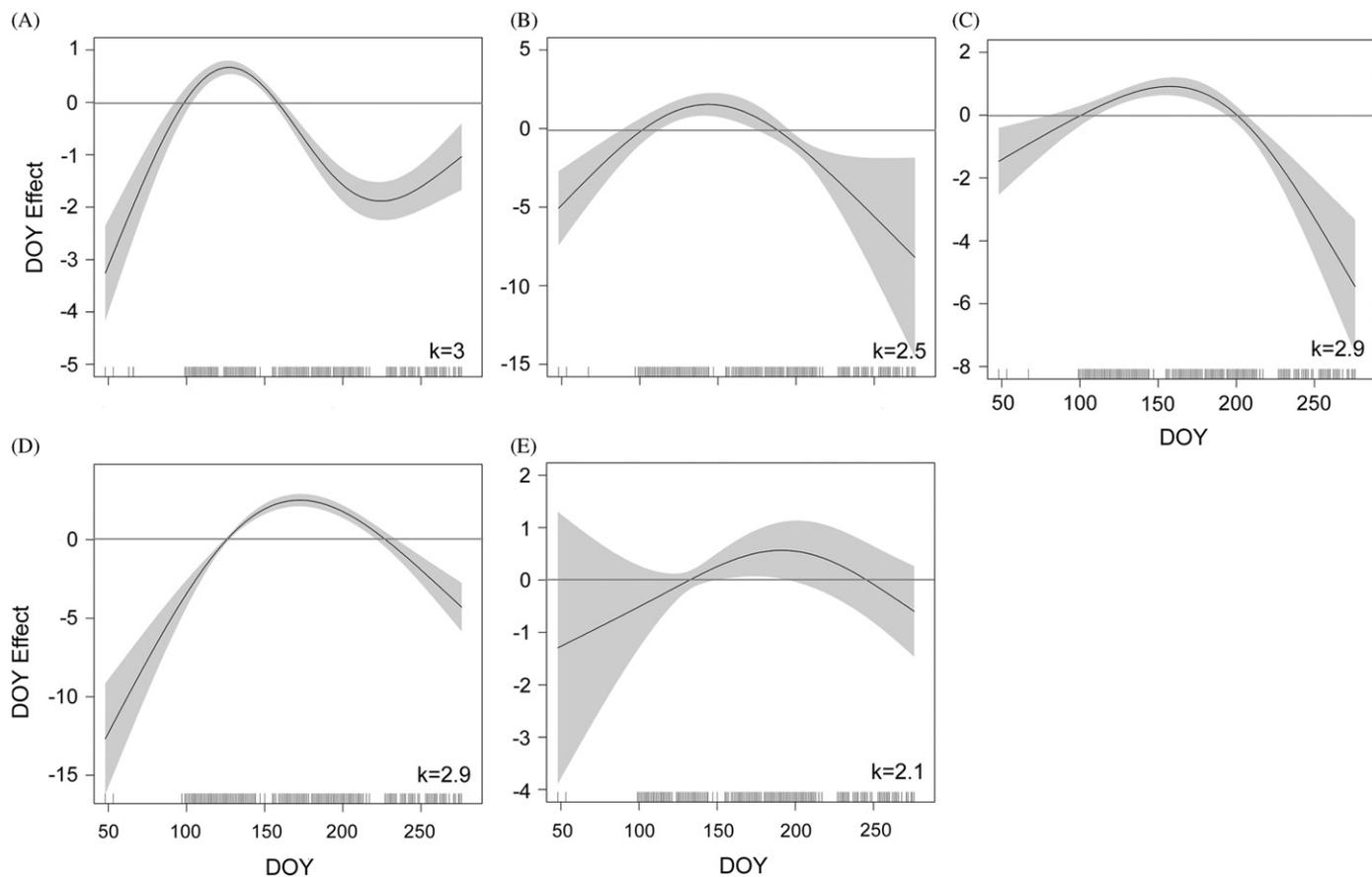


Fig. 5. Partial effect of day-of-year. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolksac larvae, (C) preflexion larvae, (D) late larvae, and (E) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

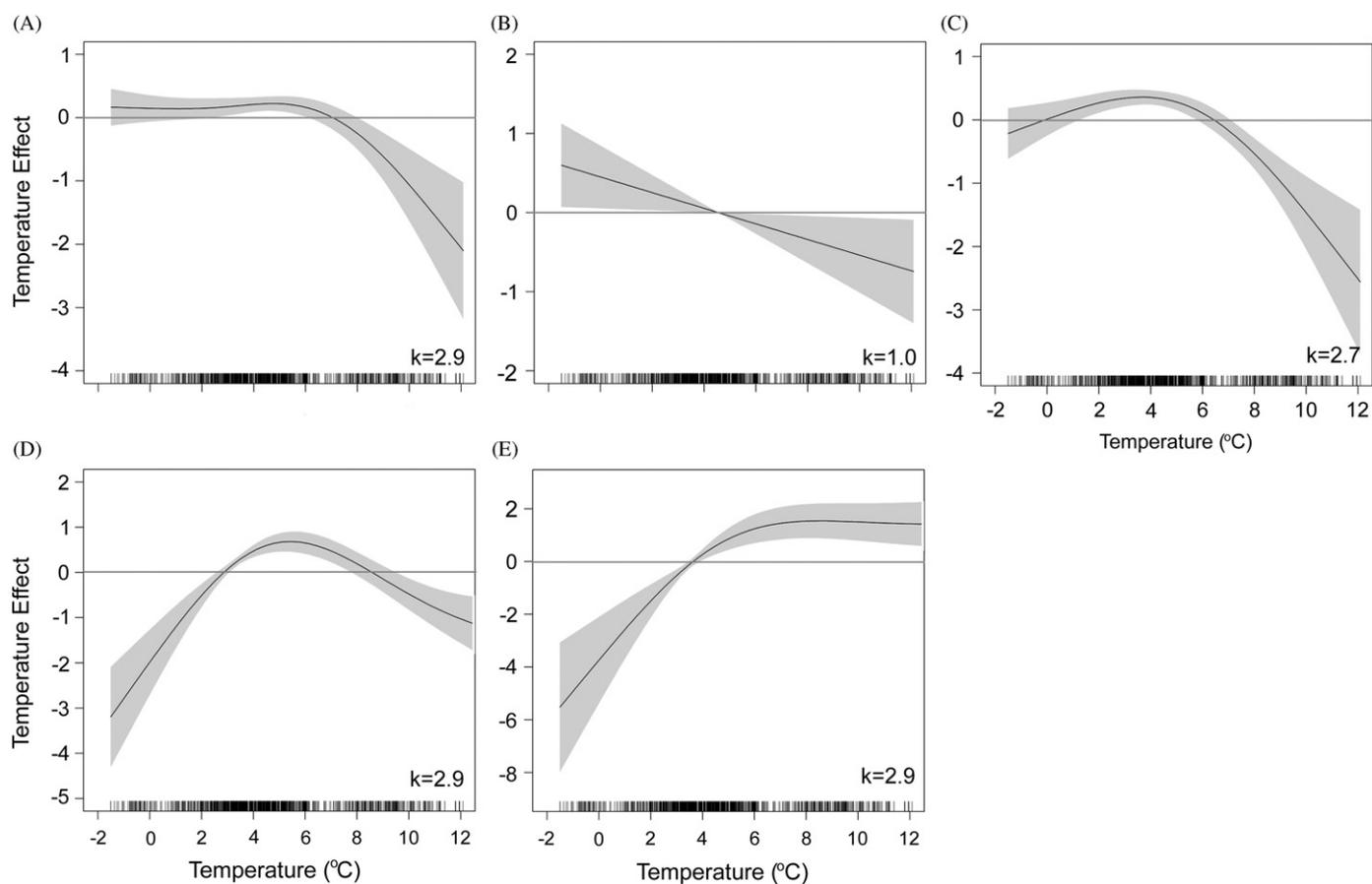


Fig. 6. Partial effect of surface water temperature. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolksac larvae, (C) preflexion larvae, and (D) late larvae and presence of (E) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

effect was highest between -2 and 5 °C for yolk sac larvae, between 1 and 6 °C for preflexion larvae, between 3 and 8 °C for late larvae, and between 4 and 12 °C for juveniles. The relationship with wind speed effect strength was positive for the early stages (eggs, yolk sac larvae), but became negative for late larvae (Fig. 7). Most samples containing each stage were collected at low wind speeds, and variability in effect strength increased above wind speeds of 8 m s⁻¹. The relationship between copepod concentration and feeding stages (preflexion larvae, late larvae, and juveniles) was positive across the entire data range (Fig. 8). The number of positive samples decreased above 4000 copepods m⁻³. Variability in effect strength also increased above this threshold (Fig. 4).

3.3.2. Broad-resolution

Broad-resolution environmental covariates and spawning biomass explained between 14.5% and 29.8% of the deviance in the abundance of pollock ELS (Table 4). Interactions between broad-resolution covariates were not significant ($p > 0.05$). Spawning biomass influenced the abundance of eggs, yolk sac larvae, and preflexion larvae (Fig. 9). The partial effect of SSB was highest at the extremes for all three stages (either very low or high SSB). Variability in abundance was highest in 2008, the year of lowest SSB. The partial effect of temperature anomaly was highest at negative SSTa for eggs and yolk sac larvae, at positive SSTa for

preflexion larvae, and positive BTa (except 2008) for late larvae and juveniles (Fig. 10). Similar to fine-resolution temperature, variability in abundance was highest at the extreme values of temperature anomalies, even though sampling was distributed evenly across the temperature range. The partial effect of wind mixing was highest at high values for eggs, yolk sac larvae, and juveniles (Fig. 11). The effect of mixing on late larvae was highest at very low or high values. The partial effect of zooplankton biomass was highest in less than average and average years for preflexion larvae, late larvae, and juveniles (Fig. 12).

4. Discussion

Spawning population density, environmental conditions, location, and time influenced the abundance of walleye pollock (*T. chalcogramma*) early life stages in the southeastern Bering Sea. Pollock eggs are produced in the eastern Aleutian Islands and the Pribilof Islands, while late larvae occur north of the Alaska Peninsula and in the Pribilof Islands. Juveniles occurred around the Pribilof Islands and across the shelf above 56° N, suggesting dominant transport pathways north and east. The temporal effect indicates that juveniles reached peak abundance about 75 days after eggs, and 25 days after late larvae. Location, day of year, and

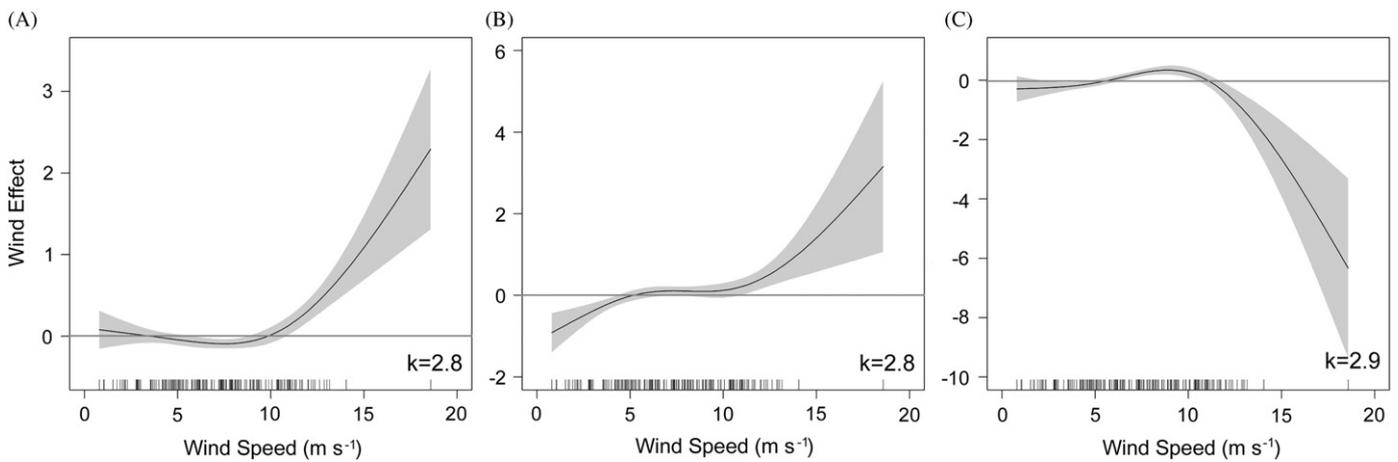


Fig. 7. Partial effect of wind speed. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolk sac larvae, and (C) late larvae. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

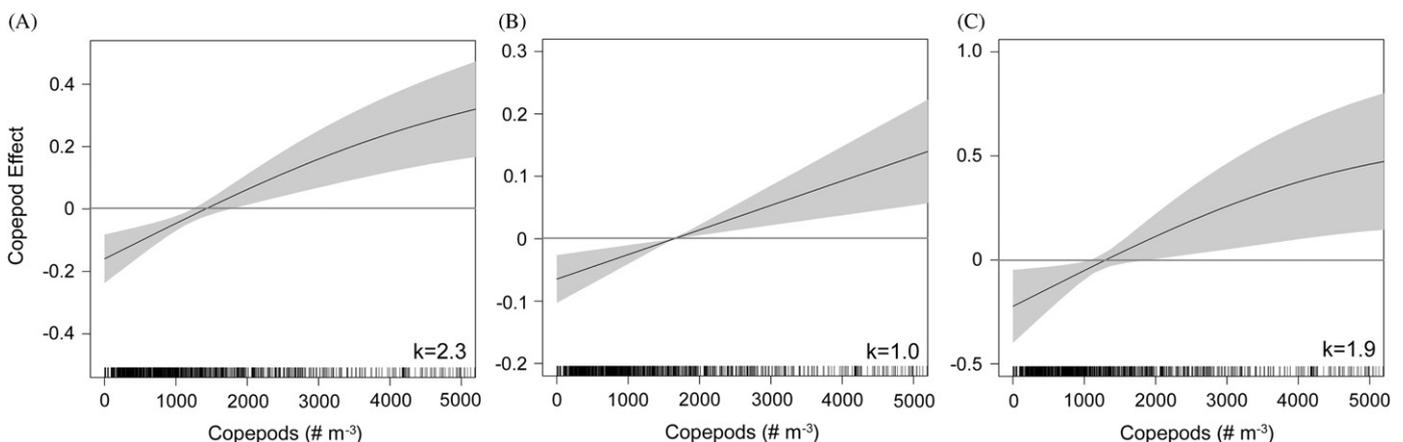


Fig. 8. Partial effect of copepod concentration. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) preflexion larvae, (B) late larvae, and (C) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

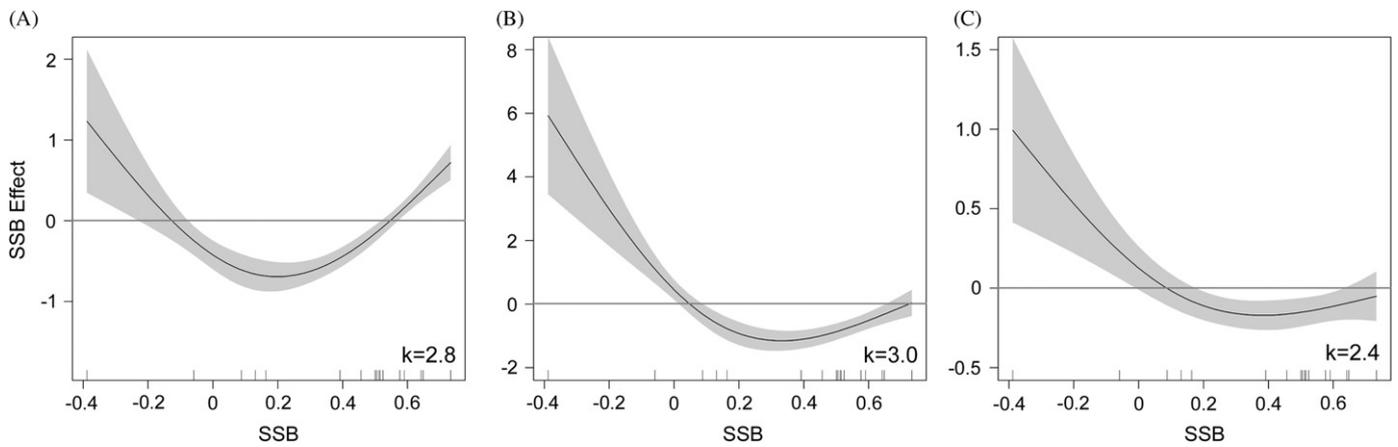


Fig. 9. Partial effect of spawning stock biomass anomaly. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolksac larvae, and (C) preflexion. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

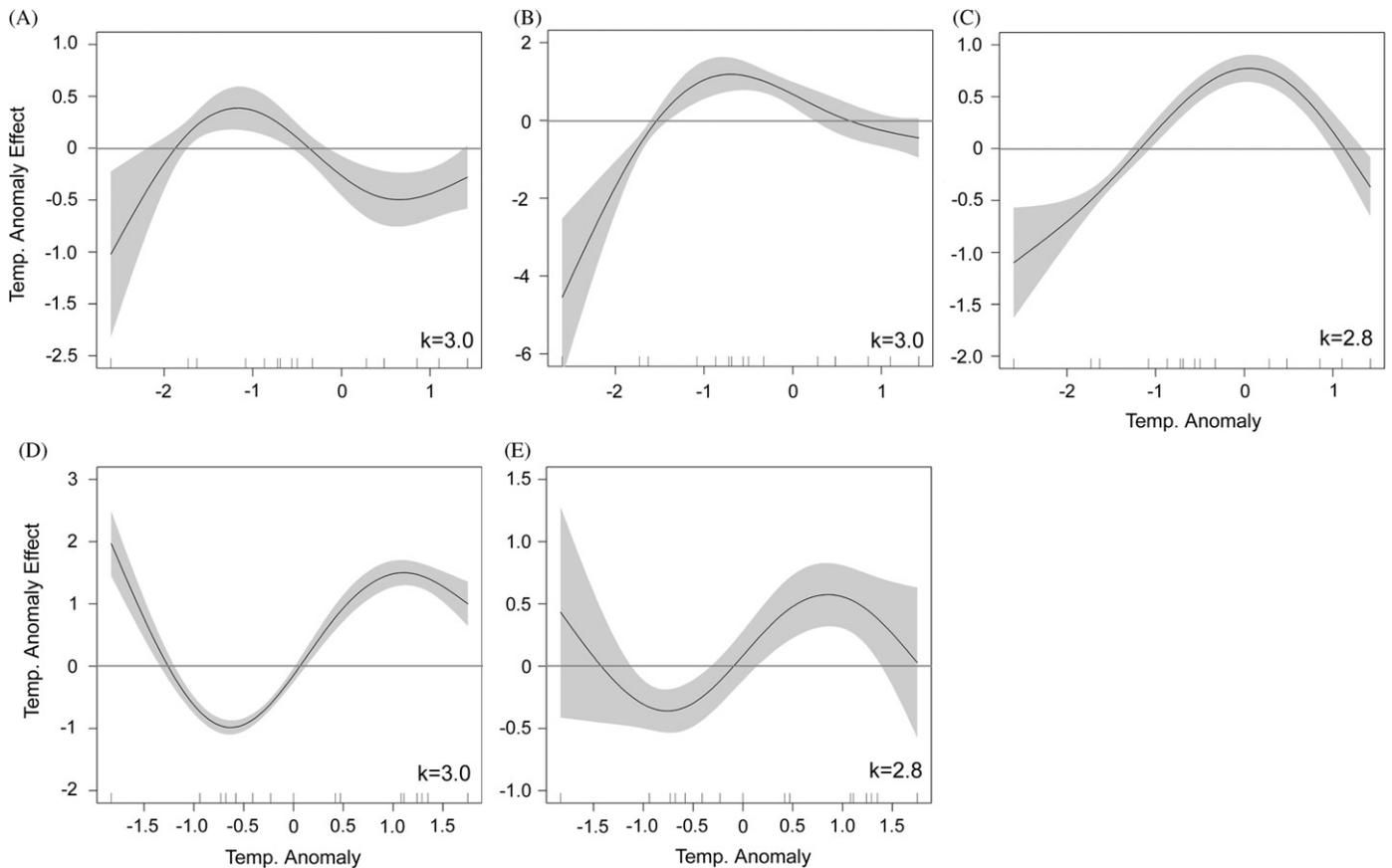


Fig. 10. Partial effect of temperature anomaly. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolksac larvae, (C) preflexion larvae, (D) late larvae, and (E) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

year accounted for most of the variation in abundance of pollock ELS relative to localized environmental covariates (Table 5). Spatiotemporal factors incorporate the aggregative and seasonal nature of spawning. As expected, SSB influenced egg, yolksac larval, and preflexion larval abundances. Within each suite of environmental conditions examined, temperature was the leading predictor of pollock ELS abundance, explaining more variation for more stages than either wind or zooplankton (Table 5).

Similar to pollock eggs in Shelikof Strait (Bacheler et al., 2009), SEBS eggs were positively associated with SSB, with the exception of 2008, a low SSB and low SSTa year. Although we would predict few eggs in 2008 based on the SSB in that year, the potential for temperature-delayed spawning and a protracted period of egg development in cold conditions would retain eggs in the water column for longer periods (Blood, 2002). We did not find a significant relationship between female maturity stage and

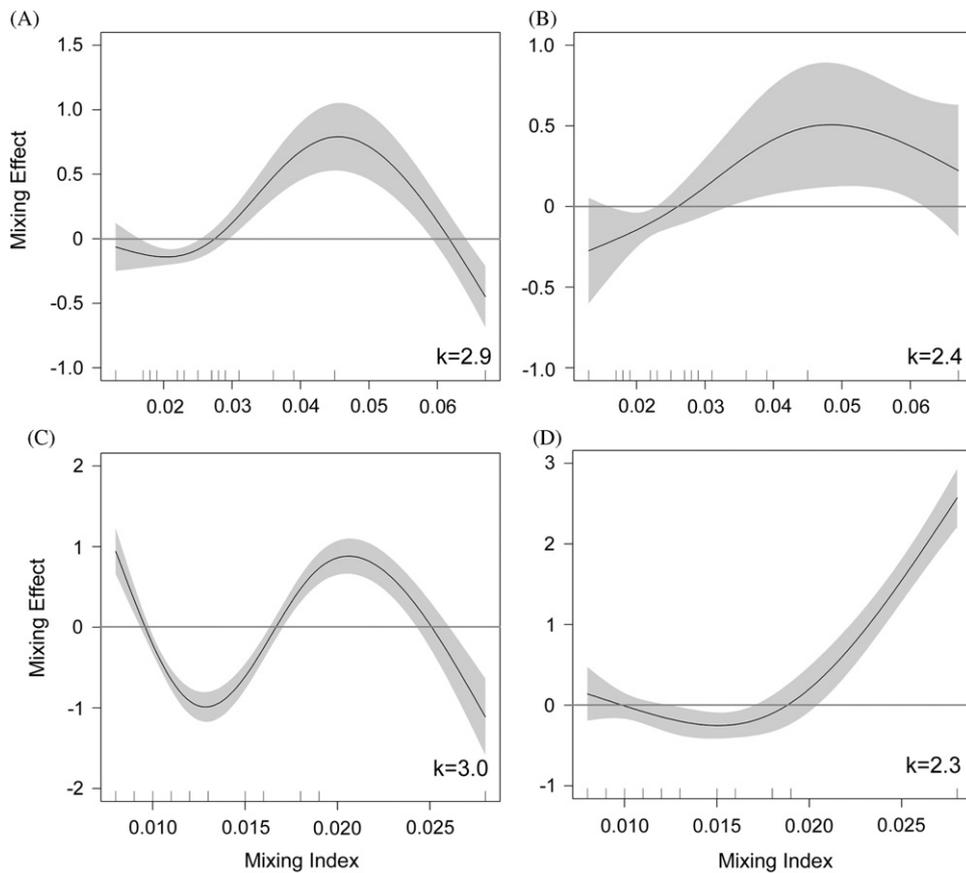


Fig. 11. Partial effect of wind mixing. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) eggs, (B) yolk sac larvae, (C) late larvae, and (D) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

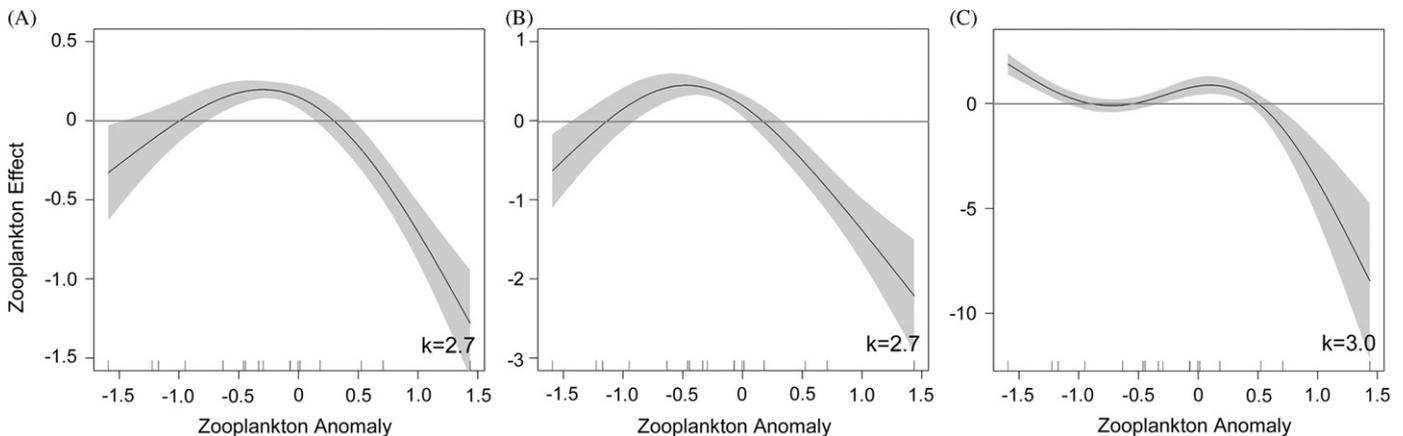


Fig. 12. Partial effect of zooplankton biomass anomaly. Positive values indicate predicted increases and negative values indicate predicted decreases in abundance of walleye pollock (A) preflexion larvae, (B) late larvae, and (C) juveniles. Shaded areas are 95% confidence intervals, tick marks on the x-axis indicate sampling intensity, and k is the number of knots.

temperature, but the positive trend highlights this as an area in need of directed investigations. The lack of a relationship between the abundance of late larvae and juveniles with SSB suggests that other sources of mortality act to modulate late larval and juvenile abundance rather than reproductive effort.

We found that temperature explained the greatest portion of variation in stage-specific abundance and the relationships changed with ontogeny. We incorrectly predicted that the abundance of Bering Sea eggs would be positively related to temperature

based on a previous study that found enhanced development and hatching rates with high temperature (Blood, 2002). Given the high numbers of eggs collected at low SSTa, it could be construed that production of pollock is higher at cooler than average temperatures (Hunt et al., 2002). We suggest that high production is not the case, but that high abundance of eggs in cold conditions results from one of two other possible scenarios. First, colder water temperatures slow rates of growth and development of ELS (Canino, 1994; Blood, 2002), so in cold conditions

Table 5

Covariate ranks derived from GAMs. Ranks are based on the total possible models that covariate was considered for, the number of models each covariate was included in, and the weighted deviance explained by that covariate. Weighted deviance is the deviance explained by a covariate in each model weighted by the deviance explained by that model summed across model types and stages.

Rank	Covariate	Possible models	Included models	Weighted deviance
1	Temperature anomaly	5	5	0.26
2	Zooplankton biomass	3	3	0.20
3	Wind mixing	5	4	0.17
4	Year	5	5	0.16
5	SSB	5	3	0.16
6	DOY	5	5	0.11
7	Location	5	5	0.04
8	Temperature	5	5	0.03
9	Wind speed	5	4	0.02
10	Copepods	3	2	0.01

slow-developing eggs accumulate in the water column along with recently-spawned eggs. Second, pollock spawning phenology is delayed at colder temperature, increasing temporal overlap between eggs and surveys. Spawning and recruitment among other gadid species are temperature-dependent (O'Brien et al., 2000; Sundby, 2000; Poltev, 2008). Pollock tended to be further along in their maturity cycle in early March at higher temperatures. However, this correlation was not significant and other methods must be employed to address changes in spawning phenology. Ichthyoplankton surveys start at about the same date and occur during a narrow temporal window relative to the timing of spawning each year. The spawning locations of pollock also change with temperature conditions, shifting onshore or to the north in warm years (Bacheleer et al., 2012). Delayed hatching under cool conditions coupled with slow growth and slow rates of starvation also would extend the yolksac stage, increase the temporal overlap of yolksac larvae with surveys, and reduce the overlap between surveys and feeding stages, and potentially increase growth-dependent mortality through extension of the larval duration.

Previous studies in the Gulf of Alaska found contrasting relationships between water temperature and abundance of pollock larvae. In the GOA, Doyle et al. (2009) found a negative relationship between pollock larval abundance and winter temperature, and no relationship between larval abundance and spring temperature. Larvae from that study were not sub-divided into length classes, which may have masked stage-specific abundance patterns. Bailey et al. (1995) found reduced larval abundance in Shelikof Strait in an anomalously cold spring relative to an average spring. Although Chan et al. (2010) found a negative relationship between larval abundance and pre-spawning temperature, they found that higher than normal temperatures during the larval period in the GOA increased larval survival rates relative to those measured at lower temperatures. Bering Sea feeding-stage larvae and juveniles were associated with higher local and summer temperatures, consistent with either advanced growth rates or high survival.

Wind speed measurements provide a proxy for small-scale turbulent mixing (Oakey and Elliott, 1982), which can impact feeding and growth of pollock larvae (Megrey and Hinckley, 2001). The turbulence-encounter rate theory predicts optimal turbulence intensity for successful attacks by fish larvae (MacKenzie and Leggett, 1991), resulting in a dome-shaped relationship between turbulence or wind speed and feeding (Sundby and Fossum, 1990). We expected to find a similar curvilinear relationship between wind speeds and larval pollock

abundance, assuming that growth and survival are dependent on prey capture ability. We did not find supporting evidence for this theory other than the negative effect of wind speeds greater than 12 m s^{-1} on abundance of late larvae. However, the number of samples within this range was low and overall wind speed did not have a large effect on abundances of feeding stages. We did find evidence of the potential for turbulence to bring early stages up from spawning depth into the range of our collection gear (shallower than 300 m) in the positive relationships between wind speed or mixing and egg and yolksac larval abundances, as would be predicted based on the prevalence of upwelling over the shelf break.

Chan et al. (2010) linked early larval survival in the GOA to enhanced transport from the spawning area when sea surface winds were high. Typically, eggs spawned offshore or near Unimak Island would be transported either north in the Bering Slope Current or east by the Aleutian North Slope Current (Fig. 1). Winds along the peninsula tend to move from east to west and strong winds from the east are associated with high northward flow along the slope from Unimak Pass (Kalnay et al., 1996). Wind speed data from buoys examined in this study were located relatively close to the peninsula, and although we were unable to examine wind direction, high wind speeds likely indicate enhanced northward flow along the slope due to Eckman transport. Wind-enhanced transport would result in transport of the larval population toward the northern end or out of our survey area over time. One potential result would be a reduction in later stages that would be either missed by our surveys or occur at the northern end only. Indeed, both late larvae and juveniles were most common toward the outer shelf and northern half of our survey area. In a parallel observation, Wespestad et al. (2000) suggested that wind-driven transport promoted the movement of age-1 pollock to the north and outer shelf.

As expected, feeding stages were positively related to copepod concentration as this indicates favorable feeding conditions. Copepod eggs and nauplii constituted a high proportion of pollock larval diet and are expected to be available as prey in spring and summer, particularly to first-feeding stage larvae included in the preflexion length range (Theilacker et al., 1996; Napp et al., 2000). Surprisingly, feeding stages were not positively related to zooplankton biomass. Rather than positive relationships, zooplankton biomass suggested that poor zooplankton conditions supported high abundances of pollock ELS. Zooplankton biomass anomaly was based on zooplankton abundance over the middle shelf in the summer. The feeding stages were collected primarily in other areas, such as the peninsula and the Pribilof Islands. The spatial discrepancy between where feeding stages occurred and where zooplankton biomass was estimated may explain the lack of the expected relationship. For preflexion larvae, there also was a temporal mis-match with zooplankton biomass anomaly. Preflexion larvae were most abundant in the spring and the anomaly was based on summer zooplankton estimates. In the case of prey availability, the fine-resolution copepod concentration may be a more appropriate predictor of abundance because it is estimated at the location and time at which larval feeding stages are present.

5. Conclusions

The influence of the immediate environment and overall conditions for the Bering Sea was stage-specific for walleye pollock early life stages. Previously, environmental influence was examined at one stage or at one scale (e.g. Blood, 2002; Ciannelli et al., 2005; Doyle et al., 2009). With the exception of Mueter et al. (2006), very little work has specifically addressed

the Bering Sea. Our results emphasize the importance of including ontogeny when predicting responses to environmental change, as ecological constraints imposed on a given stage do not necessarily act on other stages in a similar manner. In the SEBS, spawning stock biomass impacted initial abundances, but had no effect on walleye pollock developed larvae or juveniles. Following initial production, pollock ELS were most affected by temperature, followed by wind conditions, and prey production over the shelf. Spatial distributions of individual stages indicated that north- and eastward flowing currents are responsible for drift pathways. When available, fine-resolution environmental data were useful for modeling and predicting responses of individual stages to changing conditions. When fine-resolution data was unavailable or limited, patterns from broad-resolution indices paralleled those of some of their fine-scale counterparts, with the caveat that broad-resolution factors may not have been measured in similar locations or at similar times where pollock ELS occurred. Of particular interest, the relationship between temperature and abundance was stage-specific, with an oscillation between early stages at low temperatures and late stages at high temperatures. Eggs and newly hatched larvae were abundant in cool temperatures, while feeding larvae and juveniles were abundant at warm temperatures. Temperature in the SEBS is a dominant force structuring hydrography (Stabeno et al., 2012), zooplankton communities (Stabeno et al., 2012), ichthyoplankton communities (Siddon et al., 2010), and spawning locations (Bacheler et al., 2012). For walleye pollock, temperature potentially impacts spawning and growth cycles and available habitat during the crucial first months of life, thus setting the stage for future recruitment.

Acknowledgments

Many thanks to the members of NOAA's Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) who were involved in the collection and processing of the ichthyoplankton samples. L. Ciannelli assisted with statistical analyses and interpretation. A. Yamaguchi of the Hokkaido University Graduate School of Fisheries provided zooplankton data for biomass anomalies. Earlier versions of this manuscript benefited from comments by Kevin Bailey, Jerry Berger, and three anonymous reviewers. This research was supported by the BSIERP program of the North Pacific Research Board (NPRB); this is NPRB contribution number 337 and BEST-BSIERP Bering Sea Project publication number 51. This paper is EcoFOCI Contribution no. N753-RAOA-0 to NOAA's North Pacific Climate Regimes and Ecosystem Productivity research program.

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