

Alternating temperature states influence walleye pollock early life stages in the southeastern Bering Sea

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ABSTRACT: Water temperatures in the southeastern Bering Sea influence the density of walleye pollock *Theragra chalcogramma* early life stages, potentially influencing spatial distributions and the phenology of reproduction and development. We quantified stage-specific changes in spatial and temporal distributions under cold- and warm-water conditions using generalized additive models. Analyses showed that walleye pollock egg and yolk sac larval spatial distributions are unaffected by temperature, suggesting that spawning locations are stable. Preflexion larvae, late larvae, and juveniles shift onto the shelf under warm conditions, similar to spatial shifts observed in distributions of sub-adults and adults. Temporal distributions were used to address the hypothesis that timing of the density peak at each stage is delayed under cold conditions. Differences in the timing of density peaks supported the hypothesis that the timing of spawning, hatching, larval development, and juvenile transition are temperature-dependent. The current analysis represents the best support available for the importance of temperature to walleye pollock in determining early life stage development and population trends in the eastern Bering Sea. Our data indicate that future changes in water temperatures could influence the early life stages of an ecologically dominant member of the Bering Sea community by changing phenology and habitat use in the first several months of life.

KEY WORDS: *Theragra chalcogramma* · Temperature · Distribution · Phenology · Bering Sea

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INTRODUCTION

In the eastern Bering Sea, interannual variation in the extent of sea ice over the continental shelf determines water temperatures during the spring and summer when many fish species reproduce (Hunt & Stabeno 2002). *Theragra chalcogramma* (walleye pollock, hereafter pollock) is one of the most common spring and summer shelf-spawning species in the Bering Sea ecosystem. Juvenile and adult popula-

tions change in abundance and distribution in response to changes in water temperatures. Juvenile pollock (<130 mm fork length) densities in surface trawls were higher and spatial distributions were broader during 2 recent warm summers relative to 2 recent cold summers (Moss et al. 2009). The authors hypothesized that warm conditions promote growth and survival in this population. Sub-adult (<30 cm fork length) and adult biomasses and spatial distributions have been shown to correlate with summer

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temperature during the pollock post-spawning feeding season (Kotwicki et al. 2005). Biomass increased with summer temperatures and the feeding migration progressed farther north and inshore (east) from spawning grounds as temperature increased. Kotwicki et al. (2005) hypothesized that warmer water temperatures advance the post-spawning feeding migration by advancing the timing of spawning. They did not address the alternate hypothesis that spawning distribution changes in response to temperature conditions.

Colder than average years are characterized by late sea-ice retreat from the shelf in the spring, water column temperatures $<2^{\circ}\text{C}$ over the shelf during spring and summer, and abundant large-bodied zooplankton (Hunt et al. 2002, Coyle et al. 2011). Warmer than average years are characterized by early ice retreat, continental shelf water temperatures $>2^{\circ}\text{C}$ during spring and summer, and small-bodied zooplankton. Sea-ice conditions also determine the extent and location of a pool of cold bottom water in the summer over the middle shelf (50 to 100 m depth, Stabeno et al. 2012a). Pollock distributions generally are restricted to areas $>2^{\circ}\text{C}$, such as those found outside the cold pool (Wyllie-Echeverria & Wooster 1998). Therefore, in warm years, a larger area of thermally-suitable habitat is available to pollock over the continental shelf, particularly over the middle shelf.

Smart et al. (2012) identified temperature in spring and summer as a leading environmental factor influencing stage-specific densities of pollock early life stages (ELS) in the southeastern Bering Sea (SEBS). Lower than average temperature years have high densities of eggs and newly hatched yolksac larvae, regardless of the size of the adult spawning population. Average and higher than average temperature years have high densities of feeding larvae (pre- and postflexion) and early juveniles (<65 mm standard length). One hypothesis to explain the oscillation between early and developed stages is high egg production under cold conditions. Spawning stock biomass in recent cold years has been low, while egg densities have been high (Janelli et al. 2009, Smart et al. 2012). An alternate hypothesis is that the oscillation between early and late stages results from shifts in spawning and development phenology. Maturity stage of SEBS pollock females in late winter tends to be advanced in warm relative to cold years (Smart et al. 2012), although the impact of temperature on spawning has not been rigorously tested. Temperature influences hatching time in laboratory-reared Bering Sea pollock eggs: eggs at 2°C , typical of cold

conditions, require almost a week longer to hatch than eggs raised at 3.8°C , typical of warm conditions (Blood 2002). In the Gulf of Alaska, lower than average temperatures contribute to high mortality rates of field-observed larvae (Bailey et al. 1995).

The current study has 2 objectives: (1) to determine whether pollock ELS undergo spatial shifts in response to changing temperature conditions and (2) to test whether temperature affects the phenology of developmental events.

MATERIALS AND METHODS

Field surveys

The SEBS is bordered to the east by the Alaska mainland, to the south by the Alaska Peninsula and eastern Aleutian Islands, to the west by the Aleutian Basin, and to the north by a change in vertical structure of the water column and hydrography near 60°N latitude (Stabeno et al. 2012b) (Fig. 1). The shelf in the SEBS is very broad (~ 500 nautical miles). Northwest flow is driven by the Bering Slope Current and flow through Aleutian passes (Napp et al. 2000). East-west flow is driven by the Aleutian North Slope Current. The SEBS shelf can be divided into 3 bathymetric domains, each with its own characteristic hydrography (Coachman 1986). The inner shelf (or coastal domain, <50 m in depth) is weakly stratified and influenced by freshwater run-off, the middle shelf (50 to 100 m) is strongly stratified and home to the cold pool in summer; and the outer shelf (100 to 200 m) is an area of intermittent upwelling in the spring and summer, high productivity, and stratification (Hunt et al. 2002).

Depth-integrated densities (no. of ind. 10 m^{-2}) of pollock ELS were determined from a time series of ichthyoplankton surveys conducted by the NOAA Alaska Fisheries Science Center Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) program (Seattle, WA, cf. Matarese et al. 2003). Surveys varied in spatial and temporal coverage and in the number of tows conducted and gears used. To account for these variations, we limited the tows considered for analysis to include pollock spawning areas, areas of potential transport, and the spawning season. Data were limited to tows conducted south of 60°N latitude and east of the Aleutian basin, where a majority of spawning occurs (Fig. 1). Pollock spawning in the SEBS occurs from February through November (Bacheler et al. 2010), but since sampling at the start or end of the spawning season is

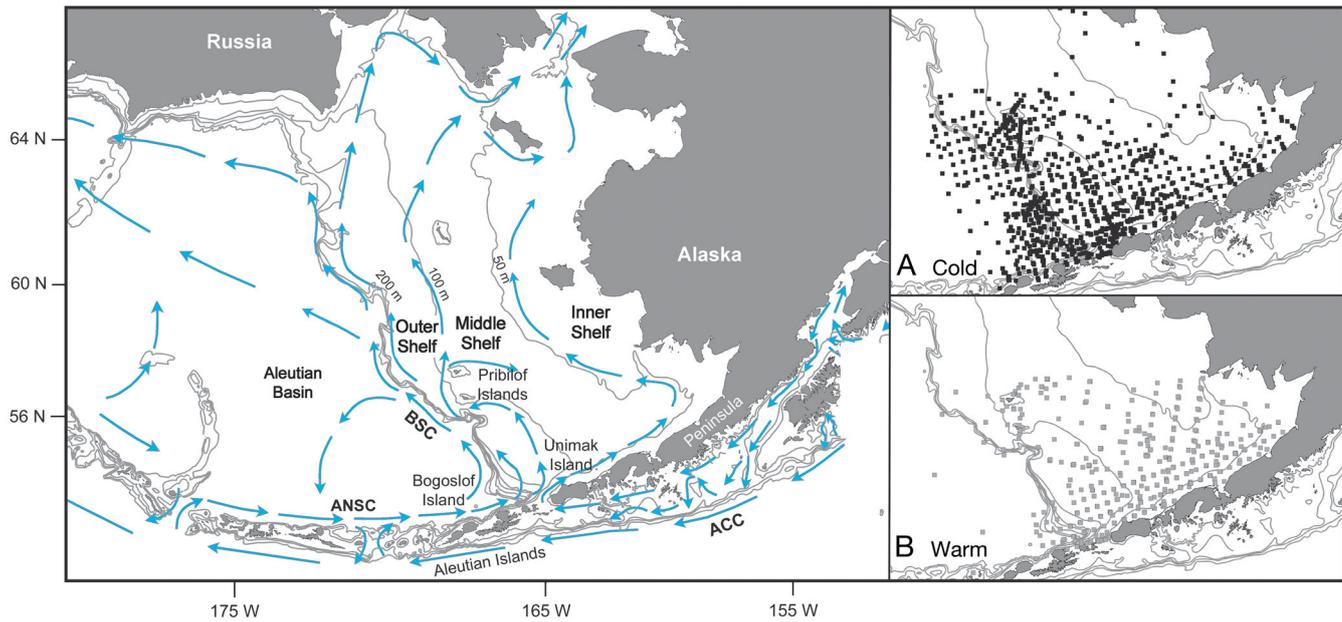


Fig. 1. (Left panel) Dominant eastern Bering Sea currents including the Aleutian North Slope Current (ANSC), the Bering Slope Current (BSC), and inflow through passes driven by the Alaska Coastal Current (ACC). The eastern Bering Sea is divided into 3 shelf domains based on hydrography: outer, middle, and inner. (Right panels) Locations of cumulative sampling in (A) 10 cold and (B) 7 warm years from 1988 to 2009

rare, we limited catch records to between March and September (Fig. 2). Fifteen years in the time series met these spatial and temporal criteria (see Table 1 for details).

Gear types employed included obliquely towed bongo nets, a 1 m² multiple opening and closing net and environmental sensing system (MOCNESS), and 1 m Tucker trawls, all equipped with 333 or 505 μ m mesh. Differences in selectivity between bongo, MOCNESS, and Tucker gears are generally minor and are appropriate for the length ranges of pollock examined in this study (Wiebe et al. 1976, Shima & Bailey 1994). Volume filtered by each gear type was determined by calibrated flow meters mounted in the mouth of each net. Catches were divided into 5 developmental stages: eggs, yolk sac larvae (<4.4 mm standard length, SL), preflexion larvae (4.5 to 9.9 mm SL), late larvae (10.0 to 24.5 mm SL), and early juveniles (25 to 64.5 mm SL). In addition to standard length, divisions were based on developmental attributes outlined in the Ichthyoplankton Information System (NOAA 2011). The upper size limit for early juveniles was selected based on the reduced catchability of larger fish with the current gear types.

Monthly mean sea surface temperatures in May are a good indicator of overall conditions throughout the pollock spawning period, correlating with both sea-ice state and summer temperatures (Moss et al. 2009, Stabeno et al. 2012a). Sea surface temperature

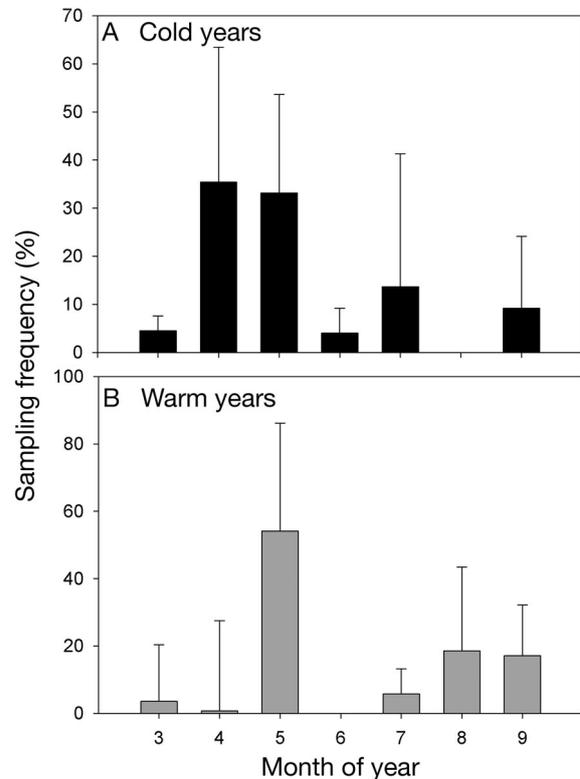


Fig. 2. *Theragra chalcogramma*. Monthly sampling frequency (mean + SD) for walleye pollock in the southeastern Bering Sea shown by percent of tows conducted within each month in a given year for early life stages during the walleye pollock spawning season in (A) cold and (B) warm years from 1988 to 2009

Table 1. Survey years for collection of walleye pollock included in analysis according to their sea surface temperature anomaly (SSTa) as either cold (negative) or warm (positive). Cruise start and end dates (mm/dd), mean day of year (DOY), and the number of tows collected are included. Growth and mortality rates were derived from sequential cruises in similar geographic areas within each year

Year	SSTa	Cruise Start date	Cruise End date	Mean DOY	No. of tows
Cold					
1994	-0.16	04/15	04/30	113	101
		09/05	09/13	253	19
1995	-0.52	04/17	05/01	114	152
		05/04	05/18	131	139
		09/11	09/18	258	14
1997	-0.18	04/16	04/25	111	32
		05/04	05/13	128	31
		07/01	07/13	189	86
1999	-1.09	04/14	04/18	138	43
		05/15	05/20	138	15
		07/13	07/23	199	56
2000	-0.05	05/07	05/11	131	14
		06/22	07/02	178	6
		07/28	07/31	212	8
		09/18	09/22	265	12
2006	-1.01	05/09	05/18	134	96
		06/22	06/25	174	21
		09/11	09/22	259	84
2007	-1.09	04/11	05/11	114	35
		04/24	04/25	114	6
		05/08	05/18	133	89
		06/08	06/22	167	12
		07/01	07/11	184	11
		07/25	07/29	208	8
2008	-1.86	05/13	05/21	138	66
		06/03	06/16	162	14
		06/19	06/28	175	5
		07/04	07/15	192	43
2009	-1.95	04/27	05/03	120	12
		05/08	05/18	133	89
		06/05	06/17	163	9
		06/20	07/06	177	10
		07/12	07/30	201	10
		09/25	09/30	274	60
Warm					
1988	0.16	03/17	04/04	84	64
		04/11	04/26	110	40
1991	0.01	03/11	03/15	72	19
		04/14	05/08	115	52
1996	0.88	04/23	04/25	115	4
		05/15	05/16	136	5
		05/19	05/20	140	5
		07/21	08/04	210	12
		09/07	09/15	256	19
2002	0.71	05/13	05/21	136	77
		08/02	08/08	218	6
		08/14	08/28	234	8
		08/20	09/21	241	55
		09/08	09/30	264	8
2003	1.73	03/04	03/06	64	13
		05/18	05/24	141	69
		07/21	07/24	204	5
		09/09	09/27	256	28
2005	1.21	03/03	03/05	63	4
		05/10	05/22	134	110
		05/16	05/27	140	5
		07/15	07/18	197	9
		09/22	09/25	266	8

anomalies were derived from means of monthly sea surface temperatures in May averaged over the area 54.3° to 60.0° N and 161.2° to 172.5° W (NCEP/NCAR Reanalysis, Kalnay et al. 1996). The anomaly used in the current analysis is the deviation from the mean value (2.11°C) for the survey years from 1988 to 2009 normalized by the standard deviation (0.82°C).

Spatial distributions

Stage-specific spatial distributions were determined for each ELS using variable-coefficient generalized additive models (VCGAMs). VCGAMs allow the formulation of a nonparametric, nonlinear regression model in which the effect of predictor variables can be determined for a specific location (Hastie & Tibshirani 1993, Bachelier et al. 2010). In our case, we examined if density at each ELS was expected to increase or decrease with an increase in annual sea surface temperature anomaly for a given location. VCGAMs quantified changes in density for each ELS using the following model structure:

$$C_i = \text{offset}(\text{volume}) + a + s(\text{SSB}) + s(\text{DOY}) + s(\text{location}) + \text{SSTa} + s(\text{location}) \times \text{SSTa} + \epsilon \quad (1)$$

where C_i is the count of fish in stage i in each tow standardized (offset) by the volume of water filtered in each tow (volume, m³), a is the model intercept, SSB is the annual female spawning stock biomass (t) included to account for annual changes in spawning effort, DOY is the day of year of each tow, location is a combined term of the latitude and longitude for each tow, SSTa is the annual sea surface temperature anomaly, and ϵ is the model error. SSB was based on summer surveys for adult pollock over the eastern Bering Sea shelf (Ianelli et al. 2009). In preliminary examination of the data, there was no relationship between temperature and SSB (T. Smart unpubl. data). The negative binomial error distribution was used because of overdispersion caused by a high number of zeroes in the data set (Dupont 2002, Maunder & Punt 2004). The negative binomial error distribution also produced the best model fit using the Akaike Information Criterion (AIC) compared to Poisson, gamma, or Gaussian error distributions. The identity link function was used in all VCGAMs. The level of smoothing was minimized to between 1 and 4 knots to minimize the effects of spatial autocorrelation (Stige et al. 2006, Heinänen et al. 2008). All models were coded and analyzed using the mgcv library (version 1.4-1, Wood 2006) in R (version 2.7.1, R Development Core Team 2008). VCGAM predictions

were plotted for each $0.1^\circ \times 0.1^\circ$ degree cell for which data were available in our study area.

Temporal distributions

Generalized additive models (GAMs) were used to describe the non-linear temporal distributions for each stage to estimate temporal shifts between temperature categories. Years of positive SSTa were categorized as warm years ($n = 6$) and years of negative SSTa were categorized as cold years ($n = 9$). This method was chosen over the Kolmogorov-Smirnoff test, as the Kolmogorov-Smirnoff test cannot separate changes in peaks in the distribution from changes in the shapes of the distribution. GAMs allow a visual comparison of the shapes and peaks in density among collection dates. The use of GAMs also allowed us to account for the spatial component of our surveys, as tow locations often varied among months and years. GAMs quantified anomalies in density for each ELS using:

$$C_i = \text{offset}(\text{volume}) + a + s(\text{SSB}) + \text{factor}(\text{temperature}) + s(\text{location}) + s(\text{DOY}) + \varepsilon \quad (2)$$

where C_i is the count of individuals of stage i in each tow standardized (offset) by the volume of water filtered in each tow (volume, m^3), a is the model intercept, SSB is the annual female spawning stock biomass (t), temperature is the temperature category (cold or warm), location is a combined term of the latitude and longitude for each tow, DOY is the day of year of each tow, and ε is the model error. The negative binomial error distribution produced the best model fit based on AIC compared to the Poisson, gamma, or Gaussian error distributions. The identity link function was used in all models. The level of smoothing was minimized to between 1 and 4 knots to minimize the effects of spatial autocorrelation (Stige et al. 2006, Heinänen et al. 2008). When the effect of temperature category on density anomaly was significant ($\alpha = 0.05$), we derived the partial effect of DOY on the density anomaly within each temperature category to define the temporal distribution. The switch from negative to positive density anomalies indicated the DOY when each stage first appeared in surveys. The switch back to negative anomalies indicated the DOY when each stage of development was complete (i.e. the season for each stage). The maximum positive density anomaly predicted from DOY in GAMs indicated when each stage reached its maximum density within each temperature category.

RESULTS

Spatial distributions

Egg densities were high across much of the study area in cold years, with highest catches near Unimak Pass and the Pribilof Islands (Fig. 3A). Tows with high egg density were common off the shelf in 1988 and 1990 and sporadic over the shelf in the rest of the warm years. High-density catches of yolksac larvae were common over the shelf and around the Pribilof Islands in cold years and either over the basin or over the shelf in warm years (Fig. 3B). Preflexion larval densities were highest over the shelf and near the Pribilof Islands in cold years and over the shelf and basin in warm years (Fig. 3C). Highest densities of late larvae were found near the Pribilof Islands in cold years and over the shelf in warm years (Fig. 3D). Very few tows collected juveniles in high numbers in cold years, but these tows occurred mostly near the Pribilof Islands (Fig. 3E). In warm years, high-density juvenile catches occurred over the shelf and near the Pribilof Islands.

For all stages, annual temperature anomaly had a significant impact on location-specific density (Table 2). Eggs and yolksac larvae were predicted to decrease in density as temperature increased in all study area locations (Fig. 4A,B). Preflexion larvae were predicted to increase in density as temperature increased in the central portion of our study area (shelf break, outer shelf, middle shelf) and decrease in density over the basin and in the inner shelf (Fig. 4C). Late larval density decreased with warming over the basin and to the north and increased over the shelf and to the south with warming (Fig. 4D). Warming did not impact juvenile density over the shelf, but was predicted to decrease densities along the shelf break, over the basin, and to the north (Fig. 4E).

Temporal distributions

Temperature category affected the density of all pollock ELS in GAM analyses (Table 3). Egg density anomalies peaked prior to DOY 150 (before June 1) in cold years and before DOY 140 (before May 20) in warm years (Fig. 5A). The yolksac larval season occurred between DOY 100 and 190 (April 10 and July 10) in cold years and prior to DOY 175 (before June 25) in warm years (Fig. 5B). Among preflexion larvae, density anomalies peaked between DOY 100 and 195 (April 10 and July 15) in cold years and

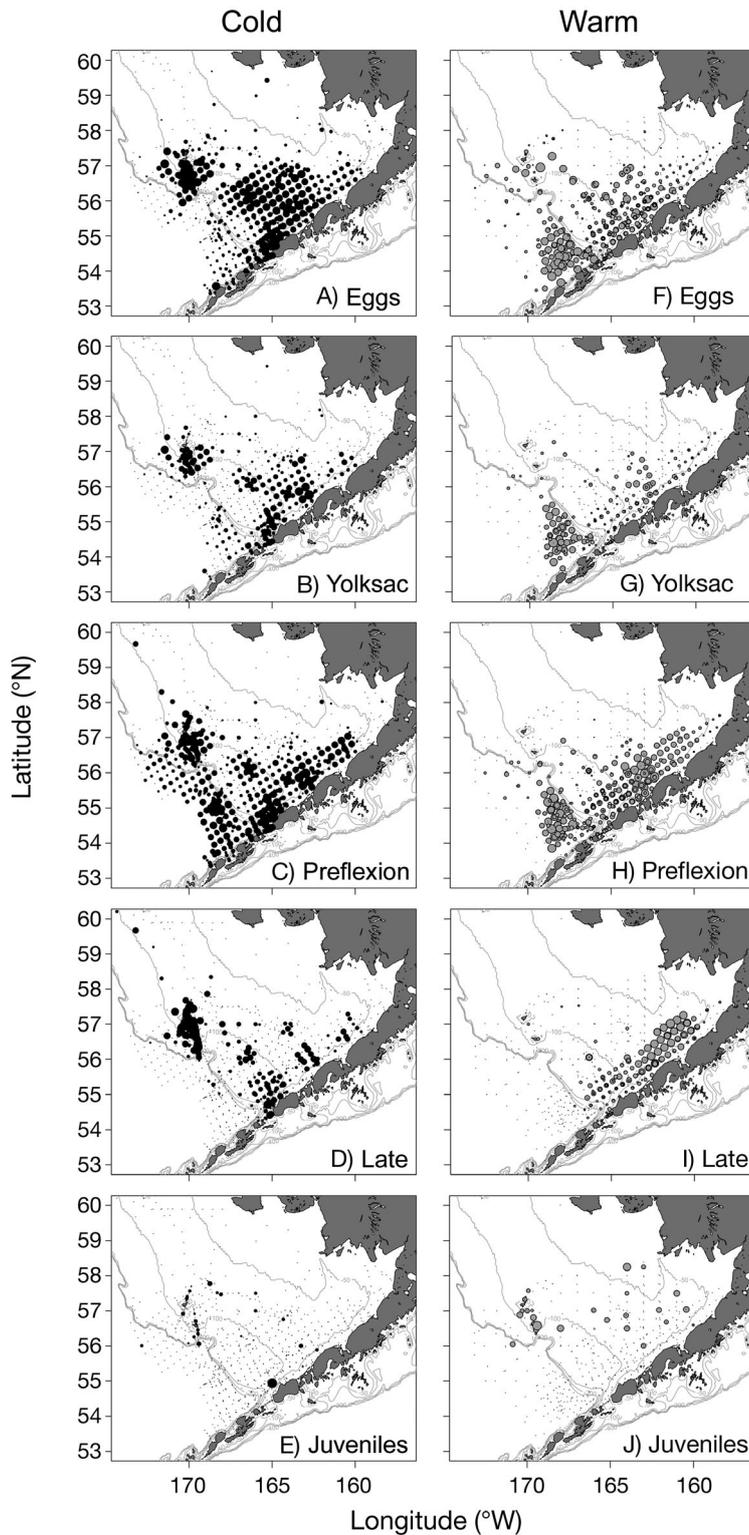


Fig. 3. *Theragra chalcogramma*. Walleye pollock early life stages in the southeastern Bering Sea showing relative abundances of (A,F) eggs, (B,G) yolksac larvae, (C,H) preflexion larvae, (D,I) late larvae, and (E,J) juveniles within (A–E) cold and (F–J) warm temperature categories. Bubble size is proportional to the largest catch within each stage

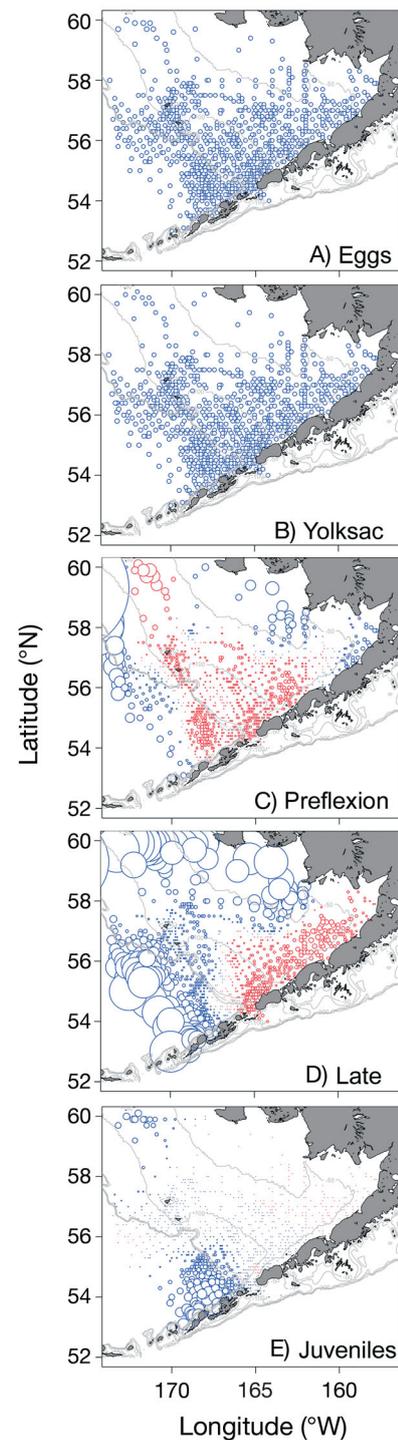


Fig. 4. *Theragra chalcogramma*. Spatially-explicit impacts of temperature on density of walleye pollock for each early life stage: (A) eggs, (B) yolksac larvae, (C) preflexion larvae, (D) late larvae, and (E) juveniles. \circ = increase and \circ = decrease in density as temperature increases in the southeastern Bering Sea. Bubble size is relative to the size of the change in density

Table 2. *Theragra chalcogramma*. Variable-coefficient generalized additive models used to develop spatial distributions of each walleye pollock early life stage within each temperature category, including the number of tows containing each stage (positive tows), number of tows lacking each stage (zero tows), % deviance explained by the model, and estimated degrees of freedom (edf) for spawning stock biomass (SSB), day of year (DOY), location, sea surface temperature anomaly (SSTa), and the spatially-explicit SSTa term. *p < 0.05, **p < 0.01, ***p < 0.001

Life stage	Tows (n)		% deviance	edf				
	Positive	Zero		SSB	DOY	Location	SSTa	Location × SSTa
Egg	1032	1003	47.9	2.995***	2.998***	2.965***	1*	29.937***
Yolksac	404	1631	50.9	2.995***	2.998***	2.993***	1***	28.930***
Preflexion	862	1173	53.0	2.986***	2.997***	2.999***	1*	29.980***
Late	345	1690	65.8	2.999***	2.995***	2.001***	1**	29.963***
Juvenile	74	1971	75.1	2.978***	2.938***	2.971***	1*	29.996***

Table 3. *Theragra chalcogramma*. Generalized additive models used to develop temporal distributions of each walleye pollock early life stage within each temperature category. The number of tows is the same as in Table 2, and % deviance explained by the model and estimated degrees of freedom (edf) for model covariates of spawning stock biomass (SSB), location, temperature, and day of year (DOY) are shown. *p < 0.05, **p < 0.01, ***p < 0.001

Life stage	% deviance	edf			
		SSB	Location	Temperature	DOY
Egg	41.5	8.980***	2.997***	1***	2.997***
Yolksac	51.4	8.981***	2.991***	1***	2.997***
Preflexion	51.1	8.980***	2.997***	1***	2.997***
Late	60.1	8.964***	2.939***	1***	2.995***
Juvenile	54.3	8.953***	2.987***	1**	2.995***

prior to DOY 185 (before July 5) in warm years (Fig. 5C). The late larval season occurred between DOY 125 and 240 (May 5 and August 25) in cold years and between DOY 100 and 215 (April 10 and August 1) in warm years (Fig. 5D). For juveniles, density anomalies peaked after DOY 130 (after May 10) in cold years and after DOY 120 (after May 1) in warm years (Fig. 5E). For the stages that we can predict start or end dates of their seasons, all seasons started or finished earlier in warm years than in cold years. However, as sampling does not typically occur prior to March, we are unable to predict start dates for eggs, yolksac larvae in warm years, and reflexion larvae in warm years. As sampling rarely occurs after October, we are unable to predict end dates for juveniles. With these limitations, we cannot at present determine whether or not the span of each stage is shortened in warm years as hypothesized.

Temporal shifts were estimated for each stage using the density maximum predicted by DOY. Differences in maxima indicated delays in peak temporal distributions of all ELS in cold compared to warm years (Table 4). These differences suggested a 40 d

delay in the egg stage maxima (spawning and hatching), a 45 d delay in the yolksac larval stage maxima (hatching and absorption of yolk reserves), a 20 d delay in the reflexion stage maxima (feeding commences), a 30 d delay in the late larval stage maxima (flexion of the notochord), and a 25 d delay in the juvenile stage maxima (completion of the juvenile transition and growth to sizes above which our collection gear are avoided).

DISCUSSION

Water temperatures in the southeastern Bering Sea influenced walleye pollock *Theragra chalcogramma* ELS in several ways. Spatial distributions of eggs and yolksac larvae were not affected by temperature, while feeding stages (preflexion larvae, late larvae, and juveniles) were affected. VCGAMs predicted decreases in the density of eggs and yolksac larvae with warming, suggesting that there is no discernible shift in spawning locations. VCGAMs predicted that densities of preflexion larvae and late larvae would increase over the shelf, while densities of preflexion larvae, late larvae, and juveniles would decrease offshore, suggesting a movement of the population onto the shelf. A likely mechanism to explain these patterns is that spawning location remains relatively constant, but larval transport varies with temperature. Temporal distributions predicted by GAMs indicated a delay in the timing of reproductive and ontogenetic events in cold temperatures. Earlier spawning, hatching, and onset of feeding could explain the low densities of eggs and yolksac larvae observed in warm years. We were unable to deter-

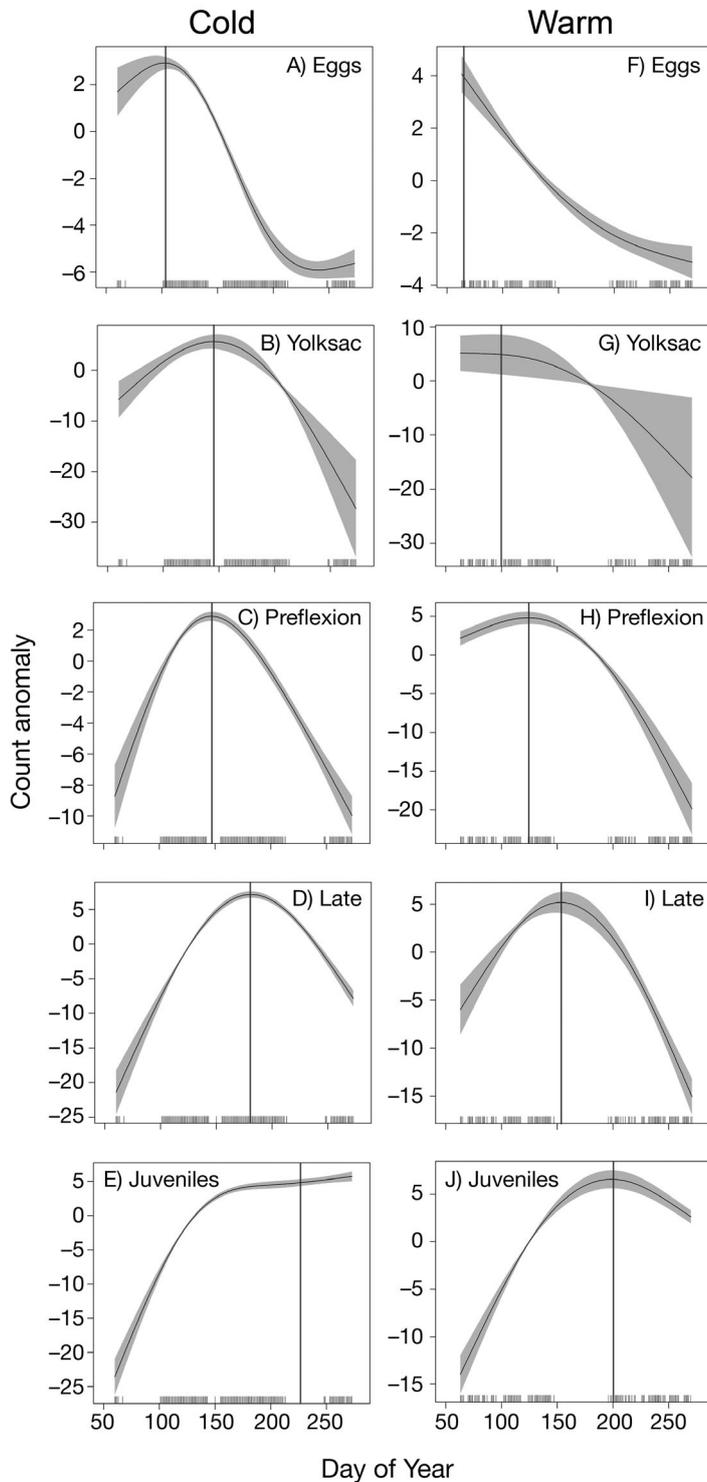


Fig. 5. *Theragra chalcogramma*. Temporal distributions of walleye pollock (A,F) eggs, (B,G) yolksac larvae, (C,H) preflexion larvae, (D,I) late larvae, and (E,J) juveniles within (A–E) cold and (F–J) warm temperature categories derived from the relationship between count (numbers or individuals) and day of year (DOY) in generalized additive models. Shaded areas are 95% confidence intervals and rug plots on the x-axis indicate sampling intensity on each DOY. The vertical line denotes the estimated DOY of the density maxima

mine rates of development because of uncertainty at the beginning and end of the sampling season. Our analysis suggests that in warm years this population reaches the juvenile stage earlier and would have more time for feeding and growth prior to the oncoming winter.

Spatial distribution shifts

Bacheler et al. (2012) found indications of shifts in pollock spawning location across the shelf using an earlier time series and VCGAMs. In support of this pattern, anchovy *Engraulis encrasicolus*, sardine *Sardina pilchardus*, and common sole *Solea solea* have all been reported to shift spawning locations in response to environmental factors (Eastwood et al. 2001, Bellier et al. 2007). We were unable to discern the same pattern for pollock eggs. An alternate explanation is that SEBS pollock spawning location does not, but subsequent transport of ELS does. The current study supplements the findings of Bacheler et al. (2012) with spatial shifts in subsequent ELS, which can isolate differential transport from shifts in spawning location. In cold years, surface currents are generally westward and faster relative to warm years (Stabeno et al. 2012a), which would transport larvae to the outer shelf or offshore if they were spawned over the shelf. In warm years, larvae are more likely to be retained over the shelf. Although we found only a small increase in juvenile density over the inner shelf with warming, we did observe a large decrease in density offshore. Together, these results suggest that juveniles move onshore in warm years although densities may be low and distributions are widespread. We attribute distributions of larvae and early juveniles to shifts in subsequent transport rather than shifts in spawning location (see also Duffy-Anderson et al. 2006).

Spatial shifts observed in pollock larvae and juveniles determine their use of 2 SEBS shelf domains which vary in productivity and zooplankton communities. The shelf tends to have a greater concentration of smaller copepods (more appropriate prey items for small larvae), while larger copepods (appropriate prey items for large larvae) are generally found in spring over the deeper outer shelf (Cooney & Coyle 1982, Vidal & Smith 1986, Baier & Napp 2003). Zooplankton present in the SEBS during cold

Table 4. *Theragra chalcogramma*. Temporal distributions of walleye pollock early life stages derived from generalized additive models, showing day of year (DOY) when each stage appears in surveys prior to the peak (start), DOY at the peak in temporal distributions (peak), and DOY when each stage appears for the final time in surveys after the peak (end). na: not available because sampling did not occur early or late enough to determine these values

Life stage	Cold			Warm		
	Start	Peak	End	Start	Peak	End
Eggs	na	105	150	na	65	130
Yolksac	100	145	180	na	100	170
Preflexion	100	145	195	na	125	185
Late larvae	125	180	240	100	150	210
Juveniles	135	225	na	120	200	na

years are larger, energetically richer, and concentrated over the outer shelf and shelf break (Coyle et al. 2011). Cold temperatures favor a larger-bodied prey for late larvae and juveniles and are predicted to increase juvenile survival if they can exploit this resource. Warm water temperatures with a smaller-sized prey field are predicted to benefit the growth of reflexion larvae, which are gape-limited (Nakatani 1988). In warm years, reflexion larvae are more likely to be in the vicinity of small prey over the shelf. In cold years, late larvae and juveniles are more likely to be in the vicinity of large prey over the shelf break. This hypothesis is supported by recent evidence that the few juvenile pollock collected in recent cold years in the SEBS were energetically richer than those sampled in recent warm years (Hunt et al. 2011). The spatial distribution shifts observed in the current study combined with the observation of spatially-distinct zooplankton communities supports the hypothesis that prey fields in cold years should support higher densities and energetically richer pollock larvae and juveniles.

Phenological shifts

Pollock ELS oscillate between high densities of early stages (eggs and yolksac larvae) in cold years and high densities of developed stages (preflexion and late larvae and juveniles) in warm years (Smart et al. 2012). One explanation for high numbers of early-staged individuals in cold years is a combination of delayed spawning and slower rates of development. Egg density temporal distribution is dependent on both the timing of spawning and the time required to develop to the hatching stage. Based on observed egg temporal distributions, either the timing of spawning events or development to hatching is

temperature dependent in the SEBS. There are currently no data available on the temperature dependence of gametogenesis in pollock. As a comparison, maturation rates and spawning in Atlantic cod *Gadus morhua* are temperature-dependent, and completion of maturation is advanced by several weeks in warm temperatures (Beaugrand et al. 2003, Yoneda & Wright 2005). Extrapolating from laboratory data, Blood (2002) estimated that egg incubation period could be delayed by 13 d during a cold (1997) compared to a warm (1998) year. In

the field, the estimated delay in peak egg density is 40 d, suggesting that both timing of spawning and development could be delayed, accounting for the interval between temperature categories in the current study.

Comparing temperature categories, we found evidence of temperature dependence in the timing of hatching, onset of feeding, flexion of the notochord, juvenile transition, or some combination of temperature dependence among any of these developmental events. Delayed hatching increases the likelihood of collecting eggs during our primary sampling period (May through September). Delayed onset of feeding retains larvae in the non-feeding yolksac stage. Jung et al. (2006) estimated that hatching was delayed by 12 to 17 d in 1976 (cold) compared to 1977 (warm) based on the staging of field-caught eggs. Under warm conditions, early-spawned eggs should rapidly develop and hatch. The newly hatched larvae could consume their yolk reserves in perhaps as little as a week (Walline 1985, Porter & Theilacker 1999). Temperature-dependent development rates in larval stages have consequences for matching with prey production cycles and for growth-dependent mortality (Gallego & Heath 1997). Currently, we cannot estimate start and end points, and by extension the time span of development, for all stages. Therefore, the timing of events must stand as a proxy supporting the hypothesis that development is delayed in cold relative to warm water temperatures.

In summary, our data demonstrated that walleye pollock ELS in the southeastern Bering Sea responded to changes in oceanographic conditions (i.e. water temperature and flows) by shifting density distributions in time and, in some cases, space. The temperature-associated oscillation between high egg and yolksac larval density and high density of more developed larvae and juveniles can be explained by

phenological shifts in spawning and development. Distributions of pollock feeding larvae and juveniles also spatially shifted between 2 habitats, the continental shelf and the shelf break or offshore, which has the potential to affect access to appropriate sized prey. We hypothesize that the lack of spatial shifts observed in pollock eggs and early larvae indicate that adults do not adjust the location of spawning in response to temperature. We further hypothesize that spatial shifts observed in larval and juvenile densities reflect differences in transport between cold and warm years. Comparable trends among life stages suggest shared habitats. As temperatures continue to change in the North Pacific, identification of spatiotemporal shifts in habitat use will be crucial to understanding short- and long-term population trends in this ecologically and economically important species.

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