**Biophysical transport model suggests climate variability determines distribution of Walleye
Pollock early life stages in the Eastern Bering Sea through effects on spawning**

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ABSTRACT

The eastern Bering Sea recently experienced an anomalously warm period followed by an
anomalously cold period. These periods varied with respect to sea ice extent, water temperature,
wind patterns, and ocean circulation. The distributions of Walleye Pollock early life stages also
differed between periods, with larval stages found further eastward on the shelf in warm years.
Statistical analyses indicated that these spatial distributions were more closely related to
temperature than to other covariates, though a mechanism has not been identified. The objective
of this study was to determine if variable transport could be driving the observed differences in
pollock distributions. An individual-based model of pollock early life stages was developed by
coupling a hydrodynamic model to a particle-tracking model with biology and behavior.
Simulation experiments were performed with the model to investigate the effects of wind on
transport, ice presence on time of spawning, and water temperature on location of spawning.
This modeling approach benefited from the ability to individually test mechanisms to

quantitatively assess the impact of each on the distribution of pollock. Neither interannual variability in advection nor advances or delays in spawning time could adequately represent the observed differences in distribution between warm and cold years. Changes to spawning areas, particularly spatial contractions of spawning areas in cold years, resulted in modeled distributions that were most similar to observations. The location of spawning pollock in reference to cross-shelf circulation patterns is important in determining the distribution of eggs and larvae, warranting further study on the relationship between spawning adults and the physical environment. The different distributions of pollock early life stages between warm and cold years may ultimately affect recruitment by influencing the spatial overlap of pollock juveniles with prey and predators.

Keywords: biophysical model; climate change; larval fish; *Gadus chalcogrammus*; *Theragra chalcogramma*

1. INTRODUCTION

The eastern Bering Sea shelf is one of the most biologically productive marine ecosystems in the world with marine resources that are integral to the culture and diet of native Alaskans and that comprise roughly 50% of the US commercial fish harvest. The continental shelf extends approximately 500 km westward from the Alaskan mainland coast to the Aleutian Basin shelfbreak and 1000 km northward from the Alaska Peninsula to the Bering Strait. The shelf can be divided into three regions based on bathymetry: inner shelf (<50 m), middle shelf (50-100 m), and outer shelf (>100 m; Coachman 1986). The inner shelf is weakly stratified and influenced by freshwater runoff, while the middle and outer shelves are strongly stratified (Coachman 1986). A large and highly variable portion of the shelf is ice-covered during winter, cooling the entire water column and resulting in a bottom layer of very cold water (the “cold pool”) over much of the middle shelf that can persist through the summer. Offshore, the Bering Slope Current (Figure 1) transports nutrient-rich waters along the slope to the northwest, replenishing nutrients on the shelf through cross-shelf exchanges associated with eddies (Mizobata et al. 2008), intrusions of water through canyons (Stabeno et al. 2008), and wind-forced cross-shelf flows (Stabeno et al. 2001, Danielson et al. 2011b). Mean circulation over the shelf is dominated by the Alaska Coastal Current, which is a seasonal current that flows roughly

parallel to the 50-m isobath northeast along the Alaska Peninsula, around Bristol Bay, and continues to the northwest off of mainland Alaska towards the Bering Strait (Figure 1). Cross-shelf and along-shelf flows provide important pathways for the planktonic stages of many species that spawn on the outer shelf or slope to reach suitable nursery areas (Lanksbury et al. 2007, Wespestad et al. 2000, Wilderbuer et al. 2013).

Walleye Pollock (*Gadus chalcogrammus*; hereafter pollock) is an ecologically and commercially important gadid in the eastern Bering Sea, supporting one of the largest single-species fisheries in the world. Adults are semi-demersal and occur primarily in regions 50-300 m deep (J. Duffy-Anderson pers. comm.). Females are iterative spawners with up to 10 batches of eggs per female per year (J. Duffy-Anderson pers. comm.). Pollock show fidelity to at least two spawning sites over the southeastern Bering Sea shelf (Figure 1). Spawning begins nearshore north of Unimak Island in March and April and later near the Pribilof Islands from April through August (Jung et al. 2006, Bacheler et al. 2010). Egg production from these two locations is highest in April or May (Bacheler et al. 2010). Eggs can be found as deep as 300 m, but the center of the vertical distribution is < 30 m (Smart et al. 2012). Depending upon water temperature, embryos hatch 18 to 34 days after fertilization and yolk sac larvae are 4.6 to 5.7 mm standard length (SL) at hatch (Blood 2002). Larvae develop in the upper 100 m of the water column and the depth of maximum abundance shifts deeper with age (Smart et al. 2013). Depth differences are related to flexion, which occurs between 10 and 17 mm SL (Matarese et al. 1989), after which larval swimming ability increases. Pollock transition from larva to pelagic juvenile when they are 30-40 mm SL (Matarese et al. 1989) and recruit into the fishery at age-3 to age-4 (Ianelli et al. 2012a).

The eastern Bering Sea recently experienced a prolonged warm period (2001-2005), followed by a prolonged cold period (2007-2012; Stabeno et al. 2012). During colder than average years, winter ice extends farther south and offshore, creating a more extensive cold pool that influences the distribution (Mueter & Litzow 2008, Barbeaux 2012, Ianelli et al. 2012a) and potentially the spawning ecology of pollock and other demersal fishes. The timing and location of pollock spawning affect the initial distribution of eggs, while their subsequent advection is a function of prevailing atmospheric and hydrographic conditions. Therefore both the initial distribution and advective forcing vary from year-to-year due to climatic variability. For example, strong northward flow and/or weaker cross-shelf flow have been observed at a

hydrographic mooring over the middle shelf during the recent warm period compared to recent cold years that had strong westward flow (Stabeno et al. 2012), which could affect the dispersal of pelagic early life stages (ELS). Modeling results suggest generally enhanced on-shelf transport when winds blow predominantly from the southeast during winter (Danielson et al. 2011a). Such southeasterly winds coincided with warm temperatures from 2001 to 2005, while the following cold years were characterized by winds from the northwest. It has been speculated that these differences in advection influence the distributions of pollock ELS, whose centers are further inshore in warm years than cold years (Smart et al. 2012).

The observed variability in distribution could be the result of differences in physical transport as hypothesized, or they could be the result of biological responses to physical variation. Preliminary analysis of roe fishery harvest data and pollock fishery observer maturity data suggest that spawning extends further onshore in warm years (S. Barbeaux unpub. data) and the onset of spawning is delayed in time by as much as 40 d in cold years (Jung et al. 2006, Smart et al. 2012). Differences in water temperature could impact not only where adults spawn, but also the development rates of ELS.

Mechanisms behind the spatial differences have not been identified, and effects of climate variation on the dispersal of pollock ELS are poorly understood. The differences in winds and water currents between cold and warm years, and the relationship between temperature and pollock spatial distribution lead to our hypothesis that physical forcing mechanisms are responsible. To gain a clearer understanding of the forcing mechanisms that underlie observed spatial differences in pollock egg and larval distribution, we developed an individual-based model of pollock biology and behavior coupled to a hydrodynamic model. Our objective was to test the effects of atmospheric (wind), oceanographic (ice, water column temperature), and biological (time and location of spawning) conditions on the distribution, development, and transport of pollock eggs and larvae. Model results are used to elucidate the dominant physical mechanisms responsible for observed changes. We present a description of the coupled biophysical model, its validation with observations, and its use to evaluate mechanisms that determine the spatial distribution of propagules during warm and cold years.

2. METHODS

2.1 Physical model

We used an implementation of the Regional Ocean Modeling System (ROMS; Shchepetkin & McWilliams 2009) as the hydrodynamic model to force the Lagrangian particle-tracking model. ROMS is a free-surface, hydrostatic primitive equation ocean circulation model. It is a terrain-following, finite volume (Arakawa C-grid) model with the following advanced features: high-order, weakly dissipative algorithms for tracer advection; a unified treatment of surface and bottom boundary layers (e.g., K-Profile Parameterization; Large et al. 1994); atmosphere-ocean flux computations based on the ocean model prognostic variables using bulk-formulae. ROMS has been coupled to a sea-ice model (Budgell 2005) consisting of the elastic-viscous-plastic (EVP) rheology (Hunke & Dukowicz 1997) and the Mellor and Kantha (1989) thermodynamics. The sea ice code is fully explicit and implemented on the ROMS Arakawa C-grid and is therefore fully parallel, just as ROMS is. The model also includes frazil ice growth in the ocean being passed to the ice (Steele et al. 2004). It currently follows a single ice category, which provides accurate results in a marginal ice zone such as the Bering Sea. Large-scale climate signals are propagated to the regional domain through the model boundaries. This global-to-regional downscaling via open boundary conditions has several desirable features for the implementation of regional models: for multi-decadal integrations, climate signals project onto the high-resolution inner domains through boundary forcing; tidal forcing is naturally implemented on the domain open boundaries; for extensive integrations a tidal potential correction is applied to ensure proper tidal phasing (Curchitser et al. 2005, Danielson et al. 2011a).

We used the ROMS model for the northeast Pacific version 6 (NEP6), an update of version 5 (NEP5; Hermann et al. 2009, Danielson et al. 2011a). The NEP model domain extends from approximately 20 °N to 71 °N, reaching about 2250 km offshore from the North American west coast at a nominal horizontal resolution of 10 km and with 50 terrain-following vertical levels stretched towards the surface boundary. The grid (a rectangle in a Lambert Conical projection) is rotated relative to lines of constant longitude so as to minimize computations over land. The coupled ocean-sea ice model was integrated in hindcast mode for the period from 1994-2012. These hindcasts derived the surface forcing from the Modern Era Retrospective-Analysis for Research and Applications (MERRA; Rienecker et al. 2011), which consists of 3-hourly winds, air temperatures, sea level pressure, specific humidity, short-wave and downwelling long-wave radiation, precipitation, and daily albedo. The air-sea fluxes were

computed using bulk formulae (Large & Yeager 2009). Riverine inputs were implemented using the Dai and Trenberth (2002) method as a surface fresh water flux. Boundary and initial conditions for this domain were derived from the Simple Ocean Data Assimilation (SODA) ocean reanalysis (Carton & Giese 2008) for the early years. Later years used boundary conditions from global HYCOM assimilative product (HYCOM Ocean Prediction website). Key model outputs have recently been validated against observations at relevant spatial and temporal scales (Curchitser et al. 2010, Danielson et al. 2011a).

The output of the hindcast was saved as daily averages to force the offline particle-tracking model, as described below. Specifically, the particle-tracking model used ROMS-generated velocities, temperature, and mixed layer depth.

2.2 Particle-tracking model

2.2.1 TRACMASS

We implemented the individual-based model with the particle-tracking tool TRACMASS. TRACMASS calculates Lagrangian trajectories from Eulerian velocity fields. The coupling is offline, using stored output from general circulation model (GCM) simulations. Offline coupling is less computationally expensive, thus it allows for more calculations of trajectories in comparison with online coupling (simultaneously with the GCM). TRACMASS accepts output from many GCMs, including ROMS. TRACMASS interpolates the GCM three-dimensional grid to its own grid and solves the trajectory path through each grid cell with an analytical solution of a differential equation, which depends on the velocities at the grid cell walls. This novel scheme was originally developed by Döös (1995) and Blanke and Raynaud (1997) for stationary velocity fields and further developed by de Vries and Döös (2001) for time-dependent fields. With time-dependent fields it solves a linear interpolation of the velocity field both in time and in space over each grid box, in contrast to the Runge-Kutta method where the trajectories are iterated forward in time with short time steps. The TRACMASS code has been further developed over the years and used in many atmospheric and oceanographic studies of large global (e.g. Drijfhout et al. 2003) and regional scales (e.g. Engqvist et al. 2006).

The particle-tracking time step was one hour. We chose to use the turbulence subroutine in TRACMASS to incorporate a sub-grid scale parameterization. This scheme adds a random horizontal turbulent velocity to the horizontal velocity from ROMS to each trajectory and each

horizontal grid wall every time step (Döös & Engqvist 2007). The amplitude of the random turbulent velocity is set to the same size as the ROMS velocity. We tested simulations of a small cluster of particles with and without sub-grid turbulence. Including turbulence resulted in less patchy distributions of ELSs, which were assumed to be more realistic, although fine-scale data to evaluate this assumption are lacking. In addition to particle trajectories, TRACMASS calculated surface light as a function of latitude, longitude, date, and time of day.

2.2.2 Number of particles

Often results from stochastic models are presented as the average of several repeated simulations with the same initial and forcing conditions. For particle-tracking models, an alternate method exists of releasing multiple particles at each time and location, each representing one possible outcome of the simulation. The results of a rigorous particle-tracking model should not change significantly between repeated simulations (Brickman et al. 2009). The number of particles released at each time and location (number of simulation repetitions) was determined by calculating the fraction of particles at four random locations downstream of the initial start locations, and finding the minimum number of particles for which those fractions did not change appreciably. Ten particles per 10 m depth increment per spawning location were deemed appropriate for producing stable results.

2.3 Observational data

2.3.1 Ichthyoplankton surveys

Observational data from the Alaska Fisheries Science Center's Fisheries Oceanography Coordinated Investigations (FOCI) surveys and Bering Ecosystem Study and Bering Sea Integrated Ecosystem Research Project (BEST-BSIERP) cruises were used for model-data comparisons. The specific cruise details are given in Smart et al. (2012). Observational data included egg and larval samples collected with Bongo nets, Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), Modified Bottom Trawls (MBTs), and Tucker trawls. Larval stages were segregated by length: yolk sac < 6 mm; 6 mm ≤ preflexion < 10 mm; 10 mm ≤ late < 40 mm (Matarese et al. 1989). Data from all four gear types were used to characterize horizontal distributions, while only depth-stratified MOCNESS samples were used for the vertical distributions since the other gear types did not provide enough vertical resolution.

Horizontal distributions were determined for each stage and for each available month and year from 1995 to 2012, by aggregating all observations within a given month and year. To quantify horizontal distributions, vertically integrated concentrations (number per 10 m²) were computed over the entire depth range sampled by depth-stratified tows (MOCNESS, MBT, Tucker) so that they were comparable to non-stratified samples (Bongo). All available data sets from 1995 and 2007, years with the best spatial and temporal coverage, were used for model selection. Data from all years (1995-2012), for the cruises listed in Smart et al. (2012), were aggregated by warm and cold years for comparison between observed and modeled distributions in warm and cold years.

2.3.2 Spawning data

Two different data sets were used to provide information on potential locations for initializing particles as eggs in the model. The first data set was derived from collections of female pollock for the roe fishery (S. Barbeaux unpub. data). These data included the day of fishing, the centroid latitude and longitude of where the boat fished that day, and the amount of roe of each quality caught that day for the years 2001-2006. The market quality of roe deteriorates as the adults near spawning and is ranked as immature, mature, overmature, or other. Hydrated, overmature roe is within a few days of spawning and of the worst quality (S. Barbeaux pers. comm.). We used only presence and absence data of the hydrated roe as a proxy for spawning times and locations.

The second data set consisted of maturity index classifications from the NOAA Fisheries North Pacific groundfish observer program. These data were obtained on pollock fillet fishery vessels from 2008-2012 and contained date, latitude, longitude, bottom depth, fishing depth, and a maturity index for each fish. Observers classify the maturity level of a random subsample of the catch using the maturity indices: immature, developing, pre-spawn, spawning, and spent. We used only the dates and locations where female pollock in spawning condition were recorded as a proxy for spawning times and locations.

These data were used together with available literature on dominant spawning areas (Bacheler et al. 2010, Hinckley 1987) to infer generalized spawning distributions for warm and cold years, respectively, as described below. We were unable to use annual observations on spawning times and locations for model initialization because neither data set spanned the whole

time period of interest from 2000 to 2012. Furthermore, we chose not to combine the two data sets because they used data from different fisheries with different classification methods, of which one only included cold years and the other only warm years.

2.4 Biological model

2.4.1 Model parameterization

The literature on pollock ELS was reviewed to determine appropriate formulations for the growth and vertical behavior routines in the biological model. When available, data from the Bering Sea population was used in preference to data from the Gulf of Alaska.

2.4.1.1 Growth

Egg development was implemented as a temperature-dependent function parameterized from laboratory data for Bering Sea pollock eggs (Blood 2002). Time to hatch, $hatch_{hrs}$ (hr) (Figure 2a), was

$$hatch_{hrs} = 895.97 \cdot e^{-0.194T},$$

with temperature, T , in °C. At each time step, an egg accumulated a fraction of the hatch time given the temperature. When the accumulated hatch time reached 1, the egg transitioned to the yolksac stage. Size at hatch was not related to incubation temperature in a laboratory study with Bering Sea eggs, thus yolksac larvae were initialized at a random hatch length drawn from a normal distribution with a mean of 5.125 mm SL and a standard deviation of 0.46 mm (Blood 2002).

Both a temperature-dependent and an age-dependent (temperature-independent) growth model were developed for larvae to allow for tests of the effect of temperature on growth and the resulting distributions of different ELS. The age-dependent routine was an empirical function for length, L_{larva} (mm), fit to otolith-estimated age of larvae collected in the Gulf of Alaska by Yoklavich and Bailey (1990) during summer 1987, a year with slightly above average temperature conditions (7-11°C in the surface layer).

$$L_{larva} = L_{hatch} \cdot \exp(7.854 \cdot (1 - \exp(-0.004 \cdot age)))$$

where L_{hatch} is length at hatch (mm), and age is days post hatch (dph; Figure 2c solid line). The temperature-based growth model fitted growth rates from laboratory studies as a function of

temperature (Canino 1994 for yolk sac, Porter & Bailey 2007 for feeding larvae). Yolk sac larvae growth, g_y (mm d⁻¹; Figure 2b), was

$$g_y = 0.0686 \cdot \log(T) + 0.0594.$$

Growth of feeding larvae (preflexion and late larvae), g_f (mm d⁻¹), was additively adjusted to account for differences in laboratory growth rates of larvae fed a natural assemblage of zooplankton vs. those fed *Artemia*. Growth (Figure 2b, 2c dotted lines) was calculated as

$$g_f = 0.0902 \cdot \log(T) - 0.0147.$$

Larval length is only updated for nonnegative growth rates at temperatures above 1.17°C, thereby preventing larvae from shrinking at lower temperatures.

2.4.1.2 Vertical behavior

Vertical behaviors were determined from depth-stratified observations of pollock ELS in the Bering Sea (Smart et al. 2013). Five different vertical behavior routines were developed and tested. They included: 1) passive (neutrally buoyant) individuals of all stages; 2) passive eggs and yolk sac larvae, and preflexion and late larvae that move to the middle of the mixed layer; 3) all stages move to the middle of the mixed layer; 4) eggs, yolk sac, and preflexion larvae move to the middle of the mixed layer, and late larvae make diel vertical migrations (DVMs) between 20 m during the day and 5 m during the night; 5) eggs and yolk sac larvae move to the middle of the mixed layer, and preflexion and late larvae make DVMs. For DVM, day was defined as times when surface light was greater than zero. Swimming speed (w) was parameterized as:

$$w = w_{\max} \cdot (-\tanh(0.2 \cdot (z - z_{\text{pref}})))$$

where z is depth (m), z_{pref} (m) is the preferred depth (middle of the mixed layer or day-time/night-time preferred depths), and the maximum vertical swimming speed, $w_{\max}$ (m s⁻¹), is

$$w_{\max} = 0.5 \cdot L_{\text{larva}} \cdot 10^{-3}.$$

Swimming speeds of larval Atlantic Cod (*Gadus morhua*), a related gadid fish, range from 0.3-0.9 body lengths s⁻¹ (Peck et al. 2006), thus a maximum speed of 0.5 body lengths s⁻¹ was a conservative estimate for sustained swimming.

2.4.2 Model initialization

Spawning polygons were created by generalizing areas with fishery-based observations of adult pollock in spawning condition. Only the dominant spawning regions on the eastern Bering Sea shelf, as identified from the literature (Hinckley 1987, Bacheler et al. 2010), were considered. Spawning observations in regions deeper than 250 m were not used, as these are likely to consist of spawners from the Bogoslof Island population, which is considered to be a separate population from that over the eastern Bering Sea shelf (Ianelli et al. 2012b). Polygons were created for 2-week periods from the middle of January to the end of April for a total of seven periods (Figure 3; release dates Jan 15, Feb 1, Feb 15, Mar 1, Mar 15, Apr 1, Apr 15). These dates cover the spawning season and represent the iterative spawning of pollock, though at a lower frequency than the natural population. Spawning was initialized at all ROMS grid points within each spawning polygon. Spawning depths occurred every 10 m from surface to bottom at each grid point. Individuals were followed from spawning time until they reached 40 mm. At approximately 30-40 mm SL pollock larvae transition to pelagic juveniles with different growth rates and enhanced swimming abilities (Matarese et al. 1989), which were not represented within the model.

2.4.3 Model selection

Two years with the most spatially and temporally resolved observations (1995, 2007; both cold years) were used to choose the growth and vertical behavior routines to be implemented in all other simulations of the model. Ten different growth-behavior combinations (two growth functions, five vertical behaviors) were run for each year, for a total of 20 different simulations.

The observational data were used to calculate the average monthly concentration for each ELS in 0.25° x 0.25° grid cells over the eastern Bering Sea (-175°W to -160°W, 53°N to 61°N) for comparisons with model output aggregated at the same spatial scale. When multiple observations occurred within the same grid cell, the mean concentration was used. A grid cell without any observations was set to “missing”.

To account for uneven spatial coverage of samples among years and to reduce the impact of small-scale sampling variability resulting from patchiness and/or sampling errors, observed concentrations were spatially smoothed using a General Additive Modeling (GAM) approach. We modeled log-transformed concentrations of each ELS in each month as a smooth function of

latitude and longitude using a flexible thin-plate regression spline (Wood 2006). Residuals were assumed to be independent and normally distributed, an assumption that was visually assessed for each model.

To minimize extrapolation beyond the observations, contours of the resulting model standard error were mapped and a threshold was visually chosen by selecting the smallest standard error contour that encompassed all of the observations. For all grid cells within the spatial domain defined by this standard error threshold, egg or larval concentrations within each grid cell were predicted from the GAM fit. The predicted concentrations were then re-scaled to correspond to the fraction of each ELS in each grid cell in each month for comparison with model output. Fractions within each grid cell were used for comparison because the model produces relative concentrations that cannot directly be compared to observed densities.

Model output (longitude, latitude, depth, egg/larval length, time) was treated in the same way as observational data. The output for all seven spawning times was aggregated, since the spawning times of eggs and larvae collected in the field were unknown. The model output was separated by month and pollock ELS. Model output for each stage, month, and year was restricted to those particles that fell within the same spatial domain over which GAM-predicted concentrations were obtained. The fraction of particles within each of the corresponding grid cells was calculated for all stages, months, and years.

The growth and vertical behavior routines were selected using multiple skill metrics (Stow et al. 2009), including correlation coefficient (R), root mean square error (RMSE), and modeling efficiency (MEF), calculated from the GAM-predicted fractions and the modeled fractions for all months with observations in the years 1995 and 2007. All three skill metrics (Table 1) indicated the same two behaviors as the best model: behaviors 1 (passive individuals of all stages) and 2 (passive eggs and yolksac larvae, preflexion and late larvae that move to the middle of the mixed layer). Combined with the two different growth formulas, three of the four combinations were the only simulations that produced results better than using the average of the observations, as denoted by positive modeling efficiencies (Table 1). The resulting depth distributions were not used for model selection, but compare favorably with observations (Figure 4).

2.4.4 Model simulations

Based on the skill results, the warm and cold year simulations were run with temperature-dependent growth and vertical behavior 2 (passive eggs and yolk sac larvae, preflexion and late larvae that move to the middle of the mixed layer). After selecting the growth and vertical behavior routines based on results of the 1995 and 2007 simulations, the biophysical model was run for each of the warm (1996, 2002, 2003, 2005) and cold (1997, 1999, 2000, 2006, 2008-2012) years using model output from ROMS NEP6 hindcasts. Years were identified as either warm or cold based on the sign of the sea surface temperature anomaly, following Smart et al. (2012). The modeled egg and larval distributions during warm and cold years were contrasted and related to physical forcing to determine potential mechanisms for the observed differences. A series of simulations was conducted to elucidate if differences in horizontal distributions of pollock ELS between warm and cold years are attributable to spawning timing, spawning location, physical transport, and/or development during transport. All simulations used year-specific physical forcing, but different scenarios for spawning time and location:

(1) Physical transport – The same spawning time and location for both warm and cold years, thus differences in distribution arise from differences in advection alone

(2) Delay spawning time – The same spawning locations, delay initialization of cold year spawning by 40 d

(3) Advance spawning time – The same spawning locations, advance initialization of warm year spawning by 40 d

(4) Contract spawning location – Contract spawning polygons in cold years by shifting the eastern edge of spawning polygons offshore to the southwest (by 0.5° to the South and 0.25° to the West around the Pribilof Islands; by 1.0° to the South and 0.50° to the West around Unimak Island).

(5) Expand spawning location – Expand spawning polygons in warm years by shifting the eastern edge of spawning polygons onshore to the northeast (0.50° to the North, 0.25° to the East).

The advance and delay in spawn timing for scenarios 2 and 3 (40 d) were chosen based on the difference in peak egg abundance between warm and cold years (Smart et al. 2012). The simple contraction and expansion of spawning polygons were used to simulate the exclusion of spawning from areas with sea surface temperatures < 2.4 °C and >3.8 °C based on the statistical model of Barbeaux (2012) that found positive adult pollock winter abundances between these

temperatures. The spawning polygons developed for the physical transport run described above were compared to the distribution of ROMS-generated SST for a few warm and cold years. General shifts were created to remove spawning from areas that tended to be $<2.4^{\circ}\text{C}$ in cold years and to expand spawning in regions usually $<3.8^{\circ}\text{C}$. Combinations of scenarios 2 with 4 and 3 with 5 were also tested but are not presented, as they did not provide any additional information. Model output of position, velocity, and length was saved at daily increments. Only model output prior to Oct 1 of each year was used to correspond to the observational time period.

2.5 Comparisons and statistics

The same $0.25^{\circ} \times 0.25^{\circ}$ grid over the eastern Bering Sea was used to constrain the model output of the scenario tests to the spatial regions containing observations in both cold and warm years. Model results were restricted to particles that fell within a grid cell with at least one observation in both a cold and warm year. The fraction of particles within each grid cell containing observations in both cold and warm years was calculated for each stage and each year, from all individuals in a given stage during the whole larval period. The mean fraction of particles in each grid cell was then computed for cold and warm years separately for visualization of the horizontal distributions.

To quantify changes in the horizontal distributions, the center of gravity and major and minor axes were calculated for each life stage by employing the approach described in Woillez et al. (2009) and implemented in R (R Development Core Team 2011). The approach calculates the abundance-weighted average latitude and longitude of individuals over a fixed grid of stations. For these calculations we used the midpoint longitude and latitude of each grid cell and the fraction of particles of each life stage occurring in a given grid cell, aggregated over the entire larval period. The overall center of gravity was then computed by thermal regime across 11 cold years and 4 warm years. For comparison, the center of gravity and major and minor axes were similarly calculated for the observations from cold and warm years, also constrained to the same grid cells with observations in both thermal regimes. Correspondingly, longitude and latitude were weighted by the mean concentration of each stage in each grid cell instead of by the fraction of simulated individuals.

A second measure of spatial differences, the local index of collocation (LIC), was utilized since multiple distributions can produce the same center of gravity. In contrast to the center of

gravity, the LIC measures local variations in distribution with grid cell-by-grid cell comparisons (Kotwicki & Lauth 2013).

$$LIC = \frac{\sum_{i=1}^n z_{i1} z_{i2}}{\sqrt{\sum_{i=1}^n z_{i1}^2} \sqrt{\sum_{i=1}^n z_{i2}^2}}$$

where z_{i1} and z_{i2} are either the fraction of particles or mean concentration by stage at grid cell i for the two cold and warm simulation distributions being compared. Values of LIC range from 0 to 1, with 0 the most different and 1 the most similar.

3. RESULTS

3.1 Sensitivity of physical transport simulation

In both cold and warm years, there was a noticeable difference only in the late larval centers of gravity in simulations with passive individuals compared to simulations with vertical behavior (Table 2). Including behavior in the model resulted in the center to be more to the east (on-shelf), with a slightly larger difference in warm years. Simulated centers of gravity were more sensitive to the growth formulation than to implementation of vertical behavior. In both cold and warm years, temperature-dependent growth resulted in different centers of gravity for yolksac, preflexion, and late larvae compared to age-dependent growth (Table 2) due to differences in stage duration. The centers of gravity of yolksac and preflexion larvae with temperature-dependent growth were more on-shelf, whereas they were more off-shelf for late larvae. The differences between temperature-dependent and age-dependent centers of gravity were greater in cold years than warm years (Table 2). This stems from the larger difference in growth rates between the age-dependent model and temperature-dependent model at lower temperatures (Figure 2c), resulting in longer stage durations in cold years when growth is temperature-dependent.

The effect of temperature-dependent growth alone on the differences in distribution between warm and cold can be seen by comparing simulations with temperature-dependent growth and either passive or vertical behavior. When passive, eggs and yolksac larvae were more off-shelf while preflexion and late larvae were more on-shelf in warm years (Table 2). The distance between centers of gravity was greater for the yolksac stages than the preflexion and late stages (Table 2). Adding behavior moved the centers of gravity of the egg, yolksac, and late stages eastwards in warm years, resulting in smaller differences between the eggs and yolksac

stages, but late larvae shifted even further on-shelf in comparison to cold years (Table 2).
Conversely, the center of gravity of preflexion larvae with behavior moved westward in warm years, producing a negligible difference between warm and cold years (Table 2).

3.2 Cold vs. warm years

3.2.1 Observations

Distributions of pollock eggs and larvae from the FOCI survey observations listed in Smart et al. (2012) exhibit large differences in the centers of gravity between cold and warm years ranging from 77 to 186 km (Table 3). Local variations in distribution were also large, with LIC from 0.06 to 0.24 (Table 3). The centers of all the larval stages were more on-shelf to the northeast in warm years, whereas the egg stage showed the reverse pattern (Table 3). The egg stage exhibited the greatest difference in local distribution, whereas the largest difference in centers of gravity occurred in the late larval stage (Table 3).

3.2.2 Physical transport

When initial conditions (egg release locations and timing) were held constant across years, such that all differences were due to variation in ocean circulation driven by climate variability, there did not appear to be large differences between the mean horizontal distributions of simulated eggs, yolk sac larvae, and late larvae between cold (Figure 5 center) and warm years (Figure 6 center). The distributions of the preflexion larval stage were noticeably different, with individuals more widespread on the outer and middle shelves in cold years (Figure 5 center, Figure 6 center). The differences in the centers of gravity quantify that, on average, the egg, yolk sac, and preflexion stages were more westward (off-shelf) in warm years, whereas the late stages were more eastward (Table 3). The distance between the centers of gravity in cold and warm years is small for the egg and preflexion stages, and slightly larger for the yolk sac and late larval stages (Table 3).

3.2.3 Delay spawning time

Similar to the physical transport scenario, there are no obvious differences between the mean modeled stage distributions between warm and cold years when spawning is delayed 40 d in cold years (Figure 5 left, Figure 6 center). In this case, the distribution of the preflexion larval

stage in cold years (Figure 5 left) is more similar to that of preflexion in warm years (Figure 6 center). Though the variations in the horizontal distribution from the physical transport case may not be apparent visually, delaying the spawning times resulted in greater differences in the centers of gravity of all stages except the yolksac larvae (Table 3). Preflexion and late larval centers of gravity were more on-shelf in warm years, whereas the eggs and yolksac larvae were slightly more off-shelf (Table 3). The differences between the centers of gravity for warm and cold years were marginal for the egg and yolksac stages, and were largest for the preflexion stage (Table 3). Compared to the physical transport case in cold years, a 40 d delay in spawning changed the distributions of the preflexion and late larvae (Figure 5 left, center). With a delay, the distribution of preflexion larvae was not as widespread as in the physical transport simulation (Figure 5 left, center).

3.2.4 Advance spawning time

Spawning 40 d earlier in warm years resulted in fewer preflexion larvae on the outer shelf and more late larvae on the middle shelf (Figure 6 left) in warm years compared to physical transport with normal spawning time in cold years (Figure 5 center). The preflexion distribution was also more widely spread in comparison with physical transport with normal spawning time in warm years (Figure 6 center). Advancing the spawning times resulted in greater differences in the centers of gravity of all life stages compared to the physical transport scenario (Table 3). The yolksac, preflexion, and late stages were more on-shelf in warm years with early spawning, and the centers of gravity grew further apart with stage (Table 3).

3.2.5 Contract spawning location

A large difference in the mean horizontal distributions occurred when spawning locations were contracted in cold years. All stages were concentrated on the outer shelf and over the slope in cold year simulations (Figure 5 right), with none over the middle shelf as seen in warm years (Figure 6 center) or physical transport simulations of cold years (Figure 5 center). The centers of gravity of all stages were more eastward in warm years by approximately 1.0-1.5° longitude (Table 3). Spawning contraction in cold years caused the largest changes in the longitudinal center of gravity and total distance between cold and warm years, with the maximum occurring in the preflexion larval stage (Table 3).

3.2.6 *Expand spawning location*

Expansion of the spawning areas onto the shelf in warm years was reflected in the modeled distributions of pollock ELS (Figure 6 right). The preflexion and late larvae were present over the middle shelf to the northeast of the Pribilof Islands, increased in relative concentration over the middle shelf to the northeast of Unimak Island, and decreased in concentration over the slope and outer shelf (Figure 6 right) compared to the transport only case (Figure 5 center). The yolk sac stage exhibited the smallest difference in center of gravity between cold and warm years (Table 3). The centers of gravity of all stages were more northeastward in warm years, though the differences between the warm and cold centers of gravity were not as large as when spawning areas were contracted in cold years (Table 3).

3.2.7 *Comparison with observations*

The simulation with spawning locations contracted in cold years produced results with longitudinal and absolute differences most like the observations for the larval stages (Table 3). However, the contracted spawning simulation (Figure 7) and all other simulations (not shown) generated centers of gravity to the northwest of the observed centers of gravity. Additionally, the simulated centers were over the outer shelf or slope, whereas observed centers of gravity of all larval stages in warm years were on the middle shelf (Figure 7). These differences in local distribution patterns were captured with the LIC measures. Most simulations produced LIC values near 1, indicating similar spatial patterns. In contrast, the LIC of observations were much closer to 0, suggesting greater differences in observed spatial patterns between warm and cold years compared to the model results (Table 3).

4. DISCUSSION

Coupled biological-physical modeling simulations revealed the importance of variations in oceanographic conditions between anomalously cold and warm years in the eastern Bering Sea on the transport and distribution of pollock early life stages. Model simulations suggest that the locations of spawning pollock can drive differences in the horizontal distribution of eggs and larvae. It appears that the influence of sea ice on the distribution of spawning pollock via water

temperatures impacts the early life stage distributions more than the hydrographic differences between cold and warm years.

4.1 Vertical behavior

Variations in egg buoyancy and the vertical behavior of larvae can alter dispersal and are important considerations when developing a biophysical model of fish (Fiksen et al. 2007), which is why five different vertical behavior routines were tested. Ontogenetic changes in egg buoyancy of the Gulf of Alaska pollock population are well understood (Kendall 1994), but egg density differs between the Bering Sea and Gulf of Alaska populations (Kendall 2001), resulting in dissimilar vertical distributions. Over the Bering Sea shelf, eggs tend to be found at depths <100 m with the greatest concentrations in the upper 20 m (Nishiyama et al. 1986, Smart et al. 2013). There appear to be changes in buoyancy such that middle stage eggs occur higher in the water column than early and late stage eggs (Nishiyama et al. 1986), which is suggested in laboratory measurements of specific gravity (Kendall 2001), though the spread of laboratory estimates of buoyancy results in a weak pattern that cannot be parameterized with confidence. Egg specific gravity would be expected to affect egg depth in stratified regions, but not in well-mixed areas (Kendall 2001). Eggs were neutrally buoyant in the model formulation that produced distributions that best matched both horizontal and vertical observations of all pollock ELS. Our use of neutrally buoyant eggs in the model is reasonable since pollock eggs are found at all depths in the Bering Sea (Smart et al. 2013), though an empirical relationship between buoyancy and egg age would improve simulations.

The model results that corresponded best with observed horizontal and vertical distributions simulated yolk sac larvae as neutrally buoyant. The swimming ability of fish larvae increases over time (Olla et al. 1996) and is rather weak until the inflation of a gas bladder by the time of first feeding (Davis & Olla 1992). As yolk sac larvae have limited swimming capability and contain a buoyant yolk sac, it seems reasonable to model their vertical behavior like eggs, in this case as neutrally buoyant. In addition to best model performance, this assumption is validated by observations of yolk sac larvae distributed throughout the upper 100 m on the Bering Sea shelf (Smart et al. 2013). Constraining preflexion and late larvae to the mixed layer with directed swimming towards the middle of the mixed layer performed better in model-observation comparisons than either model formulation with diel vertical migration (DVM). The evidence for

DVM of pollock larvae on the Bering Sea shelf is mixed and varies by larval size and location on the inner, middle, or outer shelf (Smart et al. 2013). Though an oversimplification, our vertical behavior for feeding larvae represents active swimming to stay within the depths with high prey abundance.

The routine that resulted in the highest model skill simulated eggs and yolk sac larvae as neutrally buoyant, and preflexion and late larvae as active swimmers directed towards the center of the mixed layer. This routine only differed from purely passive physical transport for two stages, and as a result the centers of gravity of the stage distributions varied little between models with and without this behavior pattern. Despite multiple vertical behavior routines that tried to represent observed vertical distributions, the second best model did not include any vertical behavior.

4.2 Growth

The model results displayed a greater sensitivity to the growth formulation than to vertical behavior. Many of the simulations with age-dependent growth performed better than those with temperature-dependent growth; however, the model formulation with the lowest RMSE and highest modeling efficiency included temperature-based growth. Comparisons of distributions between warm and cold years were made between different ELS, often defined by length. It is possible that temperature effects on growth rates alone could be responsible for differences in distributions. For example, if transport did not differ between warm and cold years, a given stage could be found at a different location in cold years because it took longer to reach that stage, thus it would be further along on its transport trajectory. This was tested by comparing distributions of simulations with neutrally buoyant ELS with temperature-dependent growth. Indeed, there was a difference in the centers of gravity for warm and cold years, with preflexion and late larvae showing the observed pattern of being more on-shelf in warm years. However, the distances between centers of gravity were not as large as those observed or those produced in other simulations (warm expansion, cold contraction), and the addition of behavior removed the pattern in the preflexion stage. However, the difference between warm and cold years increased for late larvae, thus temperature-dependent growth may play an important role in determining where the largest larvae are found.

The age-dependent growth rate used in the model simulations was derived from a length-age relationship from larvae collected in the Gulf of Alaska from May through July 1987 (Yoklavich & Bailey 1990). This is probably an overestimate for Bering Sea pollock because the Gulf of Alaska experiences warmer temperatures than the Bering Sea (Blood 2002) and these measurements were made at the warmest part of the larval period. Temperatures in the surface layer of the Gulf of Alaska ranged from approximately 7°C in mid-May to approximately 10°C in mid-July based on a seasonal model of temperature variability (F. Mueter, unpub. results) fit to data collected at the GAK 1 monitoring station (<http://www.ims.uaf.edu/gak1/>). The temperature-based growth equations of yolk sac and feeding larvae were each parameterized from three data points of fish in a narrow age range (yolk sac: 4 dph, feeding: 18-20 dph). These growth rates were measured in laboratory studies of larvae feeding on *Artemia*, which produce lower growth rates compared to a natural assemblage of zooplankton (Porter & Bailey 2007). To account for the nutritional difference between *Artemia* and natural zooplankton, the growth rate equation of feeding larvae was increased. As yolk sac larvae still gain some nutrition from their yolk sac, this adjustment was not necessary. More data are needed for a better representation of larval pollock growth rates, which are likely to increase with both temperature and larval size (e.g. Hurst et al. 2010).

Despite the coarse approximation of temperature-dependent growth, the resulting mean lengths over the larval period compare adequately with field-observed lengths sampled at different times of the year (Siddon et al. 2013). For example, mean model lengths were 15 and 18 mm on May 15, 21 and 28 mm on Jun 15, and 34 and 39 mm on Jul 14 for cold and warm years respectively (Figure 8). The observations during cold years 2008-2010 show lengths 4-14 mm on May 15, 5-16 mm on Jun 15, and 7-22 mm on Jul 15, followed by a rapid increase to lengths of 35-90 mm after mid-Aug (Figure 8). Modeled growth ceases at 40 mm, thus the longest lengths observed are never attained. The drastic change in observed lengths between May and Aug signifies a shift in energy allocation (Siddon et al. 2013). The modeled size-independent, temperature-dependent growth rate appears to overestimate growth in the earliest larval phases when much of the energy is allocated to morphological development, and underestimate growth in the later larval phases nearing the juvenile transition when growth is primarily somatic (Siddon et al. 2013), suggesting the need for multiple growth rate equations that vary by larval stage. Nevertheless, the model produced juvenile pollock around the same

time as the observed transition. Differences in observed and modeled lengths could be a result of when and where observed fish were spawned compared to modeled individuals. Additionally, there are few observations of fish 20-40 mm because they are large enough to evade traditional plankton nets but too small to be collected with standard trawl gear, implying that the observed size distribution underestimates the true size distribution. This size range is most abundant at a time of year when historically there have been fewer collections, therefore growth during this critical period is poorly understood. Growth in the wild is highly variable and the modeled growth rates of 0.0-0.2 mm d⁻¹ are within the 0.12-0.49 mm d⁻¹ rates estimated for field-caught Bering Sea pollock larvae (Walline 1985, Jung et al. 2006). If, however, growth is slower in the wild than in the model, the result would be longer stage durations and potentially larger differences in the resulting distributions of later life stages between warm and cold years. This is consistent with the observed differences being larger than the modeled differences (Table 3).

4.3 Interannual climate variability

The modeled centers of distribution of pollock eggs and larvae did not differ much between warm and cold years when spawning time and location were held constant, and when spawning times were delayed by 40 days. These results suggest that climate-related differences in ocean circulation and delays in spawning time were not sufficient to account for the observed changes in pollock early life stage distributions in the eastern Bering Sea. Simulations with the combined impact of interannual variability in ocean currents and in spatial shifts in spawning areas best captured the observed pattern of early life stages located more on-shelf in warm years compared to cold years. In particular, simulations with contraction of the spawning areas off-shelf (to the west and south) created the largest differences between warm and cold centers of gravity.

The modeled differences between warm and cold years in the “physical transport” model are broadly consistent with results from other studies. Mean currents on the middle shelf are relatively weak with current speeds ranging from negligible to about 2 cm s⁻¹ near the surface at a mooring site on the middle shelf (Stabeno et al. 2012). However, Stabeno et al. (2012) found marked differences in current speed and direction at M2 between warm and cold years with a difference in east-west velocity on the order of 1-2.5 cm s⁻¹. This implies a difference in expected transport between warm and cold years of approximately 78-195 km over a 90-day period,

compared to the estimated difference in the modeled center of gravity for late larvae of 14.6 km (Table 3). A smaller difference in the center of gravity, which reflects the average endpoint, is expected because eggs and larvae generally do not follow straight-line trajectories. Modeled transport is also highly variable over time as evident in the large differences in relative transport between different life stages in our model (Table 3), consistent with seasonal variability in currents (Stabeno et al. 2012).

Our analyses focused on differences in transport between warm and cold years, but these differences should not be interpreted as a consequence of temperature variability. Rather, differences in both temperature and transport result from variability in wind forcing, which is associated with variability in along-isobath and cross-isobath advection (Danielson et al 2011b). Cross-isobath fluxes in particular are strongly dependent on wind direction (Danielson et al. 2012) as determined by the seasonal mean zonal position of the Aleutian Low (Danielson et al. 2011b). Strong winds from the northwest are associated with larger westward transports and cold conditions, while stronger winds from the southeast are associated with enhanced eastward and northward flows and warmer conditions (Danielson et al. 2011b, 2012). However, winds during warm (cold) years are not always favorable to on-shelf (off-shelf) Ekman transport; therefore the differences in modeled transport between warm and cold years in this study may underestimate the importance of physical transport.

Nevertheless, model results suggest that spatial shifts in spawning distribution underlie the shifts in egg and larval distributions. There is a significant lack of empirical information on the factors regulating where and when adults spawn. We propose that sea ice and water temperature affect the pollock spawning distribution in the eastern Bering Sea. Some support for our hypothesis comes from 30 years of summer (May-Aug) bottom trawl survey data that demonstrates an effect of the areal extent of the cold pool defined at 0 °C on the eastern Bering Sea pollock distribution (Kotwicki & Lauth 2013). Adult distributions were compared in a pairwise manner, such that the distribution from each year was compared individually to the distributions from the 29 other years. The similarity between distributions from all years decreased with increases in the change of the cold pool extent (Kotwicki & Lauth 2013). Resembling the larval distributions, the center of gravity of adult summer distributions differed between warm and cold years, with centers located 42 km off-shelf in cold years (Kotwicki & Lauth 2013).

Thermally influenced shifts in adult distributions, spawning migrations, and ELS distributions have been noted for a number of species, such as Atlantic Cod (*Gadus morhua*; deYoung & Rose 1993) and Capelin (*Mallotus villosus*; Rose 2005), in addition to Bering Sea (Bacheler et al. 2012) and Gulf of Alaska (Bacheler et al. 2009) pollock stocks. Although Bacheler et al. (2012) found low interannual variability in the spatial and temporal dynamics of Bering Sea pollock spawning, there were changes in the abundance of adults and eggs with temperature. With 1 °C of warming a spatially explicit variable coefficient generalized additive model predicted increased egg abundance over the middle shelf to the east of the Pribilof Islands and increased adult CPUE over the middle shelf north of Unimak Island (Bacheler et al. 2012). Though the broad spawning area may not have shifted, the changes in spawner and egg abundance on the middle shelf shift the distribution within this region, resulting in greater egg production on-shelf with warmer conditions. Similarly, Bacheler et al. (2009) found spatial effects of spawning stock biomass, transport, and temperature on pollock egg abundance in Shelikof Strait. With increased temperature, egg abundance increased around the northern edge of Kodiak Island and decreased in the southwest of Shelikof Strait (Bacheler et al. 2009), suggesting shifts in spawning areas with temperature. A review of data on Newfoundland Atlantic Cod by deYoung and Rose (1993) provided evidence for shifts in adult and larval distributions in relation to temperature with a link to recruitment. They found more southerly distributions of adults in cold years that resulted in more southerly distributions of eggs and larvae, placing them in regions with lower retention (deYoung & Rose 1993). They posited that the reduced recruitment in cold years was a consequence of larvae spending less time on the shelf (deYoung & Rose 1993).

Much like the temperature-induced changes in spawning and larval distributions of Atlantic Cod off Newfoundland, the eastern Bering Sea pollock ELS distributions varied with respect to local circulation. The differences in centers of gravity between the simulations of warm years with regular spawning and cold years with off-shelf contracted spawning (Table 3, “Contracted”) arise from the lack of eggs and larvae on the middle shelf off Unimak Island and the Alaskan Peninsula in cold years (Figure 3). This difference highlights the importance of the spatial variability of the currents on the eastern Bering Sea shelf. Contraction of spawning off-shelf reduces the number of eggs and larvae exposed to the cross-shelf currents near Unimak Island, including the Alaska Coastal Current, while increasing the proportion of eggs and larvae

exposed to more energetic along-shelf currents over the outer shelf and slope (Figure 1). There is also retentive circulation around the Pribilof Islands (Kowalik & Stabeno 1999; Figure 1) that may have facilitated the presence of pollock on the middle shelf when spawning was shoalward of the 100-m isobath in the simulations without contracted spawning.

The model results emphasize the interdependencies of cross-shelf transport and thermal regime to pollock ELS and of spawning near cross-shelf features. Tests of spawning distributions were implemented as generalized off-shelf or on-shelf contractions or expansions because a consistent observational data set of adults in spawning condition that spanned cold and warm years was not available. The hypothetical variations in spawning areas were constructed from a relationship between SST and adult pollock winter abundance (Barbeaux 2012), though these shifts were imprecise. More realistic spawning locations could be generated for each year using the annual distributions of SST and initializing eggs in places with SST between 2.4 and 3.8 °C. A better approach would be to formulate a relationship between water temperature and the presence of adult pollock in spawning condition.

4.4 Expectations with climate change

Projections with Intergovernmental Panel on Climate Change climate models predict decreased sea ice extent and increased sea surface temperatures in the eastern Bering Sea (Wang et al. 2012), conditions much like the warm years of 2002-2005. During these warm years the abundance of large, energy-rich zooplankton decreased and abundance of small, energy-poor zooplankton increased (Coyle et al. 2011). The asymmetric effect of temperature on zooplankton development and growth suggest that the typically large, energy-rich copepods would have been smaller with fewer lipid reserves in warm years as well (Coyle et al. 2011). The shift in the zooplankton community has a two-fold effect on young pollock. Firstly, the decrease in lipid-rich prey would decrease the energy density of age-0 pollock, thereby reducing the probability of overwinter survival (Moss et al. 2009, Heintz et al. 2013). Secondly, age-0 pollock experience increased predation pressure from predatory fishes that would otherwise feed on the large, energy-rich zooplankton (Moss et al. 2009, Coyle et al. 2011). Combined, the decreased energy reserves for overwintering and increased predation pressure suggest lower pollock survival and recruitment in warm years.

Changes in ice extent and water temperatures are expected to alter the distribution of spawning pollock adults. Model simulations demonstrated that simplified expansions and contractions of the spawning areas affect the distributions of pollock ELS. Going beyond distributions, it is important to understand how transport pathways and connectivity differ between warm and cold years. Future studies will examine how potential prey and predators overlap spatially and temporally with ELS of pollock during transport and with the end (summer) distribution of juveniles (age-0s) in warm and cold years. To this end, we will investigate if variations in the transport pathways between warm and cold years contribute to recruitment variability, or if recruitment is more strongly related to annual shifts in the zooplankton community and processes that occur during the transition from age-0 to age-1.

4.5 Considerations

The model simulations with contracted spawning areas in cold years qualitatively captured the observed difference in horizontal distributions of pollock larvae between cold and warm years, although the modeled and observed distributions of ELS differed. The observed centers of gravity of all larval stages were more on-shelf in warm years, but both cold and warm centers were located further southeast than the simulation results. Moreover, the observed centers of gravity in warm years were over the middle shelf, whereas the modeled centers were over the outer shelf in all warm year simulations. In contrast to Smart et al. (2012), who inferred no temperature effect on egg distribution, we found that egg centers of gravity were more off-shelf in warm years.

There are a number of potential reasons that the model did not completely replicate the observed distributions of pollock eggs and larvae. One explanation is related to the differences between the observations and model results. The observations were collected in the months of March through September, while the model represented the months January through September. As indicated by the Smart et al. (2012) analysis, the field sampling missed the start and peak of the egg stage and the start of the yolksac stage in warm years, and the end of the late larval stage in cold years. Thus the observations may not represent the true distribution of these life stages in these years. Additionally, the monthly observations and model results were aggregated by year, and then by cold or warm period, rather than compared at particular times and locations. Observations occurred at discrete locations, whereas modeled particles essentially covered the

eastern Bering Sea. Though the model results were restricted to only particles in areas that were sampled in both warm and cold years, this could contribute to divergences. Second, actual spawning times and locations may result in simulated distributions more similar to the observations than the generalized spawning used in this research, as mentioned above. Third, spatial and temporal variability in both egg production and the mortality of all stages, and their seasonal and interannual changes, could significantly shape the distribution of pollock eggs and larvae. The difference in LIC measures between observations and simulations (Table 3) provide strong support for spatially-variable processes. As this study was focused on interannual differences in advection, these spatial variations were not considered because they could have masked the effect of physical transport alone.

5. CONCLUSIONS

We developed a biophysical model that was able to replicate important features of the observed distributions of eggs and larvae of Walleye Pollock in the eastern Bering Sea. An advantage of this modeling approach was the ability to individually test environmental forcing mechanisms to quantitatively assess the impact of each on the distribution of pollock. Interannual variations in advection and advances and delays in spawning time were insufficient at reproducing the observed differences in pollock early life stage distributions between warm and cold years in the eastern Bering Sea. Changes to spawning areas, especially offshore contractions in cold years, resulted in simulated distributions most similar to observations. The location of spawning with respect to cross-shelf circulation patterns was an important factor influencing the distribution of eggs and larvae. Further study is needed on the relationship between the spatial distribution of spawning pollock and the physical environment, and its effect on the distribution of early life stages. Based on our model results, future investigations will include how warm and cold year variations in distribution correlate with recruitment and how they affect age-0 survival by way of spatial overlaps with potential prey and predators.

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TABLES

Table 1. Resulting skill metrics of the combined comparisons between 1995 and 2007 observations with model results using the different vertical behavior and growth parameterizations. 1 – passive = passive (neutrally buoyant) individuals of all stages; 2 – pre & late MLD = passive eggs and yolk sac larvae, and preflexion and late larvae that move to the middle of the mixed layer; 3 – all MLD = all stages move to the middle of the mixed layer; 4 – late DVM = eggs, yolk sac, and preflexion larvae move to the middle of the mixed layer, and late larvae make diel vertical migrations (DVMs) between 20 m during the day and 5 m during the night; 5 – pre & late DVM = eggs and yolk sac larvae move to the middle of the mixed layer, and preflexion and late larvae make DVMs; age = age-dependent growth; temperature = temperature-dependent growth; R = correlation coefficient; RMSE = root mean square error; MEF = modeling efficiency.

Behavior	Growth	R	Skill metric	
			RMSE	MEF
1 - passive	age	0.12	0.0036	0.03
	temperature	0.11	0.0040	-0.19
2 - pre & late MLD	age	0.10	0.0036	0.03
	temperature	0.11	0.0035	0.10
3 - all MLD	age	0.07	0.0040	-0.18
	temperature	0.06	0.0044	-0.43
4 - late DVM	age	0.07	0.0040	-0.17
	temperature	0.06	0.0044	-0.43
5 - pre & late DVM	age	0.08	0.0040	-0.18
	temperature	0.04	0.0060	-1.66

Table 2. Center of gravity (COG) sensitivity to behavior and growth. Values for longitude and latitude are differences in the COG (°E and °N, respectively) between scenarios: Behavior minus Passive, Temperature minus Age, or Warm minus Cold (where Behavior = vertical behavior of feeding stages; Passive = all stages neutrally buoyant; Temperature = temperature-dependent growth; Age = age-based length (temperature-independent growth); Warm = warm years combined; Cold = cold years combined). Values for Distance are the corresponding absolute distances (km) between COGs.

			Stage			
			Egg	Yolksac	Preflexion	Late
Behavior - Passive	Longitude	Cold	-0.01	-0.01	0.03	0.09
		Warm	0.00	-0.02	0.04	0.15
	Latitude	Cold	0.00	0.00	0.01	0.11
		Warm	0.00	0.00	0.02	0.15
	Distance	Cold	0.54	0.47	2.31	13.32
		Warm	0.01	0.97	3.00	19.56
Temperature - Age	Longitude	Cold	0.00	1.33	0.35	-0.77
		Warm	0.00	0.31	0.44	-0.43
	Latitude	Cold	0.00	-0.04	-0.02	-0.03
		Warm	0.00	0.00	-0.01	-0.01
	Distance	Cold	0.00	83.20	22.22	48.31
		Warm	0.00	19.15	27.55	26.67
Warm - Cold (Temperature)	Longitude	Passive	-0.05	-0.76	0.37	0.34
		Behavior	-0.04	-0.23	-0.02	0.84
	Latitude	Passive	0.00	0.00	0.00	0.07
		Behavior	0.00	-0.01	-0.01	0.04
	Distance	Passive	2.85	47.59	22.82	22.66
		Behavior	2.32	14.54	1.59	52.60

Table 3. Center of gravity (COG) differences and Local Index of Colocation (LIC) between warm and cold years for observations and different simulations. Values for Δ COG longitude and latitude are differences ($^{\circ}$ E and $^{\circ}$ N, respectively) as warm minus cold. Values for Distance are the corresponding absolute distances (km) between COGs. Observed = observations from the cruises listed in Smart et al. 2012; Transport = physical transport; Delay = 40 d delay in cold years; Early = 40 d early in warm years; Contract = contract off-shelf in cold years; Expand = expand on-shelf in warm years.

		Stage			
		Egg	Yolksac	Preflexion	Late
Δ COG Longitude	Observed	-1.71	1.26	1.14	2.92
	Transport	-0.04	-0.23	-0.09	0.11
	Delay	-0.04	-0.01	0.63	0.24
	Early	-0.05	0.09	0.43	0.79
	Contract	0.96	1.24	1.62	1.24
	Expand	0.29	0.18	0.32	0.49
Δ COG Latitude	Observed	-0.41	0.19	0.25	0.28
	Transport	0.00	-0.01	-0.02	0.12
	Delay	0.02	0.01	0.01	0.15
	Early	0.02	-0.01	0.08	0.19
	Contract	-0.01	-0.08	-0.13	0.05
	Expand	0.08	0.08	0.09	0.14
COG Distance (km)	Observed	116.98	82.00	76.69	185.85
	Transport	2.31	14.37	6.11	14.63
	Delay	3.32	1.55	39.19	22.65
	Early	4.05	5.88	28.20	53.60
	Contract	59.69	77.74	101.33	76.98
	Expand	20.18	14.41	22.74	34.29
LIC	Observed	0.061	0.240	0.222	0.088
	Transport	0.998	0.983	0.940	0.941
	Delay	0.996	0.986	0.925	0.931
	Early	0.998	0.971	0.920	0.898
	Contract	0.953	0.935	0.815	0.840
	Expand	0.986	0.982	0.937	0.925

FIGURE CAPTIONS

Figure 1. The dominant currents (blue lines) and Walleye Pollock spawning areas (green ovals) of the Eastern Bering Sea. The Alaska coastline is shown in black and the 50, 100, and 200 m isobaths in gray. ACC – Alaska Coastal Current; BSC – Bering Slope Current.

Figure 2. (a) Temperature-dependent egg development time. (b) Temperature-dependent growth rates of yolk sac and feeding (preflexion and late) larvae; growth rate is independent of size. (c) Length of larvae with age-dependent (“age”, solid line) and temperature-dependent (dotted and dashed lines) growth rates given constant temperature.

Figure 3. Spawning initial locations released on the dates shown. Light grey = Cold Contracted; Dark grey = Transport; Black = Warm Expanded. Polygons are overlapping and all share the same western and southern boundaries.

Figure 4. Depth distribution of early life stages from observations (black) compared to the model parameterization with the highest skill in reproducing horizontal distributions (grey). This model had temperature-based growth and vertical behavior 2 – passive eggs and yolk sac larvae, and preflexion and late larvae that move to the middle of the mixed layer. Depth distribution is presented as a histogram of the weighted mean depth of each MOCNESS tow (observations) or each day (model).

Figure 5. Contour plots of the relative concentration of early life stages in cold year (1995, 1997, 1999, 2000, 2006-2012) simulations. Relative concentration was calculated as the fraction of the mean number of particles found in each grid cell with observations. 40 d Late = spawning times delayed by 40 d; Transport Only = same times and locations of spawning in cold and warm years; Contracted = spawning locations contracted to the southwest.

Figure 6. Contour plots of the relative concentration of early life stages in warm year (1996, 2002, 2003, 2005) simulations. Relative concentration was calculated as the fraction of the mean number of particles found in each grid cell with observations. 40 d Early = spawning times

advanced by 40 d; Transport Only = same times and locations of spawning in cold and warm years; Expanded = spawning locations expanded to the northeast.

Figure 7. Observed (circles) and simulated Contracted (triangles) centers of gravity, major axes, and minor axes for the distributions of different pollock early life stages in cold (blue; 1995, 1997, 1999, 2000, 2006-2012) and warm (red; 1996, 2002, 2003, 2005) years.

Figure 8. Mean standard length (mm) of all larvae by date in the Transport Only simulations for cold (black line; 1995, 1997, 1999, 2000, 2006-2012) and warm (grey line; 1996, 2002, 2003, 2005) years. Standard length (mm) of larval and juvenile pollock from observations in 2008-2010 (dots).

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