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Modeled connectivity between Walleye Pollock (*Gadus chalcogrammus*) spawning and age-0 nursery areas in warm and cold years with implications for juvenile survival

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ABSTRACT

Adult and early life stage distributions of the commercially important demersal fish Walleye Pollock (*Gadus chalcogrammus*) have varied in relation to the warm and cold environmental conditions on the eastern Bering Sea shelf. Previous modeling studies indicate that transport alone does not account for the disparate juvenile distributions in warm and cold years, but that spawning locations are important. Our objective was to determine the connectivity of eastern Bering Sea pollock spawning areas with juvenile nursery areas between warm and cold years. We calculated the connectivity between sources and juvenile positions that were produced by a coupled biological-physical individual-based model that simulated transport, growth, and vertical behavior of pollock from the egg until the juvenile stage. Three connectivity patterns were seen in most simulations: along-isobaths to the northwest, self-retention, and transport around the Pribilof Islands. The major differences in connectivity between warm and cold years, more northwards in warm years and more off-shelf in cold years, mimicked wind-driven flow characteristics of those years that were related to the winter mean zonal position of the Aleutian Low. Connectivity relationships were more sensitive to spatial alterations in the spawning areas in cold years, while they were more responsive to spawn timing shifts in warm years. Juvenile pollock prey and predator studies favor the Pribilof Islands and Outer Shelf regions as advantageous juvenile habitats. The strongest connectivity to these regions originated in the well-known spawning areas around Unimak Island and the Pribilof Islands, and the less well-studied North Outer Shelf. The North Outer Shelf emerged as a very large sink of pollock reaching the juvenile transition from all spawning sources, suggesting more thorough sampling across multiple trophic levels of this potentially important juvenile pollock nursery is needed.

KEY WORDS: Bering Sea, connectivity, fish early life history, pollock

INTRODUCTION

One of the most commercially important semi-demersal fishes in the eastern Bering Sea (EBS) is Walleye Pollock (*Gadus chalcogrammus*), hereafter referred to as "pollock." Over the EBS shelf, pollock spawn consistently at at least two spawning sites, one north of Unimak Island (Figure 1, region 1), and the other near the Pribilof Islands (Figure 1, region 5), beginning near Unimak and spreading towards the Pribilof Islands (Bacheler *et al.*, 2010). Eggs can be found in the water column from December to August, but the annual peak occurs in either April or May (Bacheler *et al.,* 2010). Eggs are predominantly found within the mixed layer (Smart *et al.,* 2013) and incubation time depends on temperature (Blood, 2002). After hatching, larvae develop through a series of stages known as the yolksac, preflexion, and postflexion (or late), classified by anatomical differences (Matarese *et al.,* 1989). Pollock transition from larvae to pelagic juveniles between 30 and 40 mm (Matarese *et al.,* 1989), become more bottom-oriented with age (Brodeur & Wilson 1996; Duffy-Anderson *et al.,* 2015), and finally recruit to the fishery at age-3 or age-4 (Ianelli *et al.,* 2012b).

The EBS is a very productive region, supporting large marine bird and mammal populations and several commercial fisheries. The EBS shelf extends approximately 500 km southwestward from the Alaskan coast to the shelfbreak and 1000 km northwestward from the Alaska Peninsula to the Siberian coast (Figure 1). 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 EBS has been further divided into regions for reference and comparisons across projects under the Bering Ecosystem Study – Bering Sea Integrated Ecosystem Research Program (BEST-BSIERP). These 16 regions (Figure 1) cover the EBS shelf and slope within the U.S. Exclusive Economic Zone and were delineated by bathymetry, oceanography, animal distributions, ecological domains, and established survey areas (Ortiz *et al.,* 2012). In numerical order, these regions are: 1 – AK Peninsula, 2 – South Inner Shelf, 3 – South Middle Shelf, 4 – South Outer Shelf, 5 – Pribilofs, 6 – Midnorth Middle Shelf, 7 – Midnorth Inner Shelf, 8 – North Outer Shelf, 9 – St. Matthews, 10 – North Middle Shelf, 11 – North Inner Shelf, 12 – St. Lawrence, 13 – South Bering Strait, 14 – Norton Sound, 15 – Off-shelf North, 16 – Off-shelf Southeast (Ortiz *et al.,* 2012). Baker and Hollowed (2014) found that distinct biological communities in the EBS are best delineated by depth, bottom temperature, frontal boundaries, and position north or south of 60°N; these ecoregions are well-represented by the BEST-BSIERP regions.

Recently the EBS experienced alternating periods of temperatures that were either warmer (2001-2005) or colder (2007-2012) than average (Stabeno *et al.,* 2012). In cold years, winter ice extends farther offshore creating a larger cold pool that could influence the spawning and movements of demersal fishes (Mueter & Litzow, 2008). The water circulation is also influenced by atmospheric and hydrographic conditions, which could affect the dispersal of pelagic early life stages. For example, the predominantly northwesterly winds in cold years that extend sea ice and the cold pool also promote off-shelf Ekman transport (Danielson *et al.*, 2011b; Stabeno *et al.,* 2012; Danielson *et al.,* 2012). On the other hand, the more southeasterly winds in warm years resulted in northward or weak on-shelf flows over the Middle Shelf (Stabeno *et al.,* 2012; Danielson *et al.,* 2012). Moreover, the intensity and timing of setup of the Inner and Middle Fronts, which separate the three shelves, varies with temperature, also potentially affecting the transport of larval fishes on the shelf. Concomitant with the atmospheric and oceanographic differences, the distributions of early life stages diverged in cold and warm years (Smart *et al.,* 2012), likely due to thermally-mediated variability in spawning locations of adults (Petrik *et al.,* 2014).

Early life stage transport contributes greatly to population connectivity and persistence. Studies of connectivity between spawning regions and nursery habitats advance our understanding of genetic exchange, processes during the early life period, and recruitment (reviewed in Cowen & Sponaugle, 2009). Alternate transport pathways between spawning grounds and nursery areas can influence early life survival because of spatial differences in growth and mortality (Cowen & Sponaugle, 2009). Survival to recruitment of individuals is further influenced by the distribution of individuals at the end of the larval period in regard to spatial differences in prey and predators. For example, the overlap between juvenile and cannibalistic adult pollock explains 30-50% of interannual recruitment variability (Mueter *et al.,* 2011). Additionally, match-mismatch between the spatial distribution of juvenile pollock and prey energy density may explain the low and high year classes of 2005 and 2010, respectively (Siddon *et al.,* 2013b). Thus it is important to identify the source regions and oceanographic conditions influencing the cold and warm year patterns of juvenile pollock distribution and survival.

Modeling results suggested that spawning locations and their proximity to different physical oceanographic features drove differences in the distributions of pollock early life stages (Petrik *et al.,* 2014). Following these results, it was our primary objective to determine the connectivity between spawning and nursery regions of walleye pollock in the EBS (1995-2012). Our second objective was to resolve how connectivity diverged in warm and cold years. This examination provides a projection of the potential effects of predicted future warming (Wang *et al.,* 2012). To accomplish these objectives we used an individual-based model (IBM) of pollock biology and behavior coupled to a hydrodynamics model of the EBS to simulate transport during the period from spawning to the juvenile transition. Model output was compared to observed distributions of juvenile pollock (1996-2012) to groundtruth model results.

METHODS

Coupled individual-based model

A detailed description of the coupled physical-biological IBM can be found in Petrik *et al.* (2014). To summarize, we used the Regional Ocean Modeling System (ROMS; Shchepetkin & McWilliams 2009) developed for the Northeast Pacific (NEP6) to represent the hydrodynamics of the EBS. ROMS is a free-surface, hydrostatic primitive equation ocean circulation model. It is a terrain-following, finite volume (Arakawa C-grid) model. The ROMS NEP6 model domain extends over a broader region than the EBS Shelf, from 20°N to 71°N and reaching approximately 2250 km offshore from the North American west coast. The spatial resolution is a 10 km horizontal grid in a Lambert Conical projection that is rotated relative to lines of constant longitude and has

50 terrain-following depth levels stretched towards the surface boundary in each grid cell. ROMS includes a fully parallel coupled sea-ice model (Budgell, 2005). An older version of ROMS for the Northeast Pacific (NEP5) has been thoroughly validated against observations and had significant skill reproducing aspects of the Bering Sea physical oceanography, such as the horizontal and vertical structure of tidal currents and the frequency of kinetic energy (Curchitser *et al.,* 2010; Danielson *et al.,* 2011a). The NEP6 has further improved upon this model through more comprehensive evaluations with the newly available data collected under the BEST-BSIERP program, which had much more complete spatial and temporal coverage than earlier data sets. The NEP6 coupled ocean-sea ice model was integrated in hindcast mode for the period from 1994-2012 deriving surface forcing from the Modern Era Retrospective-Analysis for Research and Applications (MERRA; Rienecker *et al.,* 2011), air-sea fluxes computed using bulk formulae (Large & Yeager, 2009), the Dai and Trenberth (2002) method as a surface fresh water flux for the riverine inputs, initial and boundary conditions for this domain from the Simple Ocean Data Assimilation (SODA) ocean reanalysis (Carton & Giese 2008) for early years, and boundary conditions from the global HYCOM assimilative product (HYCOM Ocean Prediction website) for the later ones. Daily averages of velocity, temperature, and mixed layer depth were saved and used as offline inputs to the particle-tracking model.

We utilized the particle-tracking tool TRACMASS to simulate transport of pollock early life stages. TRACMASS computes Lagrangian trajectories from Eulerian velocity fields from general circulation model simulations through an offline coupling. TRACMASS interpolates any general circulation model 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 (Döös 1995, Blanke & Raynaud, 1997; de Vries & Döös, 2001). The TRACMASS turbulence subroutine was implemented to incorporate sub-grid scale motion. Physiological and behavioral information was added to TRACMASS to create an IBM of EBS pollock (Petrik *et al.,* 2014). Individuals transitioned from eggs to yolksac larvae, preflexion larvae, and late larvae, ultimately reaching the beginning of the juvenile stage. Stages were defined by length (yolksac: <6 mm SL; preflexion: 6-10 mm SL; late: 10-40 mm SL) that was attained via stage-specific temperature-dependent growth (Petrik *et al.,* 2014). The nonfeeding eggs and yolksac larvae were modeled as neutrally buoyant, while the feeding stages, preflexion and late larvae, directed their vertical swimming towards the middle of the mixed layer (Petrik *et al.,* 2014).

Model initialization and simulations

The model simulated spawning by initializing individuals at the egg stage. Spawning locations and times were the same as those used in Petrik *et al.* (2014). The locations concentrated on the major spawning regions identified by Hinckley (1987) and Bacheler *et al.* (2010), with individual spawning polygons created from aggregated locations of mature spawning females from observer data (Figure 1). The Bogoslof Island region, defined by bottom depth > 250 m, was disregarded as a spawning ground as this likely represents a distinct population (Ianelli *et al.,* 2012a). Following the literature and the observer data, spawning started in mid-Jan near Unimak Island, then around the Pribilof Islands in Feb. Spawning expanded to the northwest as the season progressed, peaking in mid-Mar, and then contracting into Apr. The result was seven different spawning times (15 Jan, 1 Feb, 15 Feb, 1 Mar, 15 Mar, 1 Apr, 15 Apr) with spawning areas of varying sizes. Eggs were released at these times at the center of each ROMS NEP6 grid cell within the spawning polygons. Ten eggs were released per 10 m depth increment in each spawning grid cell in all cases with the exception of the "Contracted" simulation (see description below). Because spawning occurred in fewer grid cells compared to the other cases, 15 eggs per 10 m depth were spawned to achieve the total number of particles needed for stable results.

Five distinct simulations were run (Petrik *et al.,* 2014) to test the effects of advection, spawning location, and spawn timing on connectivity. In the "Transport Only" case, all years 1995-2012 shared the same initial spawning areas and times and differed only by their physical environments simulated with ROMS NEP6. This was considered the "Base" simulation and was divided into "Base Cold" (1995, 1997, 1999, 2000, 2006-2012) and "Base Warm" (1996, 2002, 2003, 2005) years using the temperature anomaly criteria of Smart *et al.* (2012). To simulate hypothesized changes in spawning locations in reference to the cold pool extent, spawning polygons were contracted off-shelf to the southwest in cold years ("Contracted") and expanded on-shelf to the northeast in warm years ("Expanded"). Finally, to represent potential shifts in peak spawn timing (Smart *et al.,* 2012), spawning times were delayed 40 d in cold years ("Late") and advanced 40 d in warm years ("Early"). In each simulation, individuals were followed from spawn until they reached 40 mm, the size at the juvenile transition (Matarese *et al.,* 1989).

Observational data

T/S Oshoro Maru

A time series of age-0 pollock juvenile abundances from mid-summer collections (1996-2005, 2007) was available from cooperative cruises conducted by the Alaska Fisheries Science Center's (AFSC) Eco-FOCI program and the Graduate School of Fisheries, Hokkaido University, Japan aboard the T/S *Oshoro Maru* (Busby *et al.,* 2014). Sampling occurred at a grid of stations over the Outer and Middle Shelves, though not all stations were sampled each year. Cumulative over the time series, sampled stations resided within a minimum of two BEST-BSIERP regions (regions 3, 4) and a maximum of seven BEST-BSIERP regions (1-7). A modified beam trawl with 5-m^2 mouth opening fitted with a 3x2 mm oval mesh net and a 1-mm mesh cod end was towed obliquely through the water column from 200 m depth (or 10 m off-bottom, whichever was shallowest) to the surface. Use of a flowmeter permitted quantitative estimates of catch. Samples were preserved in formalin, taxa were sorted, identified, and enumerated, and pollock catch was expressed as catch 10 m^{-2} sea surface area.

BASIS surface trawls

Surface trawl surveys (2008-2013) were conducted as part of the Bering Arctic-Subarctic Integrated Survey (BASIS) aboard the NOAA Ship *Oscar Dyson*. The surveys were typically conducted mid-Aug through late Sep, and occupied a systematic grid of stations over the southeast Bering Sea shelf. Near-surface fish, inclusive of age-0 walleye pollock, were collected using a 198-m long midwater rope trawl (CanTrawl) composed of hexagonal mesh wings and fitted with a 1.2-cm mesh codend liner (Farley *et al.,* 2015). The CanTrawl had a mouth opening of 55-m horizontal x 20-m vertical, with typical sampling occurring between 0 m and 20 m depth. Near-surface orientation was maintained by buoys attached to the headrope. The net was towed at speeds ranging from 3.5-5.0 knots for 30 min during daylight hours. Gridded stations typically spanned 14-16 of the BEST-BSIERP regions, but only six regions were covered in 2008.

BASIS acoustic surveys

Acoustic backscatter measurements were collected in conjunction with the BASIS surface trawl surveys (above) to determine subsurface age-0 pollock biomass (2008-2013). Measurements were collected aboard the NOAA Ship *Oscar Dyson* with Simrad EK60 echosounders from five split-beam tranducers (18, 38, 70, 120, and 200 kHz) mounted on the bottom of the vessel's retractable centerboard. Data presented herein are the results from 38 kHz-collected data. Verification of midwater and near-bottom acoustic sign was accomplished through targeted trawl sampling conducted opportunistically during daylight hours. Age-0 pollock abundance was estimated by combining echo integration data with species and size-composition information derived from targeted trawl sampling. Post-processing was conducted in accordance with other AFSC surveys (Honkalehto *et al.,* 2011). Comprehensive descriptions of acoustic methodologies are presented in Parker-Stetter *et al.* (2013) and De Robertis *et al.* (2014).

Analyses

Spawning release locations and positions of individuals upon reaching the juvenile transition were both mapped to the BEST-BSIERP regions (Figure 1). Connectivity from spawning region "A" to juvenile region "B" for a given time was defined as the number of individuals released in region “A” that were in region “B” at the time they reached juvenile size divided by the total individuals spawned in “A” at that time. As connectivity is defined as a fraction of the total number of eggs spawned in that region, it is independent of the number of eggs spawned. Connectivity for each spawning region-juvenile region pair was calculated by spawning time, year, and grouped cold or warm years. Connectivity is presented with connectivity matrices, grids with source regions on one axis and sink regions on the other axis that indicate the strength of the connection from source to sink as the value at their intersection. Retention was defined as the special case of connectivity from a region to itself.

Connectivity was analyzed a number of ways. The local index of collocation (LIC), a method for making cell-by-cell comparisons (Kotwicki & Lauth, 2013), was used to assess similarities and differences between connectivity matrices of spawning time, year, and simulation. Also, connectivity of each pair was classified as strong (>0.10), moderate (0.05-0.10), or weak (<0.05) to facilitate comparisons. Additionally, cross-shelf transport was evaluated by calculating the longitudinal difference between spawn and juvenile locations and binning results as either >10°W, 5–10°W, <5°W, <5°E, 5–10°E, or >10°E.

Eastward transport was correlated to different climate indices including the mean winter cross-shelf wind velocity, the mean winter along-shelf wind velocity, the May sea surface temperature (SST) anomaly, and the North Pacific Index in the winter (NPIw). The mean winter cross- and along-shelf wind velocity anomalies represent Oct-Apr at the NARR (NARR website) grid point of 60°N, 169.94°W (BEST-BSIERP region 9). Wind velocity anomalies were NE+/SW- for cross-shelf velocities and NW+/SE- for along-shelf velocities (Danielson unpub. data). The May SST index was calculated as mean monthly SST averaged over the area 54.3°N-60.0°N, 161.2°W-172.5°W using the NCEP/NCAR Reanalysis project data (Kalnay *et al.,* 1996). The index values are deviations from the mean value normalized by the standard deviation for the period 1961-2000 (Kalnay *et al.,* 1996). The North Pacific Index is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W that measures the intensity of the Aleutian Low (AL) (Trenberth & Hurrell, 1994). A positive NPI corresponds to a weak AL, while a negative NPI indicates a strong AL, although it does not differentiate between variations in AL zonal displacements. The winter index is the average NPI from Nov-Mar and the anomalies were normalized by the mean and standard deviation for 1961-2000 (Trenberth & Hurrell, 1994). The NPI data were provided by the Climate Analysis Section, NCAR, Boulder, USA.

Comparisons between modeled distributions of individuals at the time of reaching the juvenile transition and observations of age-0 pollock were also made with the local index of collocation (LIC) as this method of cell-by-cell comparisons has been used to compare distributions of populations (Kotwicki & Lauth, 2013; Petrik *et al.,* 2014) and is similar to the Overlap Coefficient, also used in fisheries studies of distribution overlap (e.g. Hinrichsen *et al.,* 2005). Observations of depth-integrated abundance (# surface area^{-1}) were first binned by BEST-BSIERP region to calculate a mean abundance in each region of each year. Mean depth-integrated abundances (# surface area^{-1}) were then converted into mean total areal abundances (#) by multiplying the areal extent of each region (surface area). Mean numbers of individuals were used to calculate the fraction of individuals observed in each region out of the total number of individuals in all regions observed that year. Since not all 16 BEST-BSIERP regions were sampled by all observations in all years, model-observation comparisons were only made using the regions sampled. Thus, modeled fractions of individuals were calculated as the number of individuals that reached juvenile size in each region sampled by that observation data set that year out of the total number of individuals that reached juvenile size in all regions sampled by that observation data set that year. The LIC was then calculated year-by-year for each observation data set by comparing each specific pair of observed and modeled fractions.

RESULTS

Modeled spawning only occurred in the BEST-BSIERP regions (Figure 1) AK Peninsula (1), South Middle Shelf (3), South Outer Shelf (4), Pribilofs (5), Midnorth Middle Shelf (6), North Outer Shelf (8), and Off-shelf Southeast (16), yet individuals were found in all 16 regions at the time each reached the juvenile transition. Connectivity between spawning and juvenile regions differed by spawn date, year, and simulation.

Base simulation

The greatest mean connectivity over all spawn times and years from the Base (“Transport Only”) simulation was retention within the North Outer Shelf (8) with 0.374 of all individuals spawned residing in the area as both eggs and juveniles (Table 1). The South Middle Shelf (3) and Midnorth Middle Shelf (6) were other regions with strong retention >0.10 (Table 1). Retention within the AK Peninsula (1) was moderate (0.05–0.10), while it was weak (<0.05) in the other spawning areas (4, 5, 16) (Table 1).

Consistently high connections existed from the AK Peninsula (1), historically described as a key spawning area, to the southern Middle Shelf regions and both Outer Shelf regions (3, 4, 6, 8) (Table 1). Robust connections originating from the other historic spawning ground, the Pribilofs (5), were to more northern Middle, Outer, and Off-shelf regions (6, 8, 9, 15) (Table 1). Spawning in the South Middle Shelf (3) and Midnorth Middle Shelf (6) bridged between the historic areas around Unimak (region 1) and the Pribilof Islands (region 5) and shared their connectivity patterns, with the South Middle Shelf (3) more like the AK Peninsula (1) and the Midnorth Middle Shelf (6) more like the Pribilofs (5) (Table 1). The Outer and Off-shelf spawning regions (4, 8, 15) all connected strongly to the North Outer Shelf (8) and Off-shelf North (15) (Table 1). Connectivity between all spawning areas and the Inner Shelf regions (2, 7) and northernmost regions (11-14) was very low (Table 1).

Seasonal connectivity patterns

The 15 Jan release date represented early in the season when spawning starts near Unimak Island, only occurring in the AK Peninsula (1), South Middle Shelf (3), and South Outer Shelf (4) (Figures 1, 2). As spawning spread to the northwest with time, there was additional connectivity originating in the Pribilofs (5), Midnorth Middle Shelf (6), North Outer Shelf (8), and Off-shelf Southeast (16) regions (Figures 1, 2). Seasonal connectivity in the Base simulations generally mirrored the mean connectivity with a few variations by spawn date. Retention within the North Outer Shelf (8) was the greatest connectivity for all spawning times except Jan 1 (Figure 2). Connectivity to the southern Middle Shelf (1, 3) was highest from 15 Jan – 1 Mar spawning dates, while connectivity to Off-shelf North (15) was higher from the 1 Mar – 15 Apr spawning dates (Figure 2). Connectivity to the Inner Shelf (2, 7) and northernmost regions (11-14) decreased from all spawning regions as time progressed (Figure 2). The AK Peninsula (1) and South Middle Shelf (3) tended to have the highest retention in the middle of the spawning period, while retention in the Pribilofs (5), Midnorth Middle Shelf (6), North Outer Shelf (8), and Off-shelf Southeast (16) regions increased over the spawning season (Figure 2). Similarity between connectivity patterns from one spawning time to another decreased as the time between them increased, with the exception of 15 Jan, which had connectivity patterns least like those of 15 Mar spawning and most like those of 15 Apr (Table 2). Due to its isolated spawning (Figure 1), the 15 Jan spawning simulation was the least like the other connectivity patterns (Table 2). Conversely, the most widespread spawning in 15 Feb had the greatest similarity in connectivity to all other spawning times (Table 2).

Interannual connectivity patterns

Connectivity patterns varied from year to year, but were generally more similar to each other than random, with mean annual LIC scores ≥0.55 (Table 3). Between-year variability in the connectivity patterns (σ^2=0.0094) was greater than the variability between spawning times (σ^2=0.0064). Seasonal variability in connectivity was largely driven by the small spawning area in Jan that had a mean LIC of 0.58, while the other months had mean scores ≥0.83 (Table 2).

The year with connectivity patterns most similar to all others was 1999 (cold), with a mean of 0.82, though no individual comparisons were exceptionally high (Table 3) and may be the result of more cold years simulated than warm ones. On the other hand, the years 1997 (an El Niño with a warm summer) and 2002 and 2004 (both warm) were very similar to 5 or 6 individual years (Table 3), typically to each other and warm years but also to cold years 2000, 2009, and 2011 (Table 3). Generally, connectivity patterns of individual warm or cold years did not have exclusively high LIC scores with either year type (Table 3). The most striking result was the years with the lowest similarity in connectivity to the other years: 2005 and 2007 (Table 3). Both of these years tended to have lower connectivity from all spawning areas to all juveniles areas compared to the mean Base simulation. For 11 of the 17 years, connectivity in 2007 was the most different (Table 3). Connectivity in 2007 was much like that of 2008 (LIC=0.90), but 2005 was dramatically different from 2007 (LIC=0.29; Table 3). There were much higher connections to the North Outer (8) and Off-Shelf North (15) regions from all spawning areas in 2007 than 2005. In contrast, 2005 had greater connectivity from Middle Shelf regions to regions just north of them (1, 3 to 3; 5, 6 to 9, 10). Retention in the North Outer Shelf (8) was consistently above 16% in all years, which had the greatest retention of all times and regions in 1997, whereas virtually no retention occurred Off-shelf Southeast (16) that year (Table 4). The South Outer Shelf (4), Pribilofs (5), Midnorth Middle Shelf (6), and Off-shelf Southeast (16) shared the years with maximum rates (1998), but minimum retention rates varied (Table 4). The high retention year of 1998 produced above average rates in the other regions as well (Table 4).

Connectivity patterns in different simulations

Combining all spawning times and years within each simulation likewise produced different connectivity patterns. Comparing between only the Cold and Warm years of the Base simulation highlights differences based on temperature regime, and better elucidates connections between spawning areas and different regions of the EBS (Figure 4). In these comparisons, connectivity was classified as strong (>0.10), moderate (0.05–0.10), or weak (<0.05; not pictured in Figure 3). Strong connectivity existed from the AK Peninsula (1) to the South Middle Shelf (3) and North Outer Shelf (8) in both Cold and Warm years (Figure 3A). Connections from most spawning areas (1, 3, 5, 6, 8) to the northern Middle Shelf regions (6, 9, 10) and the southern Outer and Off-shelf regions (4, 16) were stronger in Warm years, while to Off-Shelf North (15) was greater in Cold years (Figures 3A-B,D-F). Connectivity patterns from both the South Outer Shelf (4) and Off-Shelf Southeast (16) were identical in both temperature conditions: strong to northern Outer and Off-shelf regions (8,15) and moderate to the Midnorth Middle Shelf (6) (Figures 3C,G). With the exception of the North Outer Shelf (8) spawning region, most moderate and strong connections were to regions north and/or west of spawning regions, with higher off-shelf connectivity in Cold years and greater northward connectivity in Warm years (Figure 3). Retention of juveniles (not visible in Figure 3) decreased in all regions in Cold years, and increased in the South Middle Shelf (3), Pribilofs (5), and North Outer Shelf (8) in Warm years (Table 4).

When only comparing the cold year simulations (Figure 4 top), the largest differences existed for the Contract simulation because there was no spawning in the Midnorth Middle Shelf (6) (Figure 4 top). Connectivity from southern Middle Shelf regions (1, 3) to northern Middle, Outer, and Off-shelf regions (6, 8, 9, 15) increased and lessened to southern regions (1, 2, 3, 16) when spawning was contracted in cold years (Figure 4 top). Heightened connectivity was seen between the Pribilofs (5) and southern

Middle, Outer, and Off-shelf regions (1, 3, 4, 16), while links to the Inner Shelf regions (2, 7) and north to St. Matthews (9) dropped (Figure 4 top). Contraction of spawning areas in cold years reduced retention in the North Outer Shelf (8), but increased it in the Pribilofs (5) and Off-shelf Southeast (16) (Table 4). Contraction of the spawning area had the largest effect on connectivity from southern Middle Shelf spawning regions (1, 3), and to the South Middle Shelf (3), North Outer Shelf (8), and St. Matthews (9) juvenile regions.

Shifting spawning 40 d later in the Late simulation also produced differences in connectivity from the Cold Base simulation. Connections to mid-north Middle Shelf regions (5, 6) and southern Outer and Off-shelf regions (4, 16) were greater than or equal to those of the Cold simulation (Figure 4 top). Late spawning weakened connectivity from most spawning regions to the Inner Shelf (2, 7), and to the northern regions (8-11) (Figure 4 top). Late spawning reduced retention in the South Middle Shelf (3) compared to Base Cold, but was positive for all other regions (Table 4).

The warm year simulations also varied among each other, often as either an increase or decrease to a juvenile region from all source regions. Expanding spawning regions increased delivery to the southern inner and Middle regions (1, 2, 3) (Figure 4 bottom). In comparison to the Warm Base simulation, retention in the Pribilofs (5) increased as well as its connectivity to the South Outer Shelf (4) and North Middle Shelf (10) (Figure 4 bottom). Expanded spawning lowered connectivity from the Midnorth Middle Shelf (6) to many Middle Shelf regions (3, 4, 5, 6, 9, 10) (Figure 4 bottom). With the exception of this area, retention was enhanced in all regions when compared to retention in the Warm Base simulation (Table 4).

Advancing spawning times by 40 d in the Early simulation created the greatest differences between the warm simulations. Connectivity from the majority of the spawning regions to the Inner Shelf and northern Middle Shelf regions (2, 7, 10, 11, 12) was stronger, as well as to the South Middle Shelf (3) (Figure 4 bottom). Conversely, links from nearly all source regions to the Outer and Off-shelf regions and mid-north Middle Shelf regions (4, 5, 6, 8, 15, 16) fell in the Early simulations, with the exception of retention in the Midnorth Middle Shelf (6) (Figure 4 bottom). In addition, connectivity to St. Matthews (9) on the Middle Shelf increased from Outer and Off-shelf areas (4, 8, 16), but decreased from the mid-north Middle Shelf regions (5, 6) (Figure 4 bottom).

When comparing the Warm year simulations to the Cold year simulations, the Cold years tended to have much stronger connectivity to the Off-Shelf North (15) and slightly increased connectivity to the Inner Shelf (1, 2, 7), while connectivity to the Middle Shelf (3, 6, 9, 10) was greater in the Warm year simulations (Figure 4). The Contract simulation produced connectivity patterns that were the most dissimilar from other simulations (Table 5). Contracting the spawning areas resulted in greater connectivity differences from the Base Cold simulation than delaying spawning 40 d with the Late simulation, almost as large as the difference of the Base Cold from the Base Warm simulation (Table 5). In contrast, connectivity patterns with Expanded spawning were more similar to the Base Warm simulation than when spawning was 40 d Early, and the Base Warm simulation was much more like both the Expanded and Early simulations than the Base Cold one (Table 5).

East-West transport

Connectivity to more on-shelf regions was further exemplified by the fraction of juveniles transported 0°–5°, 5°–10°, or >10° longitude to the east of where they were spawned (Figure 5). The total fraction of all juveniles found east of their spawning locations never exceeded 0.4 in any year (Figure 5). Especially strong peaks in the fractions transported 0°–5°E and 5°–10°E occurred in 1998, 2000, and 2009 (Figure 5 top and middle). Dispersal >10°E of the spawning origin was much less common and showed a different interannual pattern from transport <10°E (Figure 5). While 2009 was also a year with the fraction greater than the mean; transport was very low in 1998 and 2000, and above average in 2007 (Figure 5). None of the eastward transport metrics were significantly correlated with temperature or wind indices (Table 6), but dispersal >10°E was significantly positively correlated with the winter North Pacific Index (NPIw; r=0.55, p=0.02, Table 6).

When the years were grouped by Cold and Warm in the Base simulation, there were differences in the fractions of individuals found various distances east and west of their spawning origins (Table 7). The Cold year simulations had greater fractions transported >5°W compared to the Warm simulations, but also greater fractions >5°E (Table 7). When comparing across simulations, roughly 80% or more of all juveniles were found to the west of where they were spawned, with the plurality found a distance of <5°W in all simulations (Table 7). Contracting the spawning grounds off-shelf led to greater westward transport, whereas advancing spawning time by 40 d with the Early simulations increased eastward transport more than Expanding the spawning areas on-shelf (Table 7).

Comparisons with juvenile survey observations

Agreement between the model and different sets of observations varied by year and observational method (Table 8). The BASIS surface observations had the lowest LIC values in all years and simulations indicating less than 50% mean overlap (Table 8). On the other hand, model agreement with the *Oshoro Maru* and BASIS acoustics observations were much better, with 76% and 67% mean collocation, respectively (Table 8). The model showed the highest agreement with the *Oshoro Maru* observations in all simulations except when spawning was delayed 40 d in the Late simulation, which had a greater LIC with the BASIS acoustics (Table 8). There was only one year (2007) that had all three types of observations collected. In this year, the model overlapped greatly with the *Oshoro Maru* data and poorly with both of the BASIS data sets (Table 8, Figure 6). This year was not the best representation of how the model and observations differed. In most years the model overestimated juveniles in the AK Peninsula (1), South Outer Shelf (4), and Midnorth Middle Shelf (6) and underestimated juveniles in the south Inner and Middle Shelves (2, 3) compared to the *Oshoro Maru* observations (Figure 7), whereas in 2007 there are greater fractions of modeled juveniles in all regions except for the South Outer Shelf (4) (Figure 6 top). The over-prediction of modeled juveniles in the North Outer Shelf (8) compared to the BASIS surface trawl observations was seen in 2007 (Figure 6 middle), but this year lacked the general trend of more northward displaced modeled juveniles (regions 6, 9, 10, 15) (Figure 8). Compared to the BASIS acoustics, the model simulated fewer juveniles on the south Inner and Middle Shelves (2, 3), and more juveniles elsewhere (Figure 9), of which the decreased fractions in the South Middle Shelf (3) were seen in 2007 (Figure 6 bottom).

DISCUSSION

Relationship with oceanography and climate

The strong and moderate connectivity between spawning and juvenile regions exhibited three patterns: along-isobath flow to the northwest, self-retention, and in the vicinity of the Pribilof Islands. Most of the consistently high connections existed from spawning regions to the southeast to juvenile regions to the northwest, suggesting transport via flows like the BSC (Figure 1) and the baroclinic flows along the 100-m and 200-m isobaths. These along-isobath flows carried individuals to regions directly northwest of the spawning region, or to regions located either off- or on-shelf from the spawning region and sharing a common border with the 100-m and 200-m isobaths. The highest connectivity for all spawning times (except 15 Jan), years, and simulations was retention within the North Outer Shelf (8). Though technically retention, transport within the North Outer Shelf could also be considered northwesterly. This long, narrow region that spans a wide range of latitudes could easily retain individuals that were spawned in the south of the region near the Pribilofs (5) and were transported along-shelf to more northwestern parts of the same region. Unlike the North Outer Shelf, the AK Peninsula (1), South Middle Shelf (3), and Midnorth Middle Shelf (6) are not as long in the northwest direction. The strong (3, 6) and moderate (1) retention in these regions must be related to their locations on the Middle Shelf. Some of the retention in region 1 could be the result of on-shelf advection by the ACC (Figure 1) that flows northeastward along the Peninsula, while other retention in regions 1, 3, and 6 is likely related to the Inner and Middle Fronts inhibiting cross-shelf flow (Coachman, 1986; P. Stabeno, pers. comm.).

The third connectivity feature that appeared was transport in and around the Pribilof region (5). The Pribilof Islands are a major spawning ground (Hinckley, 1987; Bacheler *et al.,* 2010) and are known for anti-cyclonic flow that can retain drifters for 20-200 d (Kowalik & Stabeno, 1999; Stabeno *et al.,* 2008). The weak modeled retention of this region could be explained by its small size that would account for anticyclonic transport into the adjacent regions (3, 6, 8) with strong and moderate connectivity. Transport from the Outer Shelves (4,8) to the Midnorth Middle Shelf (6) is evidence of the anti-cyclonic flow extending into other regions. Off- and on-shelf transport across two major fronts rarely occurred, with a few exceptions. Movement from the Middle Shelf into the slope region of Off-shelf North (15) persisted with strong connectivity from the Pribilofs (5) and moderate connectivity from the South (3) and Midnorth Middle (6) Shelves. The greatest on-shelf connection was moderate from Off-shelf Southeast (16) to the Midnorth Middle Shelf (6). All of these on- and off-shelf pathways required crossing both the Middle Front and the BSC, likely via the anti-cyclonic Pribilof flow. The inadequate size of the BEST-BSIERP Pribilof region is further supported by a study that characterized the spatial extent of the Pribilof Islands habitat using ecosystem energetics and foraging theory with data spanning 1990-2000 (Ciannelli *et al.,* 2004). Both methods estimated a radius of approximately 100 nautical mi (185.2 km), which is consistent with the size of the clockwise gyre during summer (Stabeno *et al.,* 1999). This area is much larger than the BEST-BSIERP region 5 (<50 nmi) and would contain parts of regions 3, 4, 6, 8, 15, and 16.

Temporal variability within a season

General connectivity patterns did not vary much across spawning times, though some connections changed with time. The strong link between the AK Peninsula (1) and South Middle Shelf (3) was greatest earlier in the spawning season. Similarly, the weak connections to northernmost regions 10-14 decreased as the spawning season progressed. The fluctuations in connectivity and retention with the Early spawning simulations arose from these relationships. Connectivity strengthened to Inner Shelf and northern regions and weakened to Outer and Off-shelf regions with 40 d Early spawning.

The AK Peninsula (1) and South Middle Shelf (3) tended to have the highest retention in the middle of the spawning period, while retention in the Pribilofs (5), Midnorth Middle Shelf (6), North Outer Shelf (8), and Off-shelf Southeast (16) regions increased over the spawning season. Modeled connectivity and retention with 40 d Late spawning corresponded to these seasonal patterns and inverted the results of the Early simulation. Connections to the Inner and north Middle Shelves and retention within the South Middle Shelf (3) were reduced when spawning times were shifted later. In contrast, Late spawning improved retention in all other regions, most of which had higher retention rates later in the Base spawning season.

Taken together, these results suggest that northward and on-shelf transport was greater in the late winter and early spring compared to the rest of the spawning season. In fact, advancing spawning time by 40 d with the Early simulations increased eastward transport more than Expanding the spawning areas on-shelf. Ekman surface currents are strongest in the winter and decrease through the spring to minima in the summer (Danielson *et al.,* 2011b; Stabeno *et al.,* 2012; Danielson *et al.*, 2014), accounting for the greater overall transport in the Early simulations and greater retention in Late simulations. In addition to strength, current direction varied by month. For example, at station M2 on the Middle Shelf (region 3) the mean monthly surface currents during 1995-2010 were to the northwest in Jan and Feb, and then shifted to the west/southwest as they weakened through the spring (Stabeno *et al.,* 2012). The warm years showed a different pattern with strong northward flow in Jan and Feb and weak eastward flow in May and Jun (Stabeno *et al.,* 2012). Similarly, the BSC is strongest Jan-Mar and weakens as the year progresses (Ladd, 2014). Additionally, seasonal stratification establishes the Inner Front and Middle Front in Apr and May (Kachel *et al.,* 2002; Gibson *et al.,* 2013). The absence of these fronts in the early spring substantiates the strong connectivity from region 1 to region 3 during early spawning times by allowing transport across the 50-m isobath, while their presence in the late spring and early summer supports the higher retention rates in most regions with Apr, May, and Jun spawning times by preventing cross-shelf transport of individuals. Additionally, the warmer temperatures of later spawning times would raise growth rates, thus reducing the time to reach the juvenile stage and potentially transport distance thereby increasing retention.

Spatial variability within a region

The alterations in connectivity, retention, and E-W transport in simulations with Contracted and Expanded spawning areas revealed spatial variability of currents within regions. The Contract simulation had the largest differences among the cold year simulations and was the most dissimilar from all simulations. These divergences included no spawning in the Midnorth Middle Shelf (6) and increased off-shelf transport. Connectivity from the Middle Shelf regions (1, 3) rose to the north Middle, Outer, and

Off-shelf regions (6, 8, 9, 15). Greater off-shelf advection was also demonstrated with increased fractions of individuals transported west of their spawning locations. Contracting spawning areas to the southwest increased south and southwestern transport from the Pribilofs (5) as well as retention within this region. On the other hand, contracted spawning reduced retention in the AK Peninsula (1), South Middle Shelf (3), and North Outer Shelf (8) and led to greater transport to the northwest, most likely by concentrating the individuals spawned in each region closer to northwestern baroclinic flows along the 100-m and 200-m isobaths and the BSC.

When spawning areas were Expanded on-shelf, delivery from most source regions increased to the south Inner and Middle Shelves and subsequently decreased to the Outer Shelves and Off-shelf North. In contrast to the Contracted simulation, Expansion increased the fractions of individuals transported to the east. Furthermore, retention was amplified in all regions except for the Midnorth Middle Shelf (6). The Expanded on-shelf spawning locations resulted in more eastward movement that facilitated improved retention in all other regions by placing eggs in regions with weaker flows, that were further from northwestward currents, and/or near eastward currents such as the ACC. Alternatively, Expanded spawning lowered connectivity from the Midnorth Middle Shelf (6) to south and west regions (3, 4, and 5), suggesting that more on-shelf individuals in region 6 were transported northwestward, while more off-shelf individuals in the region were influenced by the anti-cyclonic circulation near the Pribilofs. This is further supported by the increased Pribilofs retention and southwestward connectivity when spawning sites were contracted off-shelf.

Interannual variability and cold/warm years

The years with the lowest similarity in connectivity to the other years, 2005 and 2007, were anomalous for different reasons, thus accounting for their low similarity to each other. 2005 was one of the warmest years on record in the EBS, leading to strongly stratified conditions in the southern shelf during the summer (Stabeno *et al.,* 2010) and very high on-shore Ekman transport (Danielson *et al.,* 2011b). Stratification was also strong in 2007, but wind velocities and thus Ekman transport were very low (Danielson *et al.,* 2014). This strong stratification and low wind mixing reduced nutrient flux to surface waters and may have ultimately led to poor pollock recruitment success in 2007 through bottom-up processes, an unanticipated outcome of cold year conditions (Gann *et al., in press*). Additionally, 2007 was a year where ichthyoplankton species and stations groups characterized by Busby *et al.* (2014) were unique from all other years (1996-2007), with pollock contributing most to the differences.

Especially high fractions of individuals were transported 0°–5°E and 5°–10°E in 1998, 2000, and 2009. Many physical and biological characteristics of the EBS were anomalous in 1998 (Stabeno *et al.,* 2001). This year had strong winds from Jan into Jun and enhanced on-shelf transport (Stabeno *et al.,* 2001). This on-shelf transport was beneficial for retention, which was above average in all regions in 1998. Both 1998 and 2000 had negative winter North Pacific Index values, indicative of strong Aleutian Lows, yet the fractions of individuals transported 0°–5°E and 5°–10°E were not significantly correlated to the winter NPI, nor any climate indices. In contrast, dispersal >10°E of the spawning origin was significantly positively correlated with the winter NPI, denoting more eastward transport during weak ALs, often linked with cold temperatures

(Rodionov *et al.,* 2007), which is consistent with greater fractions transported >10°E in the cold simulations. However, the fraction of juveniles found >10°E from their spawning locations was very small in all simulations, and neither the fractions 0°–5°E nor the summed fractions >0°E were higher in cold years. This discrepancy between eastward transport and AL strength is rectified by the fact that it is the mean position of the AL, not the strength, that affects winds and cross-isobath fluxes on the Bering shelf (Danielson *et al.,* 2014), and that the position is more closely related to winter air temperatures in the Bering Sea than the strength of the AL (Rodionov *et al.,* 2007).

When the mean winter position of the AL is more westward, the EBS shelf experiences southeasterly winds that drive coastal convergence and northward flow along the Alaskan coast (Danielson *et al.,* 2014). Over the Middle Shelf flow is on-shelf in the south (regions 1, 3) and is northwards along isobaths in the midnorth (regions 6, 9), while the north Outer Shelf (region 8) currents cross isobaths to the northeast (Danielson *et al.,* 2014). Additionally, western storm paths drive on-shelf Ekman transport (Danielson *et al.,* 2014). The warm period 2000-2005 coincided with westward-displaced ALs, thus supporting the modeled warm year patterns of more eastward transport over the shelf, stronger connectivity to northern regions, and greater connectivity from the North Outer Shelf (8) northeast to the Midnorth Middle Shelf (6) and St. Matthews (9). When Ekman flows in warm years were not to the north, they were very weak in the cross-shelf direction (Danielson *et al.*, 2011b; Stabeno *et al.,* 2012). The high retention rates and smaller fractions of individuals transported >5° to the west and east of their spawning locations in warm years reflected these weak cross-shelf flows.

In contrast, the AL was shifted eastward into the Gulf of Alaska during the cold period of 2006-2011 (Danielson *et al.,* 2014). With an eastward-displaced AL, winds over the EBS shelf are more northwesterly, northerly, and northeasterly forcing coastal divergence and advection along isobaths to the southwest over the southern Middle Shelf (regions 1, 3) (Danielson *et al.,* 2014). These characteristics account for the greater westward transport and stronger off-shelf connectivity to regions such as the North Outer Shelf (8), Off-shelf North (15), and Off-shelf Southeast (16) in the cold year simulations. Additionally, greater fractions of individuals traveled further distances, in both eastward and westward directions, in cold years compared to warm years. Correspondingly, the stronger off-shelf currents in cold years (Danielson *et al*., 2011b; Stabeno *et al.,* 2012; Danielson *et al.,* 2014) support the greater travel and decreased retention in the Cold Base simulation.

Comparisons with observations

There are important considerations as to why modeled and observed juvenile distributions were not identical. For one, there is a difference in time between the two distributions. Modeled distributions were the locations of individuals when they reached 40 mm; this could be any time between Mar and the following Jan, but were typically Jun-Jul. On the other hand, most of the observations were taken later in the year (late Jul-early Oct) where age-0 pollock could include fish up to 130 mm (Moss *et al.,* 2009), and exclude fishes ≤40 mm by gear selectivity (e.g. BASIS surface trawl). Over the course of this time, simulated juveniles would continue to be transported, possibly to different nursery areas. The reason that simulations were not run until this time is the second potential difference between the model and observations: the fact that swimming ability increases as pollock juveniles get older and larger (Brodeur & Wilson, 1996; Duffy-Anderson *et al.,* 2015) and they cannot be considered passive drifters in the horizontal direction. Thirdly, in addition to horizontal swimming, vertical migration increases with age resulting in different depth distributions of juveniles, with midwater abundances often exceeding those at the surface (Parker-Stetter *et al.,* 2013). The spatial distributions of age-0 pollock at the surface and deeper in the water column were similar in warm years (2006, 2007), yet diverged in cold years (2009, 2010) when densities were low in the surface and high in the midwaters (Parker-Stetter *et al.,* 2013). Thus, surface net tow observations, like those from the BASIS survey may be representative of the total water column distribution of juvenile pollock in warm years, but not in cold ones where they would diverge from model results and the BASIS whole water column acoustic surveys. These differences in depth distributions may account for why the agreement between the model and BASIS surface tow data was higher in the warm years 2004 and 2005 and lower in the cold years 2007, 2009, and 2010, and why full water column observations such as the *Oshoro Maru* and BASIS acoustics data sets were always a better match with simulated results.

In contrast to observations, modeled juveniles were found on the Inner Shelf (regions 2, 7, 11), especially in cold years. The simulations are consistent with the observed extension of a Middle Shelf zooplankton community into the Inner Shelf in cold years, which may be the result of a weaker Inner Front in cold years (Eisner *et al.,* 2014) or one that develops in August rather than June as was observed in 1998 and 1999 (Kachel *et al.,* 2002). Observed transport of zooplankton to the Inner Shelf implies that either behavior and/or mortality are responsible for the lack of observed juveniles on the Inner Shelf. High mortality on the Inner Shelf may be related to its low prey energy density (Siddon *et al.,* 2013b), the lack of stratification that prevents energy conservation by vertical migration, and/or the shallower depths that inhibit vertical migration to avoid visual predators. Analogously, mortality in all regions, which is not represented in the simulations, is yet another factor that could account for differences between modeled and observed juvenile distributions.

Consequences of connectivity

The connectivity presented here is representative of potential connectivity. Ultimate population connectivity would be determined from survival processes both during and after dispersal until recruitment into the fishery. Some information about survival of age-0 juveniles can be gleaned from the spatial distributions of prey and predators in reference to the modeled regions of juvenile metamorphosis.

Nursery areas

Historically good juvenile habitat is near the Pribilof Islands (region 5; Duffy-Anderson *et al.,* 2015). Tides and winds around the Pribilof Islands create a structural front that enhances nutrient vertical fluxes, and primary and secondary productivity (Brodeur *et al.,* 1997; Stabeno *et al.,* 1999; Stabeno *et al.,* 2008). This high productivity in combination with a retentive clockwise circulation pattern around the islands create an ideal rearing location (Swartzman *et al.,* 2005). Studies of the Pribilof Islands (Brodeur *et al.,* 1997; Ciannelli *et al.,* 2002; Swartzman *et al.,* 2002; Swartzman *et al.,* 2005) examined nursery suitability of all mixed, frontal, and stratified zones of the southeastern Bering Sea by using the Pribilof Islands, which contained all three, as a representative mesocosm. Their findings suggest that the Pribilof Islands and other stratified (like the Outer Shelf regions 4 and 8) and frontal habitats of the EBS would be favorable feeding and rearing habitats for juvenile pollock.

More recent studies during the warm and cold time periods acknowledge the Outer Shelf (regions 4 and 8) as beneficial feeding areas for age-0 pollock juveniles. EBS zooplankton communities were significantly different in warm and cold year surveys from mid Aug to early Sep for 2003-2009 (Eisner *et al.,* 2014). These species compositions are consequential, as zooplankton differ in their size and lipid content, which affects their suitability and quality as juvenile pollock prey. For example, the equivalent biomasses and distributions of copepods *Oithona* spp. in warm and *Pseudocalanus* spp. and *Acartia* spp. in cold years do not necessarily denote equal juvenile feeding, condition, and survival. *Oithona* spp. is a less preferred prey in age-0 diet analyses (Strasburger *et al.,* 2014) that could be determined either passively if its smaller size reduces encounter rates (Petrik *et al.,* 2009), or actively if individuals choose to target other taxa when available. Juvenile pollock gut fullness was not significantly different in warm years (Heintz *et al.,* 2013), which does not suggest that feeding success suffered. Despite high abundance and statistically similar average weight and percent gut fullness, age-0 pollock energy density was lower in warm years compared to cold (Heintz *et al.,* 2013). The large zooplankton *Thysanoessa* spp. and *Calanus marshallae* and the small zooplankton *Pseudocalanus acuspes* and *Pseudocalanus minutus* store sizeable amounts of lipids (Coyle *et al.,* 2011). Due to these zooplankton, the Outer Shelf (4, 8) in all years and the Middle Shelf (1, 3, 5, 6, 9, 10) in cold years have higher energy densities of prey, while the small zooplankton of the Inner Shelf (2, 7, 11) give it the lowest energy density (Coyle *et al.,* 2011; Siddon *et al.,* 2013b). There was greater coincidence of age-0 pollock with regions of high prey energy density in cold years (e.g. 2010; Siddon *et al.,* 2013b), accounting for the higher proportion of euphausiids in their diet and the higher energy density of pollock in cold years compared to warm years (Moss *et al.,* 2009; Coyle *et al.,* 2011; Heintz *et al.,* 2013).

During warm years, the reduced availability of large lipid-rich prey items led to age-0 pollock becoming a large portion of the diet of many fishes, such as juvenile pollock and salmon (*Oncorhynchus* spp.; Moss *et al.,* 2009; Coyle *et al.,* 2011), Pacific herring (*Clupea pallasii*; Andrews *et al., accepted*), and age-0 Pacific cod (*Gadus macrocephalus*; Farley *et al.,* 2015). In addition to the absence of preferred high lipid prey, the lower per capita prey availability produced by greater juvenile densities and decreased prey biomass (Heintz *et al.,* 2013) could have been accountable for the higher proportion of cannibalism in warm years (Moss *et al.,* 2009; Coyle *et al.,* 2011; Heintz *et al.,* 2013).

The distribution of predatory fishes also varied across the shelf by region and warm or cold period (L. Eisner, pers. comm.) producing different predation rates based on the amount of overlap with each species. During warm years juvenile pollock distributions often overlapped with herring and sockeye salmon (*O. nerka*) on the north and south Middle Shelf (1, 3, 5, 6, 9, 10; L. Eisner, pers. comm.) Juvenile pollock co-occurred with capelin (*Mallotus villosus*) and herring on the northern parts of shelf (6, 9, 10, 11) and with Pacific cod and yellowfin sole (*Limanda aspera*) along the Inner Front (and in regions 1 and 3 in 2010) (L. Eisner, pers. comm.). Only the Outer Shelf regions (4, 8) lacked strong associations between juvenile pollock and predatory fishes (L. Eisner, pers. comm.). These Outer Shelf regions are home to Arrowtooth flounder, a voracious predator of pollock (Lang *et al.,* 2000), that has increased in abundance and biomass over the past 30 years (Zador *et al.,* 2011; Hunsicker *et al.,* 2013). The cluster of arrowtooth flounder in the northern half of the North Outer Shelf (8) would pose the greatest threat to age-0 pollock since these arrowtooth flounder were the largest, had the lowest proportion of non-empty stomachs, and consumed age-0s more frequently than clusters in other areas in the 2000s (Zador *et al.,* 2011).

Juvenile survival

Swartzman *et al.* (2005) found a significant difference in the 1995-2001 T/S *Oshoro Maru* net tow abundance of age-0 pollock between the Pribilof Islands and non-Pribilof shelf areas (1-4, 6-9), with greater abundances within 100 nmi of the islands. The increased contribution of the Pribilofs to recruitment in 1997-1999 (Swartzman *et al.,* 2005) led to use of the abundance of age-0 pollock near the Pribilof Islands as an index of year class strength (Macklin & Hunt, 2004). Year-class strength at recruitment (age-3) was correlated with age-0 density, the spatial relationship between juveniles and euphausiids, and the centricity of age-0 distributions around the Pribilof Islands for the years 1994-1999, having a positive relationship with euphausiid overlap (Winter & Swartzman, 2006). Consistent with later diet and condition studies (Moss *et al.,* 2009; Heintz *et al.,* 2013; Siddon *et al.,* 2013a), Winter and Swartzman (2006) hypothesized that age-0 juveniles must transition their diet from copepods to euphausiids by Sep to maximize survival potential. The Pribilof Island studies strengthen the idea that transport to the Islands alone are a good predictor of recruitment success that would be enhanced when this area had high concentrations of euphausiids and low concentrations of predators.

Later studies of recruitment demonstrate that recruitment at age-2 is related to predation mortality on age-1 juveniles (Mueter *et al.,* 2006). The variability in survival to age-1 is best described by a model that includes temperature variability and predation, such that survival is higher when temperatures and predation are lower to average (Mueter *et al.,* 2011). Survival from age-0 to age-1 was poor in warm years as indicated by high abundances of age-0s but below average recruitment year-classes (Moss *et al.,* 2009; Hunt *et al.,* 2011). The higher energy density and smaller lengths of age-0s in cold years vs. warm years suggest survival to age-1 via an energy allocation strategy towards lipid storage rather than growth (Moss *et al.,* 2009; Siddon 2013a). However, growth to a minimum size would be advantageous because comparisons of length frequencies of age-0 pollock in stomachs and trawls imply that both age-1 pollock and small arrowtooth flounder (<20cm) have age-0 pollock upper size limits of 62 mm and 55 mm respectively (Lang *et al.,* 2000). The number of age-1 recruits per spawner during the warm and cold periods (2001-2010) was significantly positively related to age-0 weight, energy density, and total energy (weight × energy density), with total energy density explaining the most variability (Heintz *et al.,* 2013). This relationship with total energy density indicates that survival to age-1 requires both high energy condition going into winter to prevent starvation and a large size to store and use lipids more efficiently (Heintz *et al.,* 2013) and to avoid predation. High age-0 survival and ultimately recruitment would occur from transport to regions with lower temperatures or stratified water columns and high concentrations of energy-rich prey, to promote gaining mass and lipids, as well as low concentrations of predators to prevent predation mortality.

Through synthesis of the information above, the Pribilofs (5), South Outer Shelf (4), and North Outer Shelf (8) emerge as the most favorable age-0 nursery habitats, regardless of temperature regime, based on high-energy prey communities and lower predation risk. Though arrowtooth flounder, salmon, and older pollock are present in these regions, arrowtooth flounder consume more pollock of ages 1-3 than age-0 (Zador *et al.,* 2011; Hunsicker *et al.,* 2013), and the deeper depths of the Outer Shelf allow pollock to vertically avoid salmon near the surface and arrowtooth flounder and older pollock near the bottom (Hollowed *et al.,* 2012). The Base simulation mean connectivity to the North Outer Shelf (8) was strong from all spawning regions in all years except from the Midnorth Middle Shelf (6) in warm years, with the greatest connectivity from retention. Mean connectivity to the South Outer Shelf (4) was strong or moderate from the AK Peninsula (1) and South Middle Shelf (3) spawning regions in all years. Mean connectivity to the Pribilofs (5) was always weak, most likely due to its small areal size. The greatest proportions of juveniles that were transported to the Pribilofs came from the AK Peninsula (1) and the South Middle Shelf (3) followed by retention within the region and was higher in warm years compared to cold. If the Pribilof habitat is best represented by a radius of 100 nmi, then it would contain parts of regions 3, 4, 6, 8, 15, and 16. Accordingly, some connectivity to these regions would be just as beneficial as to region 5, though it would depend on the final transport location being within 100 nmi of the center of the Pribilof habitat.

In cold years, the Middle Shelf (1, 3, 6) also hosted large populations of high energy prey, however none of these regions offer particularly favorable predation risk with herring, salmon, Pacific cod, and older pollock present. Though large zooplankton were less abundant and had reduced lipid stores in warm years, northern parts of the shelf (regions 9, 10, 11) had moderate amounts of prey energy density (Siddon *et al.,* 2013b) and euphausiids were prevalent in the diet of other fishes (Andrews *et al., accepted*). The North Inner Shelf (11) is too shallow to avoid the abundant capelin, which may be a predator on or prey competitor with age-0 pollock, and connectivity to this region was very weak. If there are refuges in regions 9 and 10 from herring, salmon, and older pollock, then the simulated increased connectivity to these regions in warm conditions may also be beneficial.

Unsurprisingly, the greatest connectivity to favorable juvenile nurseries stemmed from the historic spawning areas off of Unimak Island (1, 3) and the Pribilof Islands (5). Spawning adults in these vicinities could be protected if management goals are for increased production of juveniles to advantageous habitats. As climate projections forecast increasing temperatures (Wang *et al.,* 2012), the rather invariant Outer Shelf (4, 8; Siddon *et al.,* 2011; Eisner *et al.,* 2014) will become increasingly important for its high abundances of energy rich prey that are advected onto the shelf from the slope waters (Gibson *et al.,* 2013) and for its greater depths that allow vertical energy conservation and predator avoidance. Transport patterns and connectivity in warm years increased connectivity to the South Outer Shelf (4) from its dominant source regions the AK Peninsula (1) and South Middle Shelf (3) in these years. However, these connections were reduced if either spawning areas were expanded or spawning times were advanced under warm conditions. The reduced off-shelf transport in warm years decreased mean connectivity to the North Outer Shelf (8) from the historic spawning regions (1, 3, 5) in all warm simulations (Base, Expand, Early), which would place increased emphasis on spawning in all other regions with warmer water temperatures regardless of whether spawning locations and times remain the same, extend on-shelf, or advance.

In addition to the regional differences in feeding and predation conditions, juvenile survival rates may be the consequence of their origin or the specific transport route taken such that all juveniles that reach a particular habitat do not fare equally well. For example, individual condition and survival could be impacted by maternal condition at spawning (Solemdal, 1997; Berkeley *et al.,* 2004) or sublethal effects of temperature at the time and location of spawning (e.g. abnormal development; Blood, 2002). Additionally, juvenile size and condition will be affected by the temperatures and prey types and abundances encountered during transport.

Perspectives

There was strong connectivity to Off-Shelf North (15) from 2 of the 7 of the spawning areas in warm years and 6 of the 7 of the spawning areas in cold years of the Base simulations. Juvenile pollock surveys do not regularly include stations in this region and Off-shelf Southeast (16), and only a fraction of the North Outer Shelf (8) is sampled (south of 60°N). The overall retention rate in all 16 BEST-BSIERP regions ranged from 0.65 to 0.83 across the different simulations, with a retention rate of 0.73 of the total spawning in the Base simulation (Table 9). Juveniles in regions 8, 15, and 16 represented 0.34-0.51 of all the individuals spawned, which was greater than the proportion in the other 13 regions in all simulations except for Early spawning (Table 9). Acoustic surveys by the AFSC Midwater Assessment and Conservation Engineering Program have found a strong pollock acoustic signal all over the northern Outer Shelf (Honkalehto *et al.,* 2011). These observations in conjunction with the simulations suggest expansion of the early life and juvenile surveys into Outer Shelf and Slope regions of the EBS. Simulations such as the ones run in this study could be used to aid sampling plan design to include times and locations with large predicted patches of juveniles and other early life stages.

The EBS is not isolated from other sources of pollock, but is connected to the Gulf of Alaska by passes through the Aleutian Islands. A similar biophysical individual-based model of pollock in the Gulf of Alaska was used to assess connectivity of that stock. Spawning in the Gulf of Alaska resulted in high modeled densities of surviving age-0 pollock juveniles in potential nursery areas of the Bering Sea (C. Parada, pers. comm.). Mean connectivity from the eastern, central, and western Gulf of Alaska varied from 0.004-0.183 to the Inner and Middle Shelves combined and from 0.031-0.628 to the Outer Shelf and Basin combined (C. Parada, pers. comm.). Individuals were advected into the Bering Sea through Unimak pass and dominated by source regions in the western Gulf of Alaska (C. Parada, pers. comm.). Though this high potential connectivity may represent a substantial loss to the Gulf of Alaska, it is doubtful that transport of Gulf of Alaska pollock subsidizes the EBS stock if these juveniles survive and remain, given the fact that the Gulf of Alaska stock is an order of magnitude smaller than the EBS stock (Ianelli *et al*., 2012b). Some support for this idea is lent by one study that found that pollock early life stages were not a significant contribution to the larval fish species assemblage associated with Unimak Island during 2002-2008 (Siddon *et al.,* 2011). Flow through Unimak Pass was unidirectional in cold years and bidirectional in warm years of the study, suggesting that the increased density of early life stages of pollock near Unimak Island in warm years was the result of reverse direction flow from the EBS shelf population (Siddon *et al.,* 2011). Low mixing between the EBS and Gulf of Alaska stocks is additionally substantiated by morphological, demographic, and genetic differences (O'Reilly *et al.,* 2004; Grant *et al.,* 2010) that separate the two stocks. Yet genetics would not resolve any increased input of juveniles into the EBS from shifts in spawning into the western Gulf of Alaska post 1989 (Ciannelli *et al.,* 2007). As the realized connectivity from the Gulf of Alaska to the adult EBS population is unknown, it would be beneficial to validate the simulated potential connectivity, possibly with natural tags such as otolith microchemistry.

Conclusions

The three connectivity patterns of along-isobath flow to the northwest, self-retention, and transport around the Pribilof Islands were seen in most simulations. The major differences in connectivity between warm and cold years, more northwards in warm years and more off-shelf in cold years, mimicked wind-driven flow characteristics of those years (Danielson *et al.,* 2011b; Stabeno *et al.,* 2012) that were related to the winter mean zonal position of the Aleutian Low (Danielson *et al.,* 2014). Connectivity relationships were more sensitive to spatial alterations in the spawning areas in cold years, as seen with the Contracted case, while they were more responsive to spawn timing shifts in warm years, demonstrated with the Early simulation. Early spawning favored transport to the Inner Shelf and northern regions, whereas Late spawning increased retention in most regions and delivery to the South Outer Shelf (4), Pribilofs (5), Midnorth Middle Shelf (6) and Off-shelf Southeast (16). Contracted spawning increased connectivity in the off-shelf direction, while Expanded spawning facilitated retention within regions. Synthesis of juvenile pollock prey and predator studies promote the Pribilofs (5), South Outer Shelf (4), and North Outer Shelf (8) regions as very favorable juvenile habitats due to their high densities of energy rich prey and deeper water columns that allow for vertical separation from predators. The strongest connectivity to these regions originated in the well-known spawning areas within the AK Peninsula (1), South Middle Shelf (3), and Pribilofs (5), as well as in the North Outer Shelf (8). Surprisingly, the North Outer Shelf (8) emerged as a very large sink of pollock reaching the juvenile transition from all spawning sources, and requires more thorough sampling across multiple trophic levels since it may be a potentially important juvenile pollock nursery.

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TABLES

Table 1. Mean percent connectivity across all spawning times and years in the Base (“Transport Only”) simulation.

Sink	Source						
	1	3	4	5	6	8	16
1	8.66	7.69	0.51	0.72	0.25	0.10	0.53
2	0.74	0.94	0.10	1.16	1.13	0.08	0.06
3	20.50	20.08	1.74	6.65	4.65	0.82	1.72
4	10.79	9.89	1.95	2.68	2.02	0.63	2.13
5	2.47	2.44	0.73	1.69	1.18	0.47	0.86
6	10.96	9.95	6.09	20.73	24.12	7.67	5.60
7	0.38	0.46	0.10	1.30	1.99	0.10	0.05
8	16.60	18.71	30.97	27.73	23.32	37.45	31.87
9	3.19	3.64	3.05	12.89	26.06	5.97	2.42
10	0.40	0.48	0.53	1.28	3.01	1.18	0.51
11	0.10	0.16	0.04	0.57	1.08	0.07	0.02
12	0.03	0.10	0.38	0.13	0.14	0.49	0.38
13	0.02	0.07	0.28	0.07	0.06	0.34	0.30
14	0.00	0.00	0.00	0.00	0.01	0.01	0.00
15	9.38	9.12	16.73	10.59	5.67	13.48	15.90
16	5.08	4.55	2.74	1.04	0.18	1.12	3.64

Table 2. Local Index of Collocation comparisons of connectivity patterns between spawning times in the Base (“Transport Only”) simulation.

	15-Jan	1-Feb	15-Feb	1-Mar	15-Mar	1-Apr	15-Apr
15-Jan	1.00						
1-Feb	0.58	1.00					
15-Feb	0.58	0.98	1.00				
1-Mar	0.55	0.96	0.98	1.00			
15-Mar	0.54	0.95	0.97	0.99	1.00		
1-Apr	0.59	0.86	0.85	0.85	0.87	1.00	
15-Apr	0.61	0.84	0.84	0.84	0.86	0.99	1.00
Mean	0.58	0.86	0.87	0.86	0.87	0.84	0.83

Table 3. Local Index of Collocation comparisons between years in the Base ("Transport Only") simulation.

	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
1995	1.00																	
1996	0.70	1.00																
1997	0.74	0.92	1.00															
1998	0.67	0.67	0.66	1.00														
1999	0.85	0.85	0.85	0.78	1.00													
2000	0.77	0.91	0.92	0.79	0.87	1.00												
2001	0.78	0.70	0.65	0.72	0.89	0.65	1.00											
2002	0.78	0.89	0.92	0.71	0.90	0.94	0.66	1.00										
2003	0.68	0.96	0.91	0.58	0.79	0.86	0.65	0.84	1.00									
2004	0.73	0.89	0.97	0.71	0.87	0.95	0.66	0.94	0.87	1.00								
2005	0.62	0.82	0.86	0.50	0.68	0.86	0.45	0.84	0.83	0.87	1.00							
2006	0.77	0.69	0.63	0.64	0.90	0.66	0.95	0.69	0.64	0.65	0.48	1.00						
2007	0.66	0.42	0.35	0.43	0.66	0.43	0.76	0.46	0.38	0.37	0.29	0.87	1.00					
2008	0.74	0.53	0.49	0.65	0.78	0.60	0.83	0.59	0.49	0.53	0.42	0.88	0.90	1.00				
2009	0.64	0.81	0.91	0.70	0.80	0.84	0.62	0.83	0.82	0.90	0.77	0.58	0.29	0.47	1.00			
2010	0.85	0.57	0.55	0.61	0.74	0.59	0.85	0.57	0.60	0.56	0.50	0.82	0.75	0.82	0.51	1.00		
2011	0.67	0.90	0.88	0.77	0.88	0.92	0.73	0.90	0.85	0.92	0.81	0.73	0.48	0.69	0.84	0.61	1.00	
2012	0.87	0.65	0.59	0.72	0.83	0.64	0.93	0.62	0.61	0.58	0.43	0.90	0.83	0.87	0.52	0.90	0.65	1.00
Mean	0.74	0.76	0.75	0.67	0.82	0.78	0.73	0.77	0.73	0.76	0.65	0.73	0.55	0.66	0.70	0.67	0.78	0.71

Table 4. Mean percent retention rate of each spawning region grouped by year (all spawning times) in the Base simulation and by simulation (all spawning times and years).

Simulation	Time period	Region						
		1	3	4	5	6	8	16
Base all	1995	2.7	21.8	1.5	1.9	6.5	53.0	7.3
Base all	1996	11.3	14.9	1.9	2.9	24.7	46.5	4.3
Base all	1997	3.7	32.0	0.7	1.7	34.3	57.1	0.0
Base all	1998	18.5	23.7	12.7	4.2	50.8	41.1	16.7
Base all	1999	7.0	15.8	1.8	2.5	33.4	42.3	1.2
Base all	2000	12.0	36.3	8.0	2.9	23.5	55.2	11.5
Base all	2001	7.1	2.8	0.2	1.0	47.3	27.9	4.8
Base all	2002	7.0	40.6	2.1	2.2	19.6	52.9	0.8
Base all	2003	9.0	14.4	1.4	0.6	13.8	38.1	1.3
Base all	2004	5.4	41.0	0.5	2.5	34.9	44.2	0.2
Base all	2005	4.4	35.7	0.2	1.5	2.9	37.1	0.0
Base all	2006	4.9	4.4	0.3	1.1	31.3	30.9	0.1
Base all	2007	4.4	2.9	0.3	0.1	0.1	19.9	0.1
Base all	2008	17.6	12.1	0.4	0.7	10.0	17.6	0.7
Base all	2009	9.9	31.0	0.6	2.3	37.3	28.1	1.4
Base all	2010	6.1	3.9	0.2	0.1	11.0	16.6	0.0
Base all	2011	20.7	26.5	1.4	1.0	31.3	29.9	3.7
Base all	2012	4.0	1.4	1.0	1.3	21.5	35.6	11.3
Cold	Cold yrs	8.5	17.1	1.5	1.4	21.8	35.1	3.4
Contract	Cold yrs	4.5	7.9	1.5	1.7	--	32.4	4.4
Late	Cold yrs	13.3	16.4	2.3	3.0	34.5	36.0	7.2
Warm	Warm yrs	7.9	26.4	1.4	1.8	15.3	43.7	1.6
Expand	Warm yrs	10.3	32.6	1.7	2.7	14.2	44.2	1.6
Early	Warm yrs	8.8	31.9	1.1	1.2	17.5	33.8	0.9

Table 5. Local Index of Collocation comparisons of connectivity between simulations.

	Cold	Contract	Late	Warm	Expand	Early
Cold	1.00					
Contract	0.88	1.00				
Late	0.97	0.83	1.00			
Warm	0.86	0.76	0.81	1.00		
Expand	0.86	0.74	0.82	0.99	1.00	
Early	0.84	0.74	0.79	0.95	0.95	1.00

Table 6. Correlations between climate indices and the fraction of juveniles transported varying distances east from their spawning locations in the Base simulation. Correlations significant at the 0.05 level are in bold. NPIw: winter North Pacific Index, May SST: May Sea Surface Temperature, Cross: cross-shelf wind velocities, Along: along-shelf wind velocities.

	0°-5°E	5°-10°E	>10°E	>0°E
NPIw	-0.19	0.02	**0.55**	-0.17
MaySST	0.33	0.02	-0.11	0.30
Cross	-0.12	0.04	0.30	-0.10
Along	0.04	-0.16	-0.08	0.02

Table 7. Longitudinal transport of juveniles from spawning location presented as the fraction of the total in each simulation.

	>0°W	>10°W	5-10°W	<5°W	<5°E	5-10°E	>10°E	>0°E
Base all	0.87	0.11	0.34	0.41	0.12	0.007	2.7E-05	0.13
Cold	0.89	0.13	0.35	0.40	0.10	0.007	3.1E-05	0.11
Contract	0.92	0.15	0.38	0.38	0.07	0.005	3.0E-05	0.07
Late	0.85	0.08	0.30	0.47	0.13	0.007	2.1E-06	0.14
Warm	0.86	0.06	0.33	0.47	0.13	0.004	1.6E-05	0.14
Expand	0.82	0.05	0.29	0.48	0.17	0.006	1.4E-05	0.17
Early	0.79	0.06	0.28	0.45	0.19	0.010	5.6E-05	0.20

Table 8. Local Index of Collocation values of model-observation comparisons for individual years in the Base simulations and for all years in the alternate simulations.

	Oshoro Maru	BASIS surface trawl	BASIS acoustics
Base 1995	--	--	--
Base 1996	0.72	--	--
Base 1997	0.68	--	--
Base 1998	0.77	--	--
Base 1999	0.58	--	--
Base 2000	0.99	--	--
Base 2001	0.53	--	--
Base 2002	0.89	--	--
Base 2003	0.47	0.28	--
Base 2004	0.98	0.65	--
Base 2005	0.80	0.76	--
Base 2006	--	0.58	0.64
Base 2007	0.97	0.02	0.43
Base 2008	--	0.67	0.74
Base 2009	--	0.31	0.44
Base 2010	--	0.29	0.91
Base 2011	--	0.48	0.89
Base 2012	--	0.21	0.61
Base Mean	0.76	0.42	0.67
Cold	0.81	0.37	0.67
Contract	0.70	0.31	0.60
Late	0.65	0.37	0.68
Warm	0.72	0.52	--
Expand	0.78	0.56	--
Early	0.82	0.58	--

Table 9. Mean percent retention of all individuals spawned in the eastern Bering Sea by BEST-BSIERP juvenile region and simulation.

	All regions	Regions 1-7, 9-14	Regions 8, 15, 16
Base all	73.3	26.1	47.2
Cold	70.3	22.8	47.5
Contract	64.8	16.8	48.0
Late	77.4	26.0	51.4
Warm	80.5	34.2	46.3
Expand	83.3	40.8	42.5
Early	74.3	40.4	33.9

FIGURE CAPTIONS

Figure 1. (Large panel) Map of the Eastern Bering Sea with bathymetry (50, 100, and 200-m isobaths) and major currents shown in black and the BEST-BSIERP regions in blue. ACC: Alaska Coastal Current, BSC: Bering Slope Current, 1: AK Peninsula, 2: South Inner Shelf, 3: South Middle Shelf, 4: South Outer Shelf, 5: Pribilofs, 6: Midnorth Middle Shelf, 7: Midnorth Inner Shelf, 8: North Outer Shelf, 9: St. Matthews, 10: North Middle Shelf, 11: North Inner Shelf, 12: St. Lawrence, 13: South Bering Strait, 14: Norton Sound, 15: Off-shelf North, 16: Off-shelf Southeast. (Small subpanels) Spawning initial locations released on the dates shown. Light grey: Contracted simulation, dark grey: Base, Late, Early simulations, black: Expanded simulation. Polygons are overlapping and all share the same western and southern boundaries.

Figure 2. Mean connectivity matrices by spawning time in the Base simulation. Connectivity is presented as the fraction of individuals in a given region when reaching 40 mm length (columns) from a given spawning region (rows).

Figure 3. Mean connectivity in the Base simulation from the spawning regions AK Peninsula (A), South Middle Shelf (B), South Outer Shelf (C), Pribilofs (D), Midnorth Middle Shelf (E), North Outer Shelf (F), and Off-shelf Southeast (G) with Cold (blue) and Warm (red) years shown separately. Line thickness indicates the strength of connection; thick: strong connection >0.10, thin: moderate connection 0.05-0.10. Not pictured: weak connection <0.05.

Figure 4. Mean connectivity matrices of the different simulations. The Base simulation is grouped by warm and cold years. Connectivity is presented as the fraction of individuals in a given region when reaching 40 mm length (columns) from a given spawning region (rows).

Figure 5. Fraction of individuals advected <5°, 5°–10°, or >10° longitude to the east by year in the Base simulation. Note differences in y-axis scales.

Figure 6. Fractions of 2007 observed T/S *Oshoro Maru* (top), BASIS surface trawl (middle), and BASIS water column acoustics (bottom) age-0 abundance and the fraction of modeled juveniles in the observed regions of each data type. Unsampled regions are white and zero abundance is marked with an X.

Figure 7. Model-*Oshoro Maru* differences for the Base simulation, represented as the fraction simulated in the observed regions only minus the fraction observed. Unsampled regions are in grey.

Figure 8. Model-BASIS surface trawl differences for the Base simulation, represented as the fraction simulated in the observed regions only minus the fraction observed. Unsampled regions are in grey.

Figure 9. Model-BASIS acoustics differences for the Base simulation, represented as the fraction simulated in the observed regions only minus the fraction observed. Unsampled regions are in grey.