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Authors: Parker-Stetter, Sandra L., Horne, John K., and Urmey, Samuel S.

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ARTICLE

Vertical Distribution of Age-0 Walleye Pollock during Late Summer: Environment or Ontogeny?

Sandra L. Parker-Stetter,*¹ John K. Horne, and Samuel S. Urmy²

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195-5020, USA

Ron A. Heintz

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

Lisa B. Eisner

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, Washington 98115, USA

Edward V. Farley

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

Abstract

Variability in the late-summer vertical distribution of age-0 Walleye Pollock *Gadus chalcogrammus* in the southeastern Bering Sea has been attributed to a range of physical and biological factors. Using acoustic data (38 and 120 kHz) collected during the 2010 Bering Aleutian Salmon International Survey (BASIS) and dedicated high-resolution surveys (HR1 and HR2), we evaluated whether late-summer distributions could be explained by water column properties (environment) or whether sampling was likely occurring during the ontogenetic shift of age-0 Walleye Pollock from near-surface habitat to demersal habitat (ontogeny). Neither water column attributes (temperature, relative temperature, salinity, dissolved oxygen, and density gradient) nor the acoustic density of zooplankton prey strongly predicted the acoustic estimates of age-0 Walleye Pollock vertical presence or density. At 6 of 10 paired BASIS–HR1 stations, age-0 Walleye Pollock shifted deeper in the water column between BASIS sampling and the HR1 sampling conducted 8–34 d later. There were no consistent differences in FL ($P > 0.05$ for 2 of 4 station pairs) or energy density ($P > 0.05$ for 3 station pairs) between age-0 Walleye Pollock caught in near-surface trawls and those caught in midwater trawls. Our data suggest that the observation of both near-surface and midwater age-0 Walleye Pollock during late summer is likely due to an ontogenetic habitat shift; however, the causative factor was not clear given the limited sample sizes and explanatory variables. The timing of the ontogenetic shift, which appears to have begun before August 18, 2010, can ultimately affect survey strategies, and knowledge of this timing can provide additional insight into factors affecting the overwinter survival of age-0 Walleye Pollock.

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*Corresponding author: sandy.parker-stetter@noaa.gov

¹Present address: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Fisheries Resource Assessment and Monitoring Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA.

²Present address: School of Marine and Atmospheric Sciences, Stony Brook University, 239 Montauk Highway, Southampton, New York 11968, USA.

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In the eastern Bering Sea (EBS), Walleye Pollock *Gadus chalcogrammus* have been identified in different portions of the water column during their first year of life. In the spring and early summer, age-0 Walleye Pollock are typically found near the thermocline (~20-m depth) and/or in the upper portion of the water column (≤ 50 -m depth; Smart et al. 2013) during the day. By early summer of the following year (i.e., at age 1), they have completed their ontogenetic transition into deeper water and are found in midwater and semi-demersal habitats (Honkalehto et al. 2010; Lauth 2010). The location of age-0 Walleye Pollock within the water column between those two time periods has not been well documented. Sampling with a surface trawl during summer through early fall has caught age-0 Walleye Pollock near and above the thermocline (Moss et al. 2009), but acoustics and midwater trawling have also observed and caught age-0 Walleye Pollock deeper in the water column (> 75 -m depth) during that same time of year (Bailey 1989; Parker-Stetter et al. 2013). The observed variability in late-summer vertical distribution can ultimately influence the design and accuracy of surveys that are used to estimate the abundance and distribution of this commercially valuable species.

Studies in the EBS have suggested a variety of physical and biological explanations for the vertical distribution of age-0 Walleye Pollock. Environmental factors have included thermal preference (Tang et al. 1996; Swartzman et al. 1999), water column stratification (Francis and Bailey 1983), light levels (Olla and Davis 1990), and high potential growth at a given location (Ciannelli et al. 2002). Conversely, fish length (Bailey 1989; Miyake et al. 1996; Swartzman et al. 2002), food availability and prey size (Olla and Davis 1990; Schabetsberger et al. 2003), and cannibalism (Bailey 1989) have been suggested as biological explanations for the observed differences in age-0 Walleye Pollock vertical distribution. Combining physical and biological explanations, laboratory experiments have suggested that age-0 Walleye Pollock migrate to temperatures that benefit their energetic status, with food-deprived juveniles being found in colder water than fish with higher rations (Sogard and Olla 1996).

An alternative explanation for the distribution of age-0 Walleye Pollock in both near-surface and midwater regions is that late-summer surveys are sampling during the age-0 fish's ontogenetic transition from near-surface to semi-demersal habitats. In the Gulf of Alaska, Brodeur and Wilson (1996) observed that the mean depth of capture for age-0 Walleye Pollock generally increased from July–August to October. Although it is known that age-0 Walleye Pollock shift from near-surface to demersal habitats within their first year in the EBS, the timing and causative factors are unclear.

We evaluated factors potentially influencing the late-summer vertical distribution of age-0 Walleye Pollock from two complementary perspectives: environmental conditions and ontogenetic transition. We predicted that if late-summer

surveys are characterizing the distribution and abundance of age-0 Walleye Pollock before they undergo the ontogenetic transition to deeper water, then the variability in age-0 vertical distribution will be related to water column properties and/or the vertical distribution of potential zooplankton prey. We also predicted that if late-summer observations of age-0 Walleye Pollock coincide with an ontogenetic transition to deeper water, then (1) age-0 vertical distributions and aggregation attributes (school size and relative density) will change between observations at the same location separated in time and (2) surface- and midwater-caught fish will differ in FL, energy density, or both.

METHODS

Survey Area and Design

The Bering Aleutian Salmon International Survey (BASIS; see Farley et al. 2009) was conducted in the EBS on the National Oceanic and Atmospheric Administration (NOAA) FSV *Oscar Dyson* between August 18 and September 16, 2010 (Parker-Stetter et al. 2013). Immediately after BASIS, high-resolution (HR) surveys (HR1 and HR2) were conducted during September 17–25, 2010. Operations occurred during daytime from 1 h after sunrise to 1 h before sunset.

The HR study area was selected to encompass a region where age-0 Walleye Pollock were observed at a range of locations within the water column during the preceding BASIS, with the goal of resurveying acoustic transects and reoccupying a subset of BASIS stations in that area. The study area was bounded by 54°45'N in the south, 57°00'N in the north, 167°00'W in the west, and 166°00'W in the east (Figure 1). Bottom depth contours in the surveyed area ranged between 75 and 350 m.

For the HR surveys, north–south acoustic transects were spaced 00°30' apart (29.6–31.5 km at survey latitudes), with a shorter transect occurring on 166°30'W due to weather (Figure 1). The HR transects were surveyed between September 17 and September 24 (HR1), and the 167°00'W transect was acoustically surveyed a second time on September 25, 2010 (HR2; Table 1; Figure 1). Sections of the 167°00'W and 166°00'W transects were surveyed during BASIS between August 18 and September 9, 2010 (Table 1).

Oceanographic data were collected at all HR1 stations at a spacing of 00°15'. At reoccupied BASIS stations, a surface trawl was always performed, and a pycnocline or midwater trawl was also conducted if targets were observed below the surface trawl fishing depth. At all other stations, surface and midwater trawls were both conducted if targets were observed on the echosounder (Figure 1).

Data Collection and Processing

Conductivity–temperature–depth unit deployment and processing.—Oceanographic data were collected using a Sea-Bird Model 911plus conductivity–temperature–depth (CTD)

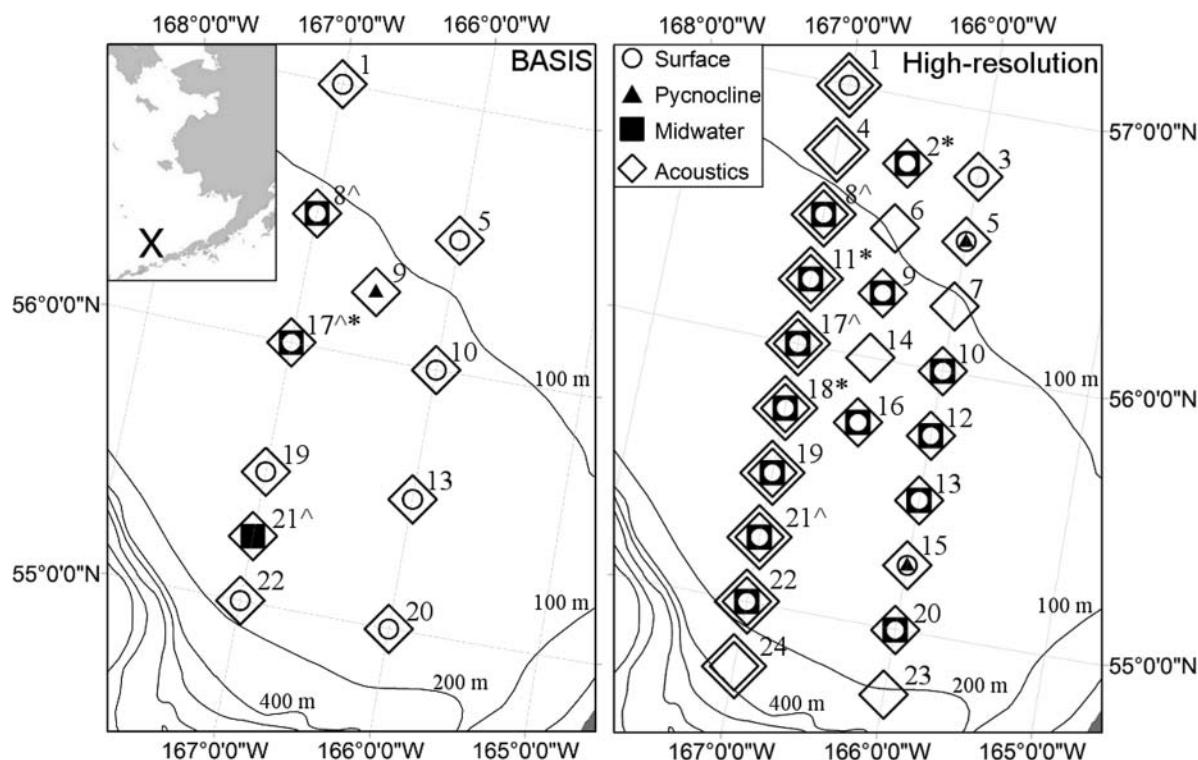


FIGURE 1. Acoustic data and trawl (surface, pycnocline, and midwater) locations used during the 2010 Bering Aleutian Salmon International Survey (BASIS; left, sampled August 18–September 9) and the 2010 high-resolution (HR1 and HR2) surveys (right, sampled September 17–25). Station numbers are referred to throughout the text. Inset shows the study area's location in the Bering Sea. The double-diamond symbol indicates sampling during HR1 and HR2; an asterisk denotes a surface–midwater comparison; and the “^” symbol denotes a BASIS–HR comparison with sufficient samples to be included in analyses.

unit (Sea-Bird Electronics, Bellevue, Washington). Casts were made from the surface to 5–10 m from the bottom. Downcast data were error-checked and averaged into 1-m vertical bins.

The Rossby radius of deformation (L_R) was used to estimate the horizontal distance from each CTD cast location at which water properties were assumed homogeneous (cf. Aletius et al. 2003). The two-layer L_R (Rossby 1938; Gill 1982) was calculated for each CTD cast station as

$$L_R = \sqrt{g'D/f}, \quad (1)$$

where D is the depth (m) of the upper layer, f is the Coriolis parameter (per second), and g' is the reduced gravity, given by

$$g' = \frac{g(\rho_2 - \rho_1)}{\bar{\rho}}, \quad (2)$$

where g is the acceleration due to gravity (m/s^2), ρ_1 and ρ_2 are the mean densities (kg/m^3) in the upper and lower layers, and $\bar{\rho}$ is the mean density (kg/m^3) over the whole water column.

Trawling.—A Cantrawl 400/601 rope trawl (25–30-m vertical opening; 1.2-cm-mesh liner in the cod end) equipped with 5-m alloy trawl doors (NET Systems, Bainbridge Island,

Washington) was used to identify targets observed on the echosounder and to collect specimens. For surface trawls, the headrope was equipped with floats, and the net's position at the surface was maintained by minor adjustments in the length of wire out. In limited instances when high backscatter from age-0 Walleye Pollock was observed near or immediately below the footrope of the surface trawl, the net was deployed without floats to headrope depths of 12–30 m in a pycnocline set (Parker-Stetter et al. 2013). For midwater trawls, the floats were removed and a Simrad FS-70 trawl sonar (Kongsberg Maritime, Horten, Norway) was used to monitor net depth and fish catch in real time (Parker-Stetter et al. 2013).

At all BASIS stations and at the reoccupied BASIS stations during HR sampling, surface trawl sets lasted 30 min. At other surface trawl stations during HR sampling, the sets lasted 15 or 30 min depending on the apparent target density indicated by the acoustics. Trawls within the pycnocline lasted 7–15 min depending on the target density shown by the FS-70 sonar. Surface and pycnocline samples were kept separate throughout our analyses. Midwater trawls (headrope depths = 50–95 m) lasted for 4–19 min depending on the target density observed using the echosounder and the FS-70 sensor during the set. For comparison, all catches were standardized to catch per 30 min of effort (number of fish/30-min trawl).

TABLE 1. Station numbers (see Figures 1 and 2), sampling dates (number of days since previous sampling is shown in parentheses), and sample type (A = acoustic; T = trawl) for the Bering Aleutian Salmon International Survey (BASIS) and the high-resolution surveys (HR1 and HR2) conducted in 2010.

Station	Bottom depth (m)	BASIS			HR1			HR2		
		Date	A	T	Date	A	T	Date	A	T
1	75	Sep 9	×	×	Sep 17 (8 d)	×	×	Sep 25 (8 d)	×	
2	80				Sep 23	×	×			
3	80				Sep 23	×	×			
4	90				Sep 17	×				
5	90	Sep 1	×	×	Sep 23 (22 d)	×	×			
6	100				Sep 22	×				
7	100				Sep 22	×				
8	105		×	×	Sep 17 (8 d)	×	×	Sep 25 (8 d)		×
9	110	Sep 1	×	×	Sep 24 (23 d)	×	×			
10	115	Aug 19	×	×	Sep 22 (34 d)	×	×			
11	120				Sep 18	×	×	Sep 25 (7 d)		×
12	120				Sep 22	×	×			
13	120		×	×	Sep 21 (34 d)	×	×			
14	125	Aug 18			Sep 24	×				
15	125				Sep 21	×	×			
16	130				Sep 24	×	×			
17	135		×	×	Sep 18 (17 d)	×	×			
18	135	Sep 1			Sep 18	×	×	Sep 25 (7 d)		×
19	135		×	×	Sep 19 (11 d)	×	×	Sep 25 (6 d)		×
20	135		×	×	Sep 21 (34 d)	×	×	Sep 25 (6 d)		×
21	145		×	×	Sep 19 (11 d)	×	×			
22	160	Sep 8	×	×	Sep 20 (12 d)	×	×			
23	195				Sep 20	×		Sep 25 (5 d)		×
24	350				Sep 20	×				

Trawl catches were sorted to species, weighed, and processed for biological information. Catches less than 1 metric ton were processed in their entirety. For catches greater than 1 metric ton, the entire catch was weighed, and a subsample of approximately 1 metric ton was randomly selected by splitting the catch. Measurements of FL (nearest mm) were taken on at least 50 individuals from each species. Up to 20 age-0 Walleye Pollock from a trawl were individually wrapped and flash-frozen for analysis of energy density (kg/J wet weight) via the method of Heintz et al. (2013).

Acoustic data collection.—Acoustic data were collected at five frequencies (18, 38, 70, 120, and 200 kHz) using a Simrad EK-60 echosounder. The 38-kHz (ES38-B; 2,000 W) and 120-kHz (ES120-7C; 500 W) data were used in this analysis. Transducers were mounted on a centerboard that was lowered to 9.15 m below the surface during the survey. Ship speed was 5.1–6.2 m/s (10–12 knots), and data were collected using a 1.024-ms pulse duration at a maximum rate of 1 pulse/s. All frequencies were calibrated prior to the survey using standard-sphere methods (Foote et al. 1987).

Acoustic data processing.—On-transect acoustic data were processed in Echoview version 5.10 (Echoview Pty Ltd, Hobart,

Australia). A sound speed of 1,470 m/s and absorption coefficients of 0.00998 dB/m (at 38 kHz) and 0.029057 dB/m (at 120 kHz) were used during processing. Noise spikes and dropped pings were removed from all files. Vessel noise was removed via linear subtraction (Watkins and Brierley 1996; Korneliussen 2000), and a 10-dB signal-to-noise ratio filter was used during processing. The bottom was detected in Echoview, inspected, and manually corrected as needed. To account for transducer depth (9.15 m) and twice the near-field range of the 38-kHz unit, data from within 15 m of the surface were excluded from the analysis. Data from within 0.5 m of the bottom were also excluded.

Age-0 Walleye Pollock aggregation acoustics.—As a pre-processing step for aggregation detection, a 3-sample \times 3-ping Gaussian blur convolution was calculated using the 38-kHz native resolution (0.18 m vertical \times 1 ping horizontal) data (Reid and Simmonds 1993). Aggregations were detected on the blurred data by using the Echoview SHAPES algorithm (Barange 1994) with aggregation detection parameter settings as follows: a minimum total/candidate school length of 0.2 m; a minimum total/candidate school height of 0.2 m; a maximum vertical linking distance of 2.0 m; a maximum horizontal

linking distance of 15.0 m; and a minimum volume backscattering strength (S_v) threshold of -60.9 dB re 1 m^{-1} . The 15.0-m maximum horizontal linking distance was selected based on the maximum distance covered by the vessel during a single pulse transmission. The -60.9 dB minimum S_v threshold represents the lower 1 SD of verified S_v sample data for age-0 Walleye Pollock (Parker-Stetter et al. 2013) and was used to conservatively delineate the outer edges of all aggregations. Aggregations were then exported from the 38-kHz native resolution data by using a minimum S_v threshold of -67 dB (Parker-Stetter et al. 2013). Aggregations that had an edge within 0.5 m of the bottom or surface exclusion lines were removed from the analysis, as their geometry may have been incorrect due to overlap with the surface or bottom exclusion zones.

Three attributes of aggregations were exported from the acoustic data files: aggregation length (horizontal; m), aggregation thickness (vertical; m), and mean S_v (hereafter, " S_v acoustic density"; a logarithmic measure in dB). Uncorrected descriptors of aggregation geometry were used in analyses because many aggregations were too small relative to the beam width for accurate geometric correction (cf. Diner 2001). To account for potential overestimation or underestimation of aggregation length due to beam width, we calculated a minimum aggregation length ($\text{length} - 0.5 \cdot [3\text{-dB beam width}]$) and a maximum aggregation length ($\text{length} + 0.5 \cdot [3\text{-dB beam width}]$).

Along-transect age-0 Walleye Pollock aggregation data were integrated within 1-m vertical \times 6-ping horizontal bins. Vertical bin size was selected to match the CTD data's 1-m vertical resolution. The 6-ping horizontal bin size corresponded to the 90th percentile for the number of pulses within an aggregation; this was selected in an effort to maximize the number of aggregations that would be contained within a single bin rather than be split across bins. Areas around aggregations were assigned 999 dB (a value ≈ 0 in the linear domain) for integration.

Zooplankton acoustics.—Because specific algorithms to categorize EBS copepods are lacking, zooplankton (i.e., copepods and euphausiids) were identified following the methods of Murase et al. (2009). The 38- and 120-kHz data were resampled into 1-m vertical \times 3-ping horizontal bins; any sample (0.18 m vertical \times 1 ping horizontal) containing an age-0 Walleye Pollock aggregation was excluded from the resample calculation as "no data." Using a -90 dB S_v threshold, a frequency difference (120 kHz–38 kHz) value was generated for each resampled bin (Murase et al. 2009). Bins containing zooplankton were identified using a frequency difference range of 7.1–22.0 dB (Murase et al. 2009). This frequency difference range also encompasses the frequency difference (120 kHz–38 kHz) values for euphausiids (10.9–16.7 dB; De Robertis et al. 2010). Methods used to determine the frequency difference range in the Murase et al. (2009) study were based on the copepod species *Neocalanus*

cristatus, which is larger than the *Calanus* spp. copepods that are typically consumed by age-0 Walleye Pollock during cold years (Coyle et al. 2011) in the Bering Sea. As our analysis was based on the relative vertical distribution of zooplankton rather than absolute abundance, any potential underestimates of *Calanus* spp. caused by using the frequency difference range from Murase et al. (2009) should be consistent within the water column and should not affect our results.

Along-transect zooplankton S_v acoustic density was exported from the 120-kHz data in 1-m vertical \times 6-ping horizontal bins by using a -90 dB data threshold (Murase et al. 2009). In empty bins (i.e., those that had been entirely filled with an age-0 Walleye Pollock aggregation), we assumed that zooplankton backscatter in surrounding bins was representative of what would be found in the empty 1-m \times 6-ping bin, and we filled those cells with the mean zooplankton S_v acoustic density from the surrounding eight cells (i.e., an 18-ping \times 3-m window).

Environment: Water Column Properties and Vertical Distribution of Age-0 Walleye Pollock

The HR1 data set was used to evaluate whether the vertical distribution of age-0 Walleye Pollock was related to environmental factors as it was more synoptically collected (sampling area $\approx 7,500 \text{ km}^2$; time = 8 d) than the EBS-wide BASIS data (Parker-Stetter et al. 2013). We used CTD cast data and zooplankton acoustic data to represent the vertical distribution of factors that might influence age-0 Walleye Pollock use of the water column as habitat.

Acoustic integration data for age-0 Walleye Pollock and zooplankton (1 m vertical \times 6 ping horizontal) within the L_R of an HR1 CTD cast were associated with that cast for the analysis. All 24 HR1 stations were used in this analysis. Because most environmental variables were only available as one-dimensional vertical profiles from CTD casts, acoustic age-0 Walleye Pollock and zooplankton integration bins within each L_R were averaged into 1-m depth intervals, thereby reducing the two-dimensional acoustic echo integration data to a one-dimensional profile with the same vertical resolution as the CTD cast. Each depth interval at each station was then treated as a data point in the analysis.

Age-0 Walleye Pollock backscatter was patchy and included many empty cells, even after averaging into one-dimensional profiles. Because these data were zero-inflated, we represented the probability of Walleye Pollock occurrence and the expected Walleye Pollock acoustic density (using logarithmic S_v acoustic density, conditional on occurrence) as separate processes in a two-part model (Stefánsson 1996; Hollowed et al. 2012). The probability of occurrence was modeled using a generalized linear model (GLM) with a logit link function and a binomial error structure; acoustic density was modeled using an identity-link GLM with a Gaussian error structure (i.e., ordinary linear regression).

We used an information-theoretic approach (Burnham and Anderson 2002) to compare the ability of seven environmental variables (hypotheses) to explain the vertical distribution of age-0 Walleye Pollock. Variables were selected to reflect common ideas in the literature as well as our own hypotheses; the variables included depth from the surface (Depth; m), vertical density gradient (Stratification; kg/m^3), water temperature (Temp; $^{\circ}\text{C}$), relative water temperature (RelTemp; unitless), dissolved oxygen (Oxygen; mg/L), salinity (Salinity; unitless), and zooplankton S_v acoustic density (ZoopS $_v$; dB) within the 1-m vertical bins. Relative temperature at a given depth was calculated by remapping the measured temperatures on a scale of zero to 1.0 (minimum to maximum). A second set of models was run using the same variables but with the inclusion of an autoregressive component, as all previous model runs had autocorrelated residuals. This autoregressive component (AdjPollock), used as a measure of age-0 Walleye Pollock aggregating behavior, was calculated for each depth interval as the average of Walleye Pollock S_v acoustic density in adjacent bins above and below each depth interval. This approach is equivalent to a first-order conditional autoregressive spatial model (Cressie and Wikle 2011).

Support for each variable or hypothesis was evaluated based on Akaike weight (w_i), an estimate of the probability that the hypothesis would be selected as the best if the analysis was repeated on a new data set (Whittingham et al. 2006). Both occurrence (binary: 0, 1) and density (numeric: S_v acoustic density) models were fitted for each hypothesis by using the glm function in R software (R Development Core Team 2013). To assess goodness of fit, we also calculated an R^2 value for each model fit. For the binomial occurrence models, R^2 values based on the residual sum of squares could not be calculated, so we calculated pseudo- R^2 values (McFadden 1974) based on the likelihood ratio of the fitted and null models (Table 2, analysis A).

We also conducted a post hoc analysis of all possible combinations of the seven variables, again by using w_i to identify the combinations of variables that were best supported by the data. The exhaustive models were run for occurrence and density, both excluding and including the autoregressive component AdjPollock. Hypotheses within the 90% confidence set, which represents the probability that the best-approximating model occurred within that set of models (Johnson and Omland 2004), are presented (Table 2, analysis B).

Ontogeny: Changes in Vertical Distribution and Aggregations over Time

In evaluating whether age-0 Walleye Pollock vertical distribution was related to ontogeny, we considered both space (i.e., sampling location) and time (i.e., sampling date) because our analyses could not decouple the two. Given the bathymetric gradient at the site, bottom depth was used to represent station

location. To represent time, sampling dates were converted to day of year.

Trawl distribution.—Trawling was conducted at 18 HR1 stations, with 18 surface trawls, 2 pycnocline trawls, and 14 midwater trawls (Figure 1; Table 1). Eleven of the HR1 stations were BASIS stations that were reoccupied between 8 and 34 d later. During BASIS, nine surface trawls, one pycnocline trawl, and three midwater trawls were conducted.

Trawl efficiency for the Cantrawl is unknown (Parker-Stetter et al. 2013); therefore, catches of age-0 Walleye Pollock were categorized in order-of-magnitude bins for comparison: ≤ 3 (0–3 fish), ≤ 30 (4–30 fish), ≤ 300 (31–300 fish), $\leq 3,000$ (301–3,000 fish), $\leq 30,000$ (3,001–30,000 fish), and $\leq 300,000$ fish/30-min trawl. These bins were used to compare trawls (surface and/or midwater) conducted at the same location during both BASIS and the HR1 survey (Table 2, analysis C).

Aggregation attributes.—Mean aggregation length, thickness, and S_v acoustic density were used to describe potential changes in the size or density of age-0 Walleye Pollock aggregations between BASIS, HR1, and/or HR2. Attributes were summarized using all aggregations within the L_R of each station. The SDs were calculated for aggregation thickness and S_v acoustic density. Given the potential effects of acoustic beam width on estimates of aggregation length, we present mean length with ± 0.5 -beam width instead of SD. In subsequent statistical analysis, minimum aggregation length is used rather than mean length to avoid potential beam width biases.

We evaluated whether aggregation attributes for a given station during BASIS, HR1, and/or HR2 were different at subsequent reoccupations of that station by using either the Dunnett-modified Tukey–Kramer test (DTK test; Dunnett 1980) or the Welch two-sample t -test (Welch test; Welch 1947). The DTK test, which corrects for multiple comparisons, was used for stations with data available from BASIS, HR1, and HR2. The Welch test was used for stations with only HR1 and BASIS data or those with only HR1 and HR2 data (Table 2, analysis D). Neither test assumes equal sample sizes or equal variances (Dunnett 1980; Ruxton 2006). For the DTK test and the Welch test, we evaluated whether the 95% confidence interval included zero as a measure of potential differences at $P < 0.05$. We acknowledge that biological significance must be evaluated using additional background information, such as theory and plausibility (Goodman 1999; Lew 2012); therefore, we use the phrase “potential significance” in reporting our results. The DTK test and Welch test methods are referenced in additional comparisons described below.

Metrics of age-0 Walleye Pollock vertical distribution.—Summary metrics were used to describe the vertical distribution of age-0 Walleye Pollock aggregations (Woillez et al. 2007; Urmy et al. 2012) during BASIS, HR1, and/or HR2. The center of acoustic mass (a measure of weighted mean depth) and the S_v acoustic density (a measure of water column density) were calculated from the 6-ping \times 1-m integration data following Urmy et al. (2012). We calculated the mean

TABLE 2. Summary of analyses used to evaluate the potential effects of environment or ontogeny on the vertical distribution of age-0 Walleye Pollock (BASIS = 2010 Bering Aleutian Salmon International Survey; HR1 and HR2 = 2010 high-resolution surveys; Depth = depth from the surface, m; Stratification = vertical density gradient, kg/m³; Temp = water temperature, °C; RelTemp = relative water temperature, unitless; Oxygen = dissolved oxygen concentration, mg/L; Salinity = salinity, unitless; ZoopS_v = zooplankton S_v, acoustic density, dB; AdjPollock = autoregressive component [see Methods]; GLM = generalized linear model).

Analysis	Data set(s)	Data type	Key characteristics	y-variable(s)	x-variable(s)	Test	Figure or table
Environment: was age-0 Walleye Pollock vertical distribution related to environmental conditions?							
A	HR1	S _v , acoustic density	24 stations	1. Occurrence 2. Density	Depth, Stratification, GLM, Akaike Temp, RelTemp, weights, R ² , or pseudo-R ² Oxygen, Salinity, and ZoopS _v (with and without AdjPollock)		Table 2
B	HR1	As above	As above	As above	As above	Post hoc all-subsets and Akaike weights	Table 3
C	BASIS, HR1	Trawl data	9 BASIS–HR1 surface pairs; 3 BASIS–HR1 midwater pairs	Fish/30-min trawl		None	Figure 2
Ontogeny: did age-0 Walleye Pollock trawl catch change over time?							
Ontogeny: did age-0 Walleye Pollock aggregation attributes change over time?							
D	BASIS, HR1, HR2	Acoustic attributes of aggregations	10 BASIS–HR1 station pairs; 10 HR1–HR2 pairs	1. Mean aggregation length 2. Mean aggregation thickness 3. S _v acoustic density		Dunnnett-modified Tukey–Kramer test (DTK test) or Welch's two-sample <i>t</i> -test (Welch test)	Figure 4, Table 4
E	BASIS, HR1, HR2	Acoustic metrics of vertical distribution	10 BASIS–HR1 station pairs; 10 HR1–HR2 pairs	1. Center of acoustic mass 2. S _v acoustic density		DTK test or Welch test	Figure 5
Ontogeny: did age-0 Walleye Pollock vertical distribution change over time?							

(Continued on next page)

TABLE 2. Continued.

Analysis	Data set(s)	Data type	Key characteristics	y-variable(s)	x-variable(s)	Test	Figure or table
F	HR1	Trawl data	Ontogeny: were there spatial differences in age-0 Walleye Pollock fork length or energy density? 8 surface; 14 midwater	FL	Bottom depth	GLM	Figure 6
G	HR1	Trawl data	4 surface; 11 midwater	Energy density	Bottom depth	GLM	Figure 6
H	BASIS, HR1	Trawl data	Ontogeny: was age-0 Walleye Pollock fork length or energy density different in surface versus midwater trawls? 1 BASIS surface– midwater pair; 3 HR1 surface– midwater pairs	FL		Welch test	Figure 6
I	BASIS, HR1	Trawl data	1 BASIS surface– midwater pair; 2 HR1 surface– midwater pairs	Energy density		Welch test	Figure 6
J	BASIS, HR1	Trawl data	Ontogeny: did age-0 Walleye Pollock fork length or energy density change over time? 3 BASIS–HR1 midwater pairs	1. FL 2. Energy density		Welch test	Figure 6

and SD of the center of mass and S_v acoustic density for bins within the L_R of each station. Comparisons of metric values for a given station sampled during BASIS, HR1, and/or HR2 were made using either the DTK test or the Welch test (Table 2, analysis E).

Ontogeny: Fork Length and Energy Density of Age-0 Walleye Pollock

Surface versus midwater.—The mean and SD of age-0 Walleye Pollock FL and energy density were calculated for all surface, pycnocline, and midwater trawls conducted during BASIS and the HR1 survey. For these analyses, data are presented for individual stations, arranged by increasing bottom depth.

To examine potential spatial differences in Walleye Pollock FL and energy density within the HR1 data, GLMs were used to evaluate relationships between fish FL or energy density at the surface and/or midwater and bottom depth for HR1 (Table 2, analyses F and G).

At stations where age-0 Walleye Pollock were caught both at the surface and midwater, we evaluated whether the FL and energy density of fish caught in surface trawls differed from those of fish caught in midwater trawls. Four stations (one from BASIS; three from HR1) were available for evaluating FL, and three stations (one from BASIS; two from HR1) were available for evaluating energy density, as surface and midwater trawls both caught over 10 fish. A Welch test was conducted to evaluate whether mean FL or energy density differed between surface and midwater trawl samples obtained at the same station (Table 2, analyses H and I).

Changes in fork length or energy density over time.—Data for this analysis came from three stations at which midwater trawls were performed during both BASIS and HR1 surveys. The limited number of comparisons resulted from the high number of HR1 surface trawls with a catch of 0 fish/30-min trawl. Mean FL and energy density of age-0 Walleye Pollock were calculated for trawls at all paired BASIS–HR1 stations and were plotted against day of year. For the three stations at which midwater trawls were conducted during both BASIS and the HR1 survey, we performed a Welch test to compare the FL or energy density of midwater-caught age-0 Walleye Pollock between the surveys (Table 2, analysis J).

RESULTS

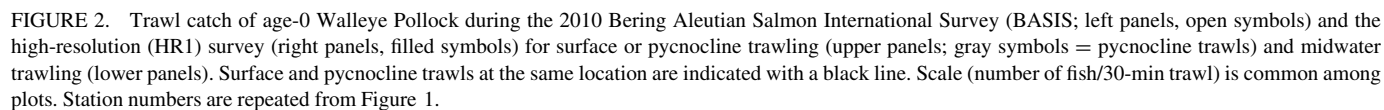
General Results

Trawling.—Trawling was conducted at 11 previously sampled BASIS stations that were reoccupied during the HR surveys (Figure 1; Table 1). The BASIS surface trawl catches ($n = 9$ trawls; Figure 2) ranged from 0 to 6,558 fish/30-min trawl, with a mean of 1,256 fish/30-min trawl. Age-0 Walleye Pollock (40–94 mm FL) were caught in seven of the nine

BASIS surface trawls, constituting between 0% and 79% (mean = 27%) of the fish catch by number. Age-0 Pacific Cod *Gadus macrocephalus* (42–88 mm FL) were frequently caught; Prowfish *Zaprora silenus* (51–117 mm FL), Bering Wolffish *Anarhichas orientalis* (161–202 mm FL), and age-0 rockfishes *Sebastes* spp. (36–56 mm FL) were also caught in three or more trawls. The single trawl within the pycnocline had a catch of 2,493 fish/30-min trawl, and 94% of the catch consisted of age-0 Walleye Pollock (43–83 mm FL). Age-0 Pacific Cod (55–93 mm FL) were also caught in the pycnocline trawl. Midwater trawl catches during BASIS contained 590–19,844 fish/30-min trawl (mean = 7,118 fish/30-min trawl; $n = 3$ trawls; headrope = 80 m; Figure 2). Age-0 Walleye Pollock (44–91 mm FL) comprised 97, 72, and 100% of the catch in the three midwater trawls, but age-0 Pacific Cod (56–91 mm FL) and Prowfish (45–91 mm FL) were also caught.

The HR survey completed trawling at 24 stations along the three acoustic transects (Figure 1; Table 1). Surface trawl catches during the HR survey were consistently low (mean = 796 fish/30-min trawl; minimum = 0 fish/30-min trawl; maximum = 6,408 fish/30-min trawl; $n = 18$ trawls) and typically contained age-0 Walleye Pollock (56–108 mm FL), age-0 Pacific Cod (57–88 mm FL), Prowfish (57–143 mm FL), and age-0 rockfishes (27–63 mm FL). Threespine Sticklebacks *Gasterosteus aculeatus* (52–82 mm FL) and juvenile Atka Mackerel *Pleurogrammus monopterygius* (150–216 mm FL) were also caught in at least three trawls. Age-0 Walleye Pollock constituted a mean of 25% (minimum = 0%; maximum = 100%) of the surface trawl catch by number and was the dominant constituent in all trawls with catches greater than 300 fish/30-min trawl. The two trawls within the pycnocline yielded catches of 24 and 1,624 fish/30-min trawl; age-0 Walleye Pollock (62–98 mm FL) constituted 25% and 96% of the catch in these trawls. Age-0 Pacific Cod (64–94 mm FL), Capelin *Mallosus villosus* (79–116 mm FL), age-0 rockfishes (35–52 mm FL), and Pacific Herring *Clupea pallasii* (323 mm FL) were also present in pycnocline catches. The HR midwater catches (mean = 27,816 fish/30-min trawl; minimum = 60 fish/30-min trawl; maximum = 213,721 fish/30-min trawl; $n = 14$ trawls; headrope = 50–95 m) were at least an order of magnitude higher than surface trawl catches. Midwater trawl catches consistently contained few species other than age-0 Walleye Pollock (55–104 mm FL), but age-0 Pacific Cod (58–100 mm FL), Prowfish (56–139 mm FL), and age-0 rockfishes (46–62 mm FL) were also caught in low numbers (≤ 300 individuals) during three or more trawls. Age-0 Walleye Pollock made up a mean of 90% (minimum = 65%; maximum = 100%) of the midwater trawl catches and constituted over 95% of the fish in all catches greater than 300 fish/30-min trawl.

Acoustics.—During BASIS, acoustic data were collected along approximately 275 km of transect within the HR study area. Overall, 3,540 aggregations occurred within the L_R (3.6–5.5 km) of BASIS CTD stations (Figure 3). In water column analyses, these aggregations occupied 791 six-ping horizontal



bins. We removed 10 surface aggregations and 15 bottom aggregations from this analysis due to their proximity to surface or bottom exclusion lines.

Acoustic data were collected along approximately 600 km of HR transects. In total, 6,034 aggregations were identified within the L_R (3.4–5.5 km) of HR CTD stations: 4,522 aggregations were identified during HR1, and 1,512 aggregations were identified during the second pass (HR2) on 167°W (Figure 3). These aggregations were contained within 4,568 six-ping horizontal bins (3,479 bins during HR1; 1,089 bins during

HR2). Overall, 49 surface aggregations and 260 bottom aggregations were removed from the HR1 or HR2 data due to the aggregations' proximity to surface or bottom exclusion lines.

Environment: Water Column Properties and Vertical Distribution of Age-0 Walleye Pollock

Explanatory water column or zooplankton variables had significant but weak effects on the vertical distribution of age-0 Walleye Pollock aggregations during the HR1 survey

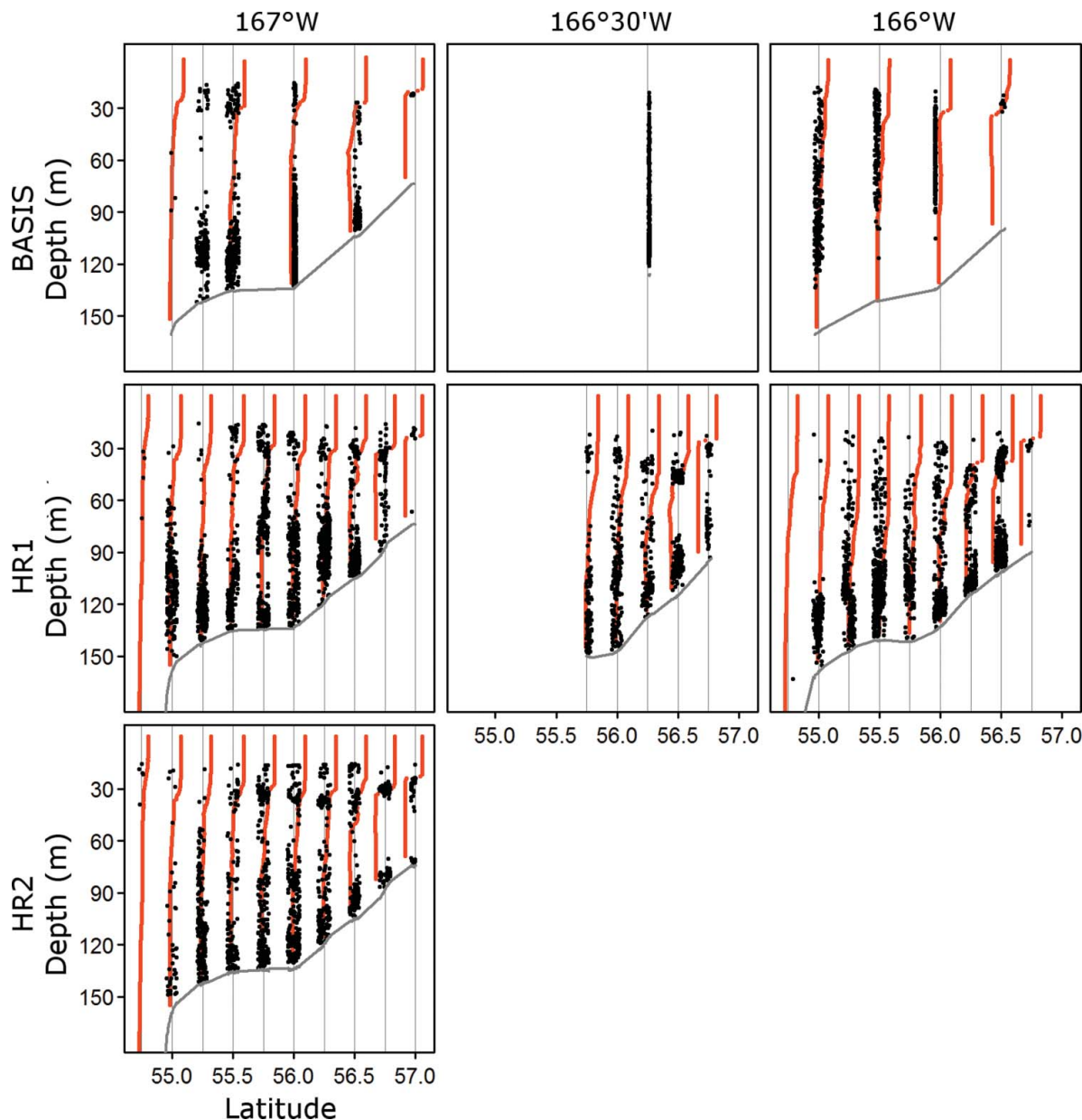


FIGURE 3. Vertical location (midpoint) of age-0 Walleye Pollock aggregations within the Rossby radius (λ_R) of each survey station on 167°W, 166°30'W, and 166°W (BASIS = 2010 Bering Aleutian Salmon International Survey; HR1 and HR2 = high-resolution surveys). Results of conductivity–temperature–depth (CTD) measurements at each station are provided for reference; gray vertical lines denote the 5°C temperature line for the CTD cast (red): values to the left are below 5°C, and values to the right are above 5°C. Bottom depth along the transect is shown (dark gray line).

TABLE 3. Hypothesis model results for the vertical distribution of age-0 Walleye Pollock occurrence and density during the high-resolution (HR1) survey in 2010. Hypothesis/variable, difference in Akaike's information criterion corrected for small sample sizes between the given model and the best-performing model in the set [ΔAIC_c for the best model in parentheses], Akaike weight (w_i), and R^2 statistic are provided. Bold italics indicate results for the best hypothesis. The R^2 value determined after the autoregressive component was added (R^2 AR) is also given.

Hypothesis/variable	Occurrence				Density			
	ΔAIC_c	w_i	R^2	R^2 AR	ΔAIC_c	w_i	R^2	R^2 AR
Depth	24,752	0	0.03	0.31	2,049	0	<0.01	0.64
Temperature	18,584	0	0.03	0.30	446	0	<0.01	0.66
Relative temperature	6,520	0	0.15	0.35	405	0	0.02	0.66
Dissolved oxygen	0 (89,249)	1	0.21	0.34	269	0	0.09	0.67
Salinity	6,452	0	0.15	0.29	0 (11,305)	1	0.21	0.67
Stratification	20,678	0	<0.01	0.25	364	0	<0.01	0.66
Zooplankton S_v	24,538	0	0.02	0.28	1,559	0	<0.01	0.63

(Table 2, analysis A). For the vertical occurrence of age-0 Walleye Pollock, the Oxygen hypothesis had the most support ($w_i = 1.0$; Table 3). Oxygen had a negative coefficient, suggesting that the probability of occurrence increased as Oxygen decreased within the water column. The Oxygen hypothesis had an R^2 value of only 0.21, but the addition of AdjPollock increased the R^2 to 0.34. For the vertical density of age-0 Walleye Pollock, Salinity was the best hypothesis ($w_i = 1.0$; Table 3). Salinity had a positive coefficient, suggesting that age-0 Walleye Pollock density increased as Salinity increased within the water column. The R^2 value for the Salinity hypothesis was initially 0.21, and the value increased to 0.67 when AdjPollock was added to the model.

Models with most or all of the available variables had the greatest support in the exhaustive all-subsets model comparison for HR1 (Table 2, analysis B; Table 4). For both occurrence and density of age-0 Walleye Pollock, there were only one or two models in the 90% confidence set. Although these models were supported by the Akaike's information criterion (AIC) values, they explained little of the variance ($R^2 = 0.27$ for occurrence and 0.23 for density). When AdjPollock was added, it was included in all of the top models for occurrence and density (Table 4). For occurrence, there was a single superior model that included all eight variables and AdjPollock ($R^2 = 0.41$). For density model selection with AdjPollock, 12 models were within the 90% confidence set, and they contained between four and six of the eight explanatory variables. The model with the most support had an R^2 value of 0.66, but the AIC value of that model was within 3 units of six other models.

Ontogeny: Changes in Vertical Distribution and Aggregation Attributes over Time

In Figures 4, 5, and 6, means of the respective measure are presented with 1 SD (except for aggregation length, which is $\pm 0.5 \cdot$ beam width) to provide insight into the distribution of data (Cumming et al. 2007).

Trawl distributions of age-0 Walleye Pollock.—Surface trawl catches of age-0 Walleye Pollock remained the same or decreased at eight of nine paired BASIS–HR1 stations (Table 2, analysis C). At five surface trawl locations, age-0 Walleye Pollock catch decreased by one to four orders of magnitude (i.e., to ≤ 3 fish/30-min trawl) between BASIS sampling and the HR1 sampling that occurred 11–34 d later (Figure 2). At three of the paired surface trawl locations (sampled 8–34 d apart), the catch of age-0 Walleye Pollock remained at ≤ 3 fish/30-min trawl between BASIS and the HR1 survey. At only one location did the surface trawl catch increase (from ≤ 3 to $< 3,000$ fish/30-min trawl) between BASIS sampling and HR1 sampling 22 d later.

Paired BASIS–HR1 midwater trawls occurred at only three locations (Table 2, analysis C). At two paired stations (sampled 11 or 17 d apart), the catch of age-0 Walleye Pollock increased by one or two orders of magnitude between BASIS and HR1 (Figure 2). At the third station, where HR1 sampling occurred 8 d after BASIS, the midwater catch of age-0 Walleye Pollock decreased by two orders of magnitude.

Attributes of age-0 Walleye Pollock aggregations.—The aggregation length (mean length \pm [0.5-beam angle]) for age-0 Walleye Pollock varied among stations but typically increased with increasing station bottom depth (Table 2, analysis D; Figure 4). Among the 20 repeated observations (10 for BASIS–HR1; 10 for HR1–HR2), there were potential differences ($P < 0.05$) for 14 observations, suggesting that minimum aggregation length changed between sampling dates (Table 5). For those 14 paired observations, there was no consistent increase or decrease in minimum aggregation length (see Methods, Aggregation attributes) between BASIS and HR1 sampling or between HR1 and HR2 sampling (Table 5). For the HR2 survey (day of the year 268), eight stations had minimum aggregation lengths within a smaller range of values (13–24 m; Figure 4) than was observed during either BASIS or the HR1 survey.

The thickness of age-0 Walleye Pollock aggregations typically increased and became more variable as the station

TABLE 4. The 90% confidence set for exhaustive selection of models describing the vertical distribution of age-0 Walleye Pollock occurrence and density during the high-resolution (HR1) survey, both with and without the autoregressive (AR) component AdjPollock (ΔAIC_c = difference in Akaike's information criterion corrected for small sample sizes, as calculated between the given model and the best-performing model in the set [AIC_c for the best model in parentheses]; w_i = Akaike weight; R^2 AR = the R^2 value determined after the AR component was added). Bold italics indicate results for the best hypothesis. Abbreviations for the variables are defined in Table 2.

Hypothesis	ΔAIC_c	w_i	R^2	R^2 AR
Occurrence				
~ Depth + Temp + RelTemp + ZoopS _v + Stratification + Oxygen + Salinity	0 (80,627)	0.90	0.27	
Occurrence with AR				
~ Depth + AdjPollock + Temp + RelTemp + ZoopS _v + Stratification + Oxygen + Salinity	0 (51,800)	1.00		0.41
Density				
~ Temp + RelTemp + ZoopS _v + Stratification + Oxygen + Salinity	0 (10,712)	0.56	0.23	
~ Depth + Temp + RelTemp + ZoopS _v + Stratification + Oxygen + Salinity	0.8	0.38	0.23	
Density with AR				
~ AdjPollock + ZoopS _v + Stratification + Salinity	0 (8,002)	0.22		0.66
~ AdjPollock + RelTemp + ZoopS _v + Stratification + Salinity	1.2	0.12		0.66
~ AdjPollock + Temp + ZoopS _v + Stratification + Salinity	1.6	0.10		0.66
~ Depth + AdjPollock + ZoopS _v + Stratification + Salinity	1.7	0.10		0.66
~ AdjPollock + ZoopS _v + Stratification + Oxygen + Salinity	1.9	0.09		0.66
~ AdjPollock + Temp + RelTemp + ZoopS _v + Stratification + Salinity	2.6	0.06		0.66
~ AdjPollock + RelTemp + ZoopS _v + Stratification + Oxygen + Salinity	3.0	0.05		0.66
~ Depth + AdjPollock + RelTemp + ZoopS _v + Stratification + Salinity	3.2	0.04		0.66
~ Depth + AdjPollock + Temp + ZoopS _v + Stratification + Salinity	3.6	0.04		0.66
~ AdjPollock + Temp + ZoopS _v + Stratification + Oxygen + Salinity	3.6	0.04		0.66
~ Depth + AdjPollock + ZoopS _v + Stratification + Oxygen + Salinity	3.7	0.03		0.66
~ AdjPollock + ZoopS _v + Stratification + Salinity	3.7	0.03		0.66

bottom depth increased (Table 2, analysis D; Figure 4). Among the 20 repeated observations (10 for BASIS–HR1; 10 for HR1–HR2), 13 stations had aggregation thicknesses that were potentially different ($P < 0.05$; Table 5). During HR2, nine stations had mean aggregation thicknesses within a range of values (0.8–1.9 m; Figure 4) that was smaller than the range for BASIS or HR1.

The S_v acoustic density of age-0 Walleye Pollock aggregations was fairly consistent as station bottom depth increased, but it was higher and more variable at bottom depths of 125 m or greater (Table 2, analysis D; Figure 4). The S_v acoustic density was potentially different ($P < 0.05$) for 13 of the 20 repeated observations, but there was no consistent pattern of increase or decrease between sampling dates (Table 5). During HR2, S_v acoustic density values were within a range (–57.5 to –51 dB) similar to that observed during BASIS and the HR1 survey.

Metrics of age-0 Walleye Pollock vertical distribution.—As station bottom depth increased, the acoustic center of mass for age-0 Walleye Pollock aggregations moved deeper in the water column (Table 2, analysis E; Figure 5). At stations 1–3, the center of mass was above the 1°C isotherm and typically in water temperatures less than 2°C. At stations 4 and 5, the center of mass was in 2°C water. At station 6, the center of mass was in 1°C water. At stations 7–24, water temperatures exceeded 3°C throughout the water column, and the center of

mass was typically deeper. Among the 20 repeated observations, 11 involved potential differences ($P < 0.05$) in the center of mass between BASIS and HR1 sampling or between HR1 and HR2 sampling, with the center of mass located deeper in the water column for nine observations (Table 5). During the HR2 survey, the acoustic center of mass was shallow (between 23 and 42 m) over the coldest water at stations 1 and 4 and at the deepest survey station (station 24, with 350-m bottom depth). All other stations had center-of-mass values between 74 and 125 m during HR2.

Water column S_v acoustic density of age-0 Walleye Pollock varied across stations but tended to be higher and more variable at stations with bottom depths of 120 m or greater (Table 2, analysis E; Figure 5). There were potential differences ($P < 0.05$) in 14 of the 20 repeated observations, but S_v acoustic density did not consistently increase or decrease between samples (Table 5). The range of S_v acoustic density values during the HR2 survey (65 to 54.5 dB) was smaller than that observed during the HR1 survey or BASIS.

Ontogeny: Fork Length and Energy Density of Age-0 Walleye Pollock

Surface versus midwater.—For age-0 Walleye Pollock sampled during the HR1 survey or BASIS, no overall pattern in FL was apparent across station bottom depths (Table 2, analysis

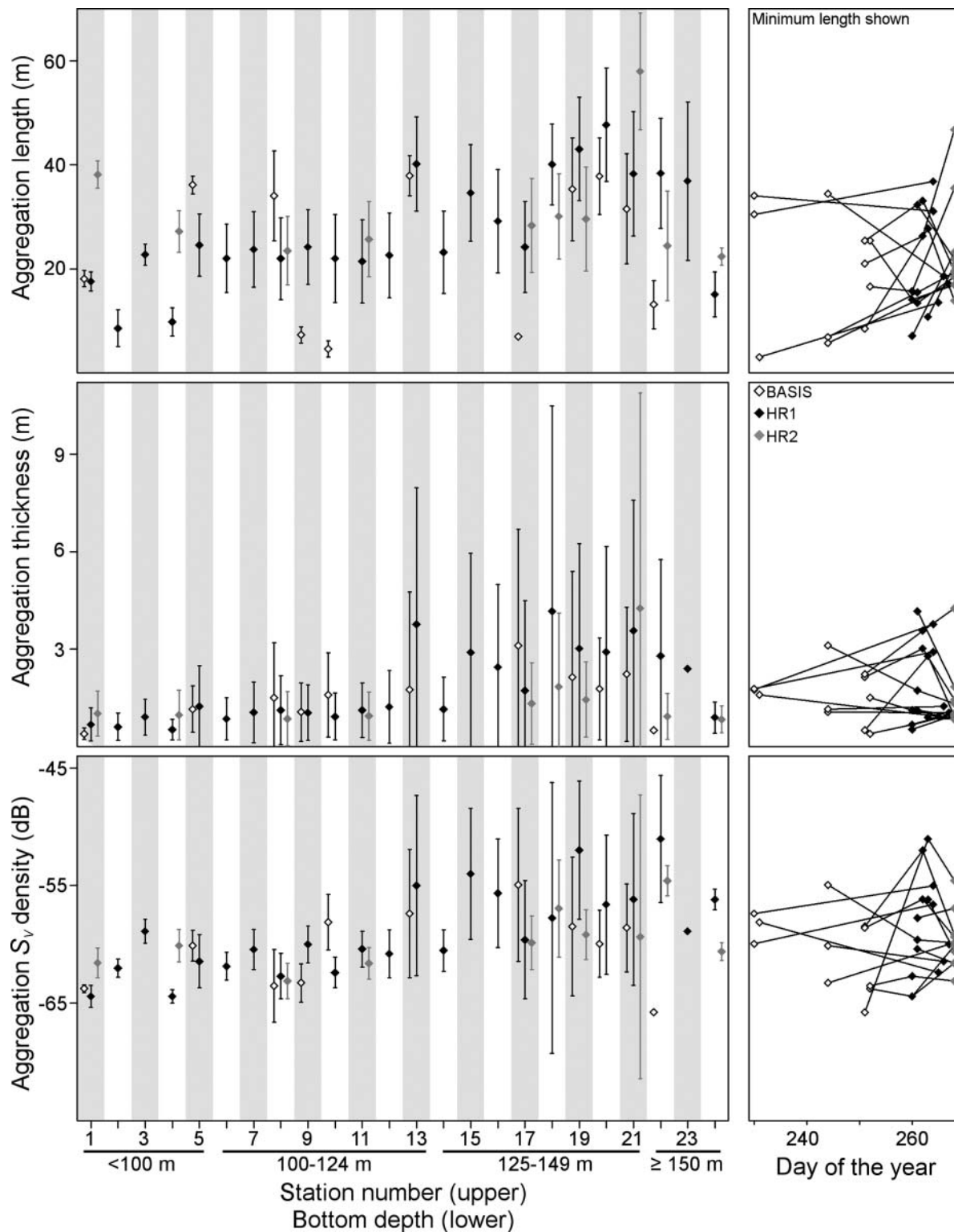


FIGURE 4. Length (upper panels), thickness (middle panels), and S_v acoustic density (lower panels) of age-0 Walleye Pollock aggregations during the 2010 Bering Aleutian Salmon International Survey (BASIS) and the high-resolution (HR1 and HR2) surveys. Means (± 0.5 -beam width) for aggregation length; \pm SD for thickness and S_v acoustic density) for each station and bottom depth are presented (left panels). Minimum aggregation length, mean thickness, and mean S_v acoustic density within a station by day of the year are also shown (right panels). Symbol descriptions apply to all panels.

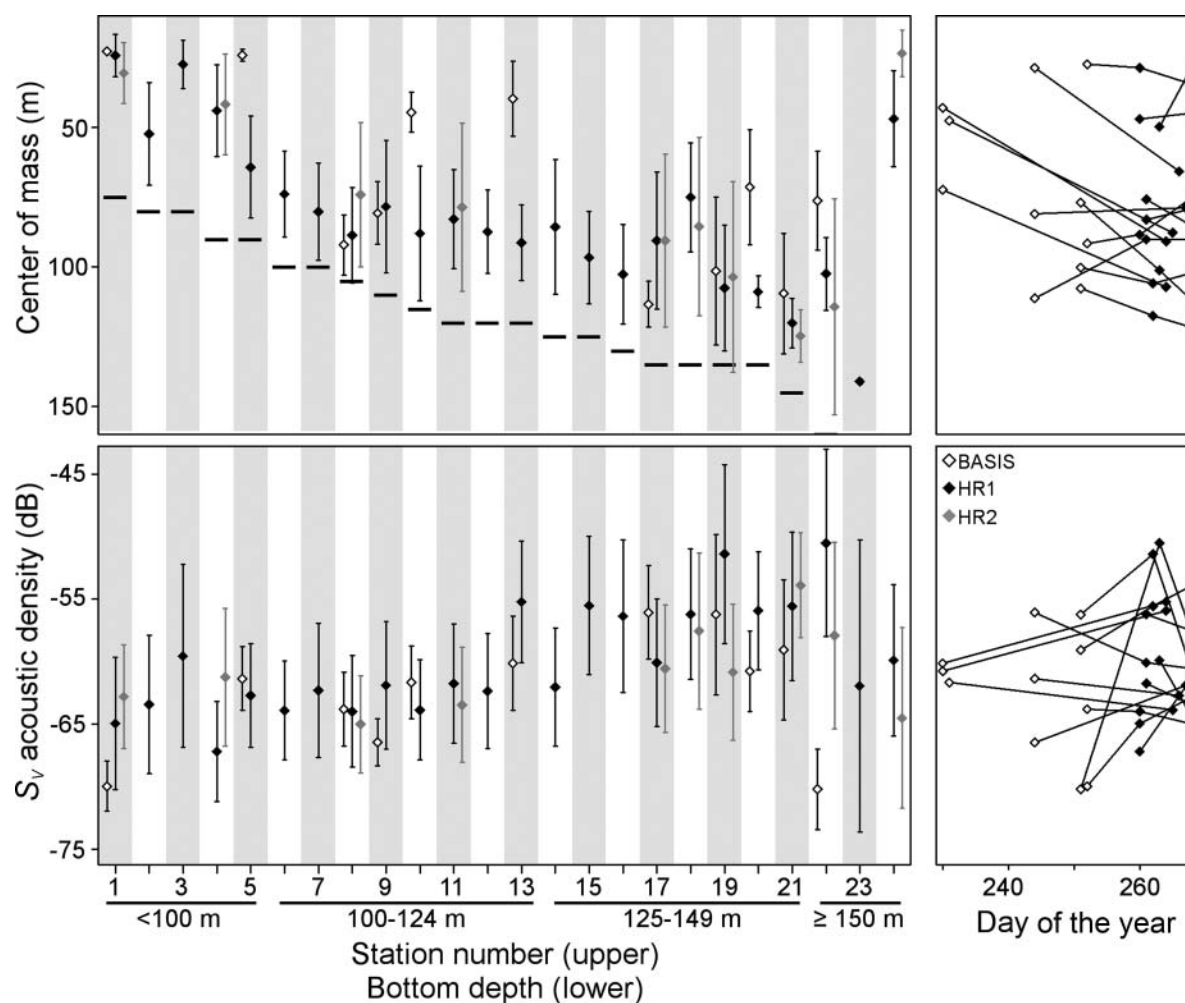


FIGURE 5. Acoustic center of mass (upper panels) and water column S_v acoustic density (lower panels) of age-0 Walleye Pollock vertical distributions during the 2010 Bering Aleutian Salmon International Survey (BASIS) and the high-resolution (HR1 and HR2) surveys. Means (\pm SD) for each station and bottom depth (left panels) and means within a station by day of the year (right panels) are shown. On the upper left panel, horizontal bars indicate bottom depth. Symbol descriptions apply to all panels.

F; Figure 6). A GLM evaluating spatial differences in age-0 Walleye Pollock FL with bottom depth during HR1 indicated potential differences ($P < 0.001$) for surface-caught fish ($df = 404$; $n = 8$ stations; bottom depth = 74–135 m) and had a coefficient of -0.22 , suggesting that as bottom depth increased the mean FL of age-0 Walleye Pollock caught in surface trawls decreased. The P -value for the surface GLM did not change when stations with low catches were removed or when pycnocline-caught fish were included in the analysis. The GLM for midwater-caught fish had a P -value of 0.15 ($df = 1,296$; $n = 14$ stations; bottom depth = 82–161 m), suggesting that Walleye Pollock FL did not differ among midwater station samples.

There was no consistent pattern between age-0 Walleye Pollock energy density and bottom depth across stations (Table 2, analysis G), but the GLM evaluating energy density of surface-caught fish versus station bottom depth during HR1 had a P -value of 0.008 ($df = 32$; $n = 4$ stations). The

coefficient for the surface GLM was -0.02 , suggesting that as bottom depth increased the energy density of age-0 Walleye Pollock caught at the surface decreased. The GLM for energy density of midwater-sampled fish had a P -value of 0.40 ($df = 89$; $n = 11$ stations), suggesting that the energy density of fish caught in midwater samples did not differ with bottom depth.

There was also no consistent difference in FL between age-0 Walleye Pollock that were caught at the surface and those caught midwater at the one BASIS station and three HR1 stations available for this comparison (Table 2, analysis H; Figure 6). At two of the three HR1 stations, the FLs of surface and midwater fish were potentially different ($P < 0.05$), with surface fish being larger at station 2 and midwater fish being larger at station 11. At the two remaining stations (BASIS station 17; HR1 station 18), the FLs of surface- and midwater-caught fish were not different ($P > 0.05$). The maximum within-station difference in mean FL was 4.01 mm.

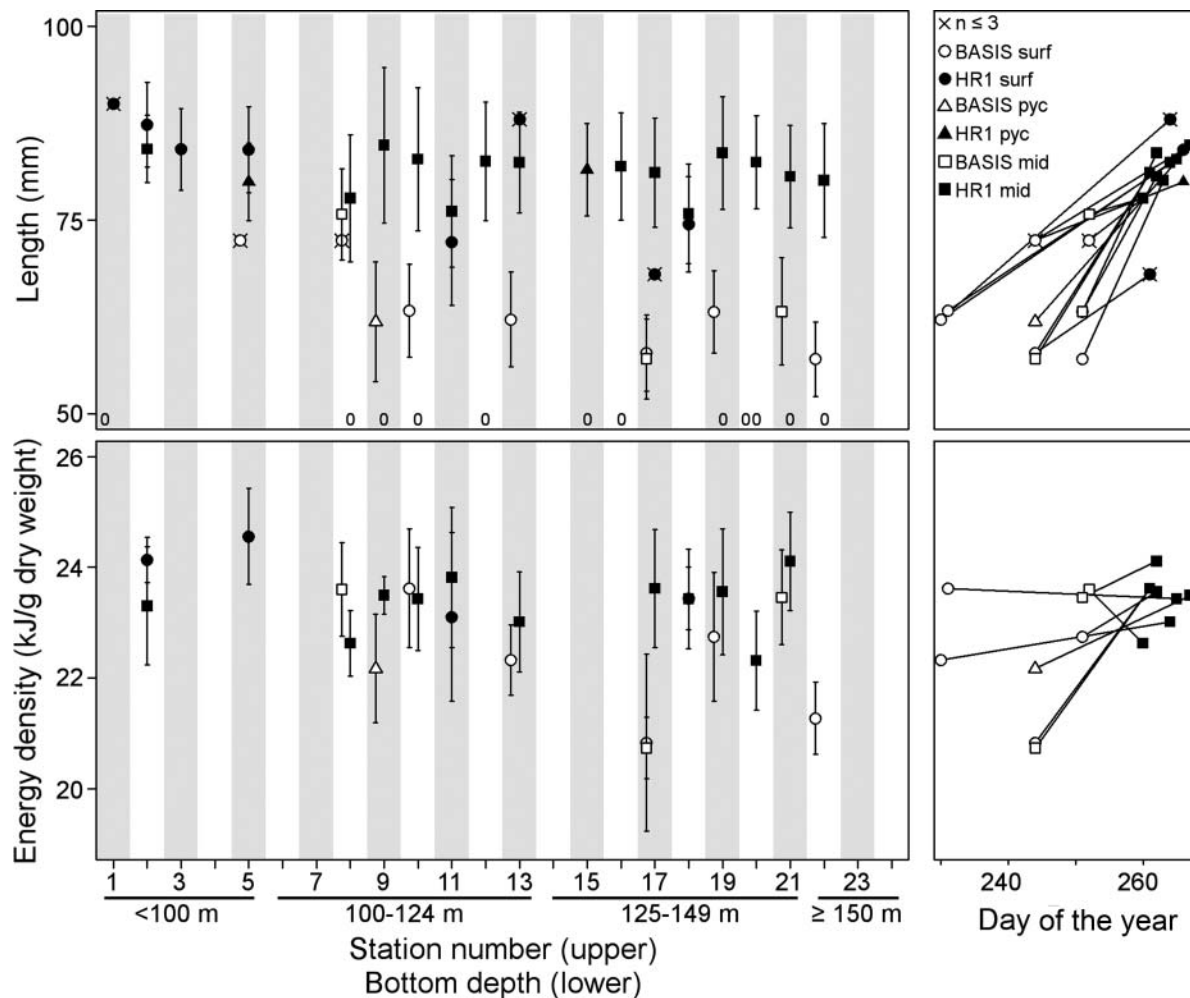


FIGURE 6. Fork length (upper panels) and energy density (lower panels) of age-0 Walleye Pollock during the 2010 Bering Aleutian Salmon International Survey (BASIS) and the high-resolution (HR1) survey. Means (\pm SD) for each station and bottom depth (left panels) and means within a station by day of the year (right panels) are shown. An “x” behind a symbol indicates that the sample contained three or fewer fish; a zero along the x-axis of the upper left panel indicates that the surface trawl catch was zero. Symbol descriptions apply to all panels (surf = surface trawl; pyc = pycnocline trawl; mid = midwater trawl).

Energy density comparisons between surface- and midwater-caught age-0 Walleye Pollock were possible for BASIS station 17 and HR1 stations 2 and 18 (Table 2, analysis I; Figure 6). The comparisons indicated that surface and midwater fish did not differ in energy density ($P > 0.05$). The maximum within-station difference in mean energy density was 0.8 J/g dry mass.

Changes in fork length or energy density over time.—As expected, mean FLs of age-0 Walleye Pollock were higher during the HR1 survey than during BASIS (Table 2, analysis J; Figure 6). Among the three stations where midwater trawls were performed during both BASIS and HR1, the mean FL of age-0 Walleye Pollock potentially increased between sampling periods at two stations (stations 17 and 21; $P < 0.05$) but not at the third (station 8; $P > 0.05$; Figure 6). Contrary to our expectation, the FLs of age-0 Walleye Pollock sampled during BASIS were not more similar to the FLs of HR1-sampled fish

when the number of days between sampling events decreased (Figure 6). During HR1 sampling, the mean FL of fish—regardless of whether they were caught near the surface or midwater—ranged from 72.1 to 87.3 mm at stations with more than three fish in the catch.

Energy densities of age-0 Walleye Pollock were similar within most stations regardless of whether the fish were sampled during BASIS or the HR1 survey (Table 2, analysis J; Figure 6). Among the three paired BASIS–HR1 midwater trawls, two stations had energy densities that were potentially different ($P < 0.05$) between sampling periods; energy density increased between BASIS and the HR1 survey at station 17, whereas it decreased between surveys at station 8. The third station (station 21) had a P -value greater than 0.05 for the comparison of energy density between BASIS and HR1 samples. Mean energy density during the HR1 survey was between 22.3 and 24.4 J/g dry mass.

TABLE 5. Summary of comparisons for age-0 Walleye Pollock aggregation attributes (length [minimum], thickness, and S_v acoustic density) and metrics of vertical distribution (center of mass and S_v acoustic density) between surveys at each station (B–H1 = comparison between the 2010 Bering Aleutian Salmon International Survey [BASIS] and high-resolution survey HR1; H1–H2 = comparison between high-resolution surveys HR1 and HR2). Days between surveys are given for each station (“^” symbol indicates that the descriptor increased between observations at $P < 0.05$; “v” symbol indicates that the descriptor decreased between observations at $P < 0.05$; “ns” indicates no significant change, $P \geq 0.05$).

Station	Aggregation attributes								Metrics of vertical distribution			
	Days between		Minimum length		Thickness		S_v acoustic density		Center of mass		S_v acoustic density	
	B–H1	H1–H2	B–H1	H1–H2	B–H1	H1–H2	B–H1	H1–H2	B–H1	H1–H2	B–H1	H1–H2
1	8	8	ns	^	ns	ns	ns	ns	ns	^	ns	ns
4		8		^		^		^		ns		^
5	22		v		ns		ns		^		v	
8	8	8	v	^	v	v	ns	ns	ns	v	ns	ns
9	23		^			ns	^		ns		^	
10	34		^		v		v		^		v	
11		7		^		v		v		ns		v
13	34		ns		^		^		^		^	
17	17	7	^	^	v	ns	v	ns	v	ns	v	ns
18		7		v		v		ns		^		v
19	11	6	ns	v	^	v	^	v	^	ns	^	v
20	34		ns		^		^		^		^	
21	11	6	ns	^	^	ns	^	v	^	^	^	^
22	12	5		v		v		v		ns		v
24		5		ns		ns		v		ns		ns

DISCUSSION

Our study examined whether environmental factors (e.g., water temperature or location of zooplankton prey) or ontogeny affected the vertical distribution of age-0 Walleye Pollock. Based on previous studies and common hypotheses, we assumed that the vertical distribution of age-0 Walleye Pollock represented a response to environmental factors, but an HR survey that sampled as many environmental and biological factors as possible was needed to refine our understanding. We also recognized that vertical distribution could be related to ontogeny, particularly since the timing of the transition from near-surface to demersal waters by EBS age-0 Walleye Pollock is not well understood (Duffy-Anderson et al. 2015).

Contrary to our initial prediction, water column properties alone did not have a strong effect on the vertical distribution of age-0 Walleye Pollock. High autocorrelation—attributed to aggregating behavior—played a larger role in explaining vertical distribution than did environmental variables. This result was not surprising given that schooling among juvenile Walleye Pollock increases their foraging success (Baird et al. 1991; Ryer and Olla 1992) and is generally thought to reduce predation risk (Pitcher and Parrish 1993). Previous studies have primarily evaluated age-0 Walleye Pollock distributions relative to environmental factors, including the thermocline (e.g., Swartzman et al. 1999, 2002), water column stability (Francis and Bailey 1983; Coyle et al. 2008), and zooplankton prey (Olla and Davis 1990; Ciannelli et al. 2004; Coyle et al.

2008). In our analysis, these variables were not significant predictors of the occurrence or density of age-0 Walleye Pollock. Instead, we found that salinity was the best predictor of age-0 occurrence and that oxygen was the best predictor of age-0 density. Most of the age-0 Walleye Pollock in this analysis occurred in the midwater of the outer domain, which is characterized by low variability in salinity and oxygen (Coachman 1986); thus, the inclusion of these variables in final model selections was not surprising.

We characterized the potential zooplankton prey field for age-0 Walleye Pollock by using acoustics rather than net tows. Acoustics provided an estimate of relative zooplankton biomass at locations within the water column, whereas net tows produce vertically integrated water column estimates (e.g., Coyle et al. 2011). Although the adopted methods from Murae et al. (2009) may have resulted in underestimation of *Calanus* spp. abundances, our analysis was based on the relative distribution of zooplankton (i.e., copepods and euphausiids) in the water column rather than absolute abundance. Additional acoustic research effort is needed to refine and expand EBS-specific acoustic classification methods for zooplankton (e.g., De Robertis et al. 2010). Knowledge of the vertical location of zooplankton relative to age-0 Walleye Pollock during the day is important, as an analysis of age-0 Walleye Pollock diets from 27 surface, midwater, crepuscular, and night trawls during the HR1 survey suggested that they fed on *Calanus* spp. and euphausiids throughout the day and were not restricted to

feeding during a diurnal cycle (N. Kuznetsova, Pacific Fisheries Research Center [TINRO], Vladivostok, Russia, personal communication).

Despite the comprehensive set of variables used in our analyses, two potential factors that have been suggested to influence Walleye Pollock vertical distributions were not included in this study. Olla and Davis (1990) and Ryer and Olla (1992) found that light levels affected the vertical distribution and shoaling of age-0 Walleye Pollock under laboratory conditions. Unfortunately, light levels at depth were not measured during our surveys due to equipment difficulties. Given that Kotwicki et al. (2013) found that bottom trawl catches of age-1 and older (age-1+) Walleye Pollock decreased with increasing near-bottom light levels, this factor should be evaluated in future studies of age-0 vertical distribution. Ryer and Olla (1992) also demonstrated that predator presence affected the degree of age-0 Walleye Pollock shoaling in laboratory experiments, but they did not evaluate the effect of predator presence on vertical distribution. Primary predators of age-0 Walleye Pollock during late summer include Arrowtooth Flounder *Atheresthes stomias* and age-1+ Walleye Pollock (Lang et al. 2000), with both species occupying demersal or semi-demersal habitats during daytime. During our surveys, we captured no Arrowtooth Flounder or age-1+ Walleye Pollock in 27 surface trawls and 17 midwater trawls. An acoustic trawl survey conducted in June–August 2010 suggested that age-1+ Walleye Pollock were primarily located over 150 km to the northwest of our study area (Honkalehto et al. 2012). Combining (1) the evidence that predator density was low in our study area with (2) our primary interest in evaluating potential factors influencing the movement of age-0 Walleye Pollock from near-surface waters to the midwater zone, we felt that the omission of predator variables from our modeling was justified.

From an ontogenetic perspective, data on trawl catch and acoustic center of mass suggested that the vertical distribution of age-0 Walleye Pollock shifted deeper in the water column between BASIS and the HR surveys. This pattern matches observations in the Gulf of Alaska by Brodeur and Wilson (1996), who reported that the depth of age-0 Walleye Pollock capture increased through the season. The presence of age-0 Walleye Pollock in the midwater zone during the 2010 BASIS (Parker-Stetter et al. 2013) suggests that movement of age-0 Walleye Pollock out of near-surface waters and into deeper waters began before August 18. Based on our single year of data, we cannot state whether the timing of the descent is consistent among years. Contrary to the concern stated by Hollowed et al. (2012) that surface trawl distributions are only representative of smaller fish (per Swartzman et al. 2002), we found no difference in FL between surface- and midwater-caught age-0 Walleye Pollock. Instead, our data suggest that the age-0 Walleye Pollock length distributions derived from the surface trawl data may represent only the proportion of the population that had not moved deeper in the water column by the time of sampling.

We predicted that aggregations of age-0 Walleye Pollock would become longer, thicker, and denser in the late summer and early fall. This pattern has been observed for other species, such as Pacific Herring (Sigler and Csepp 2007). The only consistent pattern across sampling dates was that the mean aggregation length and thickness tended to cluster around a general aggregation size (13–24 m for length; 0.8–1.9 m for thickness) by the date of the HR2 survey. This aggregation size may reflect a balance between predation risk and foraging success (cf. Pitcher and Parrish 1993). Aggregation length, thickness, and S_v acoustic density tended to increase, but characteristics became more variable with increasing bottom depth. In a study of age-1–3 Walleye Pollock, Stienessen and Wilson (2008) found that aggregation thickness increased with depth in the water column but that the density of fish (approximately comparable to our S_v acoustic density) decreased with depth. The aggregation lengths and thicknesses observed in our study were considerably smaller than those of age-0 Walleye Pollock surveyed off Japan, where maximum aggregation length was about 500 m and mean thickness was approximately 18 m during the day (Kang et al. 2006). Observation conditions for the Kang et al. (2006) study differed from ours in that sampling took place earlier in the year (June–July) and over shallower bottom depths (~75 m) than our study, so survey timing and bottom depth may have affected aggregation characteristics.

Our approach also evaluated differences in age-0 Walleye Pollock vertical distribution using growth characteristics of fish FL and energy density. Larger fish have been predicted to occur deeper than smaller fish (Miyake et al. 1996; Swartzman et al. 2002). A parallel prediction could be made for the energy densities of age-0 Walleye Pollock if midwater temperatures and food rations are bioenergetically favorable (Sogard and Olla 1996). Our limited data suggested that although station bottom depth may explain differences in FLs of surface-caught age-0 Walleye Pollock across space, midwater-caught age-0 Walleye Pollock were not consistently longer and did not have higher energy densities than surface-caught fish. When stations were resampled over a range of temporal lags, the slopes of lines connecting samples at a given station differed, but FLs and energy densities converged to a small range of values independent of the capture depth in the water column. This observed convergence of FLs and energy densities may reflect the switch between “grow longer” and “grow fatter” responses to seasonal changes, as has been proposed for EBS age-0 Walleye Pollock (Siddon et al. 2013a). We do not believe that the observed convergence of FLs was due to net selectivity, since the Cantrawl is used to catch salmon of up to 475 mm (cf. Farley et al. 2011). The range of energy densities observed during the HR surveys is similar to or higher than means reported for the 2008 and 2009 cohorts (Siddon et al. 2013b) and is similar to the mean energy densities of age-0 Walleye Pollock sampled during 2007–2012 (based on Heintz et al. 2013). Future work should increase the

number of paired surface trawl and midwater trawl samples and should involve sampling earlier in the year, when the probability of catching both surface and midwater fish is higher.

There is currently no standard methodology to determine age in juvenile Walleye Pollock; therefore, we were unable to estimate growth rates or to evaluate the influence of daily age on our results. Previous efforts to estimate the daily ages of age-0 Walleye Pollock have been inconsistent or unable to identify daily growth rings (reviewed by Duffy-Anderson et al. 2015). It is possible that differences in FL among locations could be due to different cohorts being advected away from spawning locations (cf. Smart et al. 2012). It is also conceivable that the initiation of age-0 Walleye Pollock movement from near-surface waters to the midwater zone is a function of daily age, but we observed no clear patterns in paired samples with either FL or energy density. Davis and Ottmar (2009) suggested that annual age (0+ and 1+) had a minor effect on the vertical distribution of Pacific Cod over a range of environmental conditions in the laboratory. Additional work on techniques to determine the daily age of late-juvenile Walleye Pollock (e.g., Bailey 1989) would provide insight into the condition and timing of movement from near-surface waters to deeper waters.

Two major assumptions were implicit in our processing of the acoustic data. First, we assumed that the -60 dB threshold in combination with school detection parameters would exclude jellyfish from the backscatter categorized as age-0 Walleye Pollock. De Robertis and Taylor (2014) verified that jellyfish had low backscatter contributions relative to small pelagic fishes such as age-0 Walleye Pollock, so this assumption was likely met. The second assumption was that detected aggregations of acoustic backscatter were age-0 Walleye Pollock. Age-0 Pacific Cod were present in near-surface waters of the EBS during BASIS in 2010 but at lower densities than age-0 Walleye Pollock (Parker-Stetter et al. 2013). Because age-0 Walleye Pollock were typically caught in low numbers at trawl stations with few aggregations, we felt that this assumption was valid. If aggregations contained age-0 Pacific Cod, then the location of near-surface aggregations may reflect a mixture of species rather than exclusively age-0 Walleye Pollock.

The modeling approach used here was chosen to evaluate *why* vertical distributions differed from station to station, not *whether* they differed. The use of a traditional ANOVA with “station” as a factor or the use of GLMs with separate intercepts for each station would have resulted in significant differences between or among stations. Fitting separate intercepts for each station would have overfitted the regression models since they would tell us nothing about the factors that made age-0 Walleye Pollock density higher at station x than at station y . Our intent was to infer the processes influencing Walleye Pollock vertical distribution rather than to quantify the distribution patterns. To examine whether the

1-m vertical data resolution introduced distributional artifacts, we re-ran the models with acoustic data averaged in 2-m and 5-m vertical bins. Hypotheses with the most support did not change in occurrence or density models, and R^2 remained at values less than 0.20 in the absence of the autoregressive component.

Our finding that ontogeny rather than biological or physical water column properties was likely responsible for differences in age-0 Walleye Pollock vertical distribution within and between surveys should be considered in the design of population abundance estimate surveys. If surface trawling occurs while age-0 Walleye Pollock are transitioning from near-surface to midwater depths, then abundance will be underestimated and the distribution will represent fish in the near-surface water rather than the population. Sampling earlier in the season would likely allow age-0 Walleye Pollock to be surveyed while they are in near-surface waters above or within the pycnocline (Parker-Stetter et al. 2013). Although age-0 Walleye Pollock would be mixed with jellyfish and other fish species at that time, consistent vertical distribution might increase the catches of age-0 Walleye Pollock and minimize bias. Alternatively, sampling later in the year could provide vertical separation between age-0 Walleye Pollock and other species, enabling more accurate acoustic-based estimates of population abundance and distribution.

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REFERENCES

- Alenius, P., A. Nekrasov, and K. Myrberg. 2003. Variability of the baroclinic Rossby radius in the Gulf of Finland. *Continental Shelf Research* 23:563–573.
- Bailey, K. M. 1989. Interaction between the vertical distribution of juvenile Walleye Pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. *Marine Ecology Progress Series* 53:205–213.
- Baird, T. A., C. H. Ryer, and B. L. Olla. 1991. Social enhancement of foraging on an ephemeral food source in juvenile Walleye Pollock, *Theragra chalcogramma*. *Environmental Biology of Fishes* 31:307–311.
- Barange, M. 1994. Acoustic identification, classification and structure of biological patchiness on the edge of the Agulhas Bank and its relation to frontal features. *South African Journal of Marine Science* 14:333–347.
- Brodeur, R. D., and M. T. Wilson. 1996. A review of the distribution, ecology and population dynamics of age-0 Walleye Pollock in the Gulf of Alaska. *Fisheries Oceanography* 5:148–166.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York.
- Ciannelli, L., R. D. Brodeur, G. L. Swartzman, and S. Salo. 2002. Physical and biological factors influencing the spatial distribution of age-0 Walleye Pollock (*Theragra chalcogramma*) around the Pribilof Islands, Bering Sea. *Deep Sea Research Part II: Topic Studies in Oceanography* 49:6109–6126.
- Ciannelli, L., B. W. Robson, R. C. Francis, K. Aydin, and R. D. Brodeur. 2004. Boundaries of open marine ecosystems: an application to the Pribilof Archipelago, southeast Bering Sea. *Ecological Applications* 14:942–953.
- Coachman, L. K. 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. *Continental Shelf Research* 5:23–108.
- Coyle, K. O., L. B. Eisner, F. J. Mueter, A. I. Pinchuk, M. A. Janout, K. D. Cieciel, E. V. Farley, and A. G. Andrews. 2011. Climate change in the southeastern Bering Sea: impacts on Pollock stocks and implications for the oscillating control hypothesis. *Fisheries Oceanography* 20:139–156.
- Coyle, K. O., A. I. Pinchuk, L. B. Eisner, and J. M. Napp. 2008. Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: the potential role of water-column stability and nutrients in structuring the zooplankton community. *Deep Sea Research Part II: Topic Studies in Oceanography* 55:1775–1791.
- Cressie, N., and C. K. Wikle. 2011. Statistics for spatio-temporal data. Wiley, Hoboken, New Jersey.
- Cumming, G., F. Fidler, and D. L. Vaux. 2007. Error bars in experimental biology. *Journal of Cell Biology* 177:7–11.
- Davis, M., and M. Ottmar. 2009. Vertical distribution of juvenile Pacific Cod *Gadus macrocephalus*: potential role of light, temperature, food, and age. *Aquatic Biology* 8:29–37.
- De Robertis, A., D. R. McKelvey, and P. H. Ressler. 2010. Development and application of an empirical multifrequency method for backscatter classification. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1459–1474.
- De Robertis, A., and K. Taylor. 2014. In situ target strength measurements of the scyphomedusa *Chrysaora melanaster*. *Fisheries Research* 153:18–23.
- Diner, N. 2001. Correction on school geometry and density: approach based on acoustic image simulation. *Aquatic Living Resources* 14:211–222.
- Duffy-Anderson, J. T., S. Barbeaux, E. Farley, R. Heintz, J. Horne, S. Parker-Stetter, C. Petrik, E. C. Siddon, and T. I. Smart. 2015. State of knowledge review and synthesis of the first year of life of Walleye Pollock (*Gadus chalcogrammus*) in the eastern Bering Sea, with comments on implications for recruitment. *Deep Sea Research Part II: Topical Studies in Oceanography*. DOI: 10.1016/j.dsr2.2015.02.001.
- Dunnnett, C. W. 1980. Pairwise multiple comparisons in the unequal variance case. *Journal of the American Statistical Association* 75:796–800.
- Farley, E. V. Jr., J. Murphy, J. Moss, A. Feldmann, and L. Eisner. 2009. Marine ecology of western Alaska juvenile salmon. Pages 307–329 in C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.
- Farley, E. V., A. Starovoytov, S. Naydenko, R. Heintz, M. Trudel, C. Guthrie, L. Eisner, and J. R. Guyon. 2011. Implications of a warming eastern Bering Sea for Bristol Bay Sockeye Salmon. *ICES Journal of Marine Science* 68:1138–1146.
- Foot, K. G., H. P. Knudsen, G. Vestnes, D. N. MacLennan, and E. J. Simmonds. 1987. Calibration of acoustic instruments for fish density estimation. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 44.
- Francis, R. C., and K. M. Bailey. 1983. Factors affecting recruitment of selected gadoids in the northeast Pacific and east Bering Sea. Pages 35–60 in W. S. Wooster, editor. From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska and the Eastern Bering Sea. Washington State Sea Grant, Seattle.
- Gill, A. E. 1982. Atmosphere-ocean dynamics. Academic Press, New York.
- Goodman, S. N. 1999. Toward evidence-based medical statistics I: the *P*-value fallacy. *Annals of Internal Medicine* 130:995–1004.
- Heintz, R. A., E. C. Siddon, E. V. Farley, and J. M. Napp. 2013. Correlation between recruitment and fall condition of age-0 Pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. *Deep Sea Research Part II: Topical Studies in Oceanography* 94:150–156.
- Hollowed, A. B., S. J. Barbeaux, E. D. Cokelet, E. Farley, S. Kotwicki, P. H. Ressler, C. Spital, and C. D. Wilson. 2012. Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 65–70:230–250.
- Honkalehto, T., A. McCarthy, P. Ressler, S. Stienessen, and D. Jones. 2010. Results of the acoustic-trawl survey of Walleye Pollock (*Theragra chalcogramma*) on the U.S. and Russian Bering Sea shelf in June–August 2009 (DY0909). National Marine Fisheries Service, Alaska Fisheries Science Center, Processed Report 2010-03, Seattle.
- Honkalehto, T., A. McCarthy, P. Ressler, K. Williams, and D. Jones. 2012. Results of the acoustic-trawl survey of Walleye Pollock (*Theragra chalcogramma*) on the U.S. and Russian Bering Sea shelf in June–August 2010 (DY1006). National Marine Fisheries Service, Alaska Fisheries Science Center, Processed Report 2012-01, Seattle.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.
- Kang, M., S. Honda, and T. Oshima. 2006. Age characteristics of Walleye Pollock school echoes. *ICES Journal of Marine Science* 63:1465–76.
- Korneliusson, R. 2000. Measurement and removal of echo integration noise. *ICES Journal of Marine Science* 57:1204–1217.
- Kotwicki, S., A. De Robertis, J. N. Ianelli, A. E. Punt, J. K. Horne, and J. M. Jech. 2013. Combining bottom trawl and acoustic data to model acoustic dead zone correction and bottom trawl efficiency parameters for semi-pelagic species. *Canadian Journal of Fisheries and Aquatic Sciences* 70:208–219.
- Lang, G., R. D. Brodeur, J. M. Napp, and R. Schabetsberger. 2000. Variation in groundfish predation on juvenile Walleye Pollock relative to hydrographic structure near the Pribilof Islands, Alaska. *ICES Journal of Marine Science* 57:265–271.
- Lauth, R. R. 2010. Results of the 2009 eastern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate resources. NOAA Technical Memorandum NMFS-AFSC-204.
- Lew, M. J. 2012. Bad statistical practice in pharmacology (and other basic biomedical disciplines): you probably don't know *P*: statistical inference using *P*-values. *British Journal of Pharmacology* 166:1559–1567.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. Pages 105–142 in P. Zarembka, editor. *Frontiers in econometrics*. Academic Press, New York.
- Miyake, H., H. Yoshida, and Y. Ueda. 1996. Distribution and abundance of age-0 juvenile Walleye Pollock, *Theragra chalcogramma*, along the Pacific coast of southeastern Hokkaido, Japan. NOAA Technical Report NMFS-126.

- Moss, J. H., E. V. Farley, A. M. Feldmann, and J. N. Ianelli. 2009. Spatial distribution, energetic status, and food habits of eastern Bering Sea age-0 Walleye Pollock. *Transactions of the American Fisheries Society* 138:497–505.
- Murase, H., M. Ichihara, H. Yasuma, H. Watanabe, S. Yonezaki, H. Nagashima, S. Kawahara, and K. Miyashita. 2009. Acoustic characterization of biological backscatterings in the Kuroshio–Oyashio inter-frontal zone and subarctic waters of the western North Pacific in spring. *Fisheries Oceanography* 18:386–401.
- Olla, B. L., and M. W. Davis. 1990. Behavioral responses of juvenile Walleye Pollock *Theragra chalcogramma* Pallas to light, thermoclines and food: possible role in vertical distribution. *Journal of Experimental Marine Biological and Ecology* 135:59–68.
- Parker-Stetter, S. L., J. K. Horne, E. V. Farley, D. H. Barbee, A. G. Andrews, L. B. Eisner, and J. M. Nomura. 2013. Summer distributions of forage fish in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 94:211–230.
- Pitcher, T. J., and J. K. Parrish. 1993. The functions of shoaling behaviour. Pages 363–439 in T. J. Pitcher, editor. *The behaviour of teleost fishes*, 2nd edition. Chapman and Hall, London.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org. (July 2015).
- Reid, D. G., and E. J. Simmonds. 1993. Image analysis techniques for the study of fish school structure from acoustic survey data. *Canadian Journal of Fisheries and Aquatic Sciences* 50:886–893.
- Rosby, C. G. 1938. On the mutual adjustment of pressure and velocity distributions in certain simple current systems, parts I, II. *Journal of Marine Research* 2:239–263.
- Ruxton, G. D. 2006. The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann–Whitney *U*-test. *Behavioral Ecology* 17:688–690.
- Ryer, C. H., and B. L. Olla. 1992. Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. *Animal Behaviour* 44:69–74.
- Schabetsberger, R., M. Sztatecsny, G. Drozdowski, R. D. Brodeur, G. L. Swartzman, M. T. Wilson, A. G. Winter, and J. M. Napp. 2003. Size-dependent, spatial, and temporal variability of juvenile Walleye Pollock (*Theragra chalcogramma*) feeding at a structural front in the southeast Bering Sea. *Marine Ecology* 24:141–164.
- Siddon, E. C., R. A. Heintz, and F. J. Mueter. 2013a. Conceptual model of energy allocation in Walleye Pollock (*Theragra chalcogramma*) from age-0 to age-1 in the southeastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 94:140–149.
- Siddon, E. C., T. Kristiansen, F. J. Mueter, K. K. Holsman, R. A. Heintz, and E. V. Farley. 2013b. Spatial match–mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea. *PLoS (Public Library of Science) ONE [online serial]* 8:e84526.
- Sigler, M. F., and D. J. Csepp. 2007. Seasonal abundance of two important forage species in the North Pacific Ocean, Pacific Herring and Walleye Pollock. *Fisheries Research* 83:319–331.
- Smart, T. I., J. T. Duffy-Anderson, J. K. Horne, E. V. Farley, C. D. Wilson, and J. M. Napp. 2012. Influence of environment on Walleye Pollock eggs, larvae, and juveniles in the southeastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 65–70:196–207.
- Smart, T. I., E. C. Siddon, and J. T. Duffy-Anderson. 2013. Vertical distributions of the early life stages of a common gadid in the eastern Bering Sea (*Theragra chalcogramma*, Walleye Pollock). *Deep Sea Research Part II: Topical Studies in Oceanography* 94:201–210.
- Sogard, S. M., and B. L. Olla. 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy-conserving mechanisms. *Marine Ecology Progress Series* 133:43–55.
- Stefánsson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science* 53:577–588.
- Stienessen, S. C., and C. D. Wilson. 2008. Juvenile Walleye Pollock aggregation structure in the Gulf of Alaska. Pages 271–287 in G. H. Kruse, K. Drinkwater, J. N. Ianelli, J. S. Link, D. L. Stram, V. Wespestad, and D. Woodby, editors. *Resiliency of gadid stocks to fishing and climate change*. Alaska Sea Grant College Program, Fairbanks.
- Swartzman, G., R. Brodeur, J. Napp, G. Hunt, D. Demer, and R. Hewitt. 1999. Spatial proximity of age-0 Walleye Pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. *ICES Journal of Marine Science* 56:545–560.
- Swartzman, G., J. Napp, R. Brodeur, A. Winter, and L. Ciannelli. 2002. Spatial patterns of Pollock and zooplankton distribution in the Pribilof Islands, Alaska, nursery area and their relationship to Pollock recruitment. *ICES Journal of Marine Science* 59:1167–1186.
- Tang, Q., X. Jin, F. Li, J. Chen, W. Wang, Y. Chen, X. Zhao, and F. Dai. 1996. Summer distribution and abundance of age-0 Walleye Pollock, *Theragra chalcogramma*, in the Aleutian Basin. *Ecology of juvenile Walleye Pollock, Theragra chalcogramma*. NOAA Technical Report NMFS-126.
- Urmy, S. S., J. K. Horne, and D. H. Barbee. 2012. Measuring the vertical distributional variability of pelagic fauna in Monterey Bay. *ICES Journal of Marine Science* 69:184–196.
- Watkins, J. L., and A. S. Brierley. 1996. A post-processing technique to remove background noise from echo integration data. *ICES Journal of Marine Science* 53:339–344.
- Welch, B. L. 1947. The generalization of “Student's” problem when several different population variances are involved. *Biometrika* 34:28–35.
- Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75:1182–1189.
- Wuillez, M., J.-C. Poulard, J. Rivoirard, P. Petitgas, and N. Bez. 2007. Indices for capturing spatial patterns and their evolution in time, with application to European Hake (*Merluccius merluccius*) in the Bay of Biscay. *ICES Journal of Marine Science* 64:537–550.