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Vertical distributions of the early life stages of walleye pollock (Theragra chalcogramma) in the Southeastern Bering Sea

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ABSTRACT

The present study examines vertical distributions of the early life stages of walleye pollock (*Theragra chalcogramma*) in the Southeastern Bering Sea to assess ontogenetic and diel vertical migration in relation to development and habitat. Walleye pollock demonstrated a decrease in the depth of occurrence following hatching, indicating an ontogenetic change in vertical distribution. Eggs occurred deepest in the water column and early juveniles occurred shallowest. Vertical distributions were related to the date of collection, water column depth, and thermocline depth. Non-feeding stages (eggs and yolksac larvae, <4.5 mm standard length [SL]) did not exhibit diel vertical migration. Feeding larvae exhibited diel vertical migration, although patterns varied between two feeding stages. Preflexion stage larvae (4.5–9.9 mm SL) were concentrated between 10 and 20 m during the day and deeper at night. Postflexion stage larvae (flexion and postflexion, 10.0–24.5 mm SL) underwent regular diel migrations (0–20 m, night; 10–40 m, day). Low sample sizes limited our ability to assess diel vertical migration in early juveniles, but this stage tends to occur in the upper 20 m of the water column, regardless of time of day. These results suggest that vertical distributions and diel migration potentially are driven by prey availability at sufficient light levels for preflexion larvae to feed and a trade-off between prey access and predation risk for postflexion larvae. Vertical distributions of eggs and preflexion larvae varied with habitat examined (on the continental shelf versus over the continental slope). Vertical distributions of walleye pollock eggs, yolksac larvae, and preflexion larvae in the Bering Sea are different from distributions in other ecosystems, which can impact transport and modeling efforts.

1. Introduction

Information on vertical distributions of early life history stages of fishes is critical for accurate modeling of larval transport to nursery habitats as transport can differ depending on vertical position in the water column (Fiksen et al., 2007; Kristiansen et al., 2009; Miller, 2007; Stenevik et al., 2003; Tanaka, 1991). Ontogenetic vertical migration (OVM) is a pattern in which vertical distribution changes with stage of development. Typically, OVM involves a shoaling in the depth of occurrence as eggs and larvae develop, which allows larvae to exploit high food concentrations and fast currents in surface waters (Fortier and Leggett, 1983; Hare and Govoni, 2005; Norcross and Shaw, 1984). Often OVM is accompanied by increasing complexity of vertical behaviors, such as responsiveness to changes in light intensity (Hare and Govoni, 2005; Heath et al., 1988). Diel vertical migration (DVM) is a behavioral trend in which depth of occurrence changes with time of day and light intensity. DVM typically is exhibited by feeding stages. Larval fish are visual predators, consuming a variety of zooplankton, and as such will orient themselves in the water column to overlap with prey vertical distribution and with light levels sufficient to facilitate feeding (Heath et al., 1988; Porter et al., 2005). Larval fish also are preyed upon by a variety of visual predators and may move down to darker depths during the day time to avoid predation (Hunter and Sanchez, 1976; Yamashita et al., 1985). Regular DVM is the pattern in which larvae move deeper in the water column during the day to avoid visual predators and shallower at night to feed upon zooplankton in surface waters (Kerfoot, 1985; Ohman, 1990). Reverse DVM is the pattern in which larvae migrate to the surface during the day and migrate to depth at night, often as a response to tidal currents or the presence of non-visual predators.

The continental shelf and shelf break areas of the Southeastern Bering Sea (SEBS) are important spawning and nursery grounds for commercially valuable pelagic and demersal fishes, such as walleye

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pollock (*Theragra chalcogramma*, Matarese et al., 2003). The shelf in the SEBS is very broad (~300 nmi), providing a wide area of shallow habitat for developing larvae and juveniles. Walleye pollock spawn in several areas near islands in the SEBS, along the Alaska Peninsula, and in deep-water canyons along the continental slope (Bacheler et al., 2010; Hinckley, 1987). Coupled with the locations of spawning, the dominant currents in the SEBS can deliver walleye pollock early life stages to several different habitats over the continental shelf and slope, each with unique hydrographic and biological characteristics (Coachman, 1986; Stabeno et al., 2001). A coastal domain (<50 m water depth) surrounds all islands and the Alaska mainland and peninsula. The coastal domain is well-mixed. The middle shelf domain (50–100 m water depth) is strongly stratified in summer and characterized by a pool of cold (<2 °C) bottom water in summer that is detrimental to the development of larvae (Napp et al., 2000). The coastal and middle domains are habitat for several species of copepod whose naupliar stages are preferred prey items for larval walleye pollock (Coyle et al., 2011; Hillgruber et al., 1995). The outer shelf domain (100–200 m water depth) is an area of intermittent upwelling in spring and summer, high productivity, strong stratification, and abundant potential predators (Coyle et al., 2011; Hunt et al., 2002; Springer et al., 1996). The slope domain (>200 m water depth) adjoins the Aleutian Basin and is predicted to provide lower growth potential to larvae due to lower prey availability and temperature (Napp et al., 2000). Among the hydrographic domains, walleye pollock larvae are exposed to depth strata with distinct flow regimes, thermal regimes, predation pressures, and prey availability.

Although walleye pollock spawn in a variety of habitats and water depths in the North Pacific, ontogenetic and diel vertical migrations are known for relatively few areas and we have limited knowledge of how habitat interacts with vertical distributions. Vertical distributions have been studied most extensively in the Gulf of Alaska (GOA). In the GOA, walleye pollock early life stages undergo OVM. Eggs occur between 150 and 200 m depth (Kendall et al., 1994), yolksac larvae rise gradually to the surface where feeding larvae are found above the thermocline (Davis and Olla, 1994), and juveniles are primarily pelagic (Brodeur and Wilson, 1996; Laurel et al., 2007). By comparison, in the shallow-water Funka Bay, Japan, eggs and larvae are found at depths less than 50 m with no indication of OVM (Kamba, 1977; Kendall et al., 1987). In the laboratory, regular DVM is initiated once GOA larvae reach 6 mm standard length (SL) and are feeding (Davis and Olla, 1994; Olla and Davis, 1990a). Kendall et al. (1994) found limited DVM in feeding larvae in Shelikof Strait, while larvae in Auke Bay, Alaska, responded to patches of copepod nauplii with regular DVM (Haldorson et al. 1993). Juvenile walleye pollock undergo regular DVM in the western GOA (Brodeur and Rugen, 1994; Olla and Davis, 1990b).

Our knowledge of vertical distributions of SEBS walleye pollock early life stages is limited relative to the GOA (but see Brase, 1996; Hillgruber et al., 1995; Walline, 1981). Egg distribution over the basin is much deeper (400–500 m) than over the shelf (≤ 100 m) (Nishiyama et al., 1986; Serobaba, 1974). Juvenile walleye pollock near the Pribilof Islands undergo regular DVM (similar to the western GOA), presumably in response to prey movement (Schabetsberger et al., 2000). There is currently no assessment of OVM or DVM in SEBS walleye pollock early life stages other than this example. The preferred prey of SEBS larvae, copepod eggs and nauplii, can be found in surface waters and are unlikely to undergo DVM themselves. Fish larvae in the SEBS are exposed to a variety of visual predators (e.g. walleye pollock, Pacific cod) that could drive DVM (Ohman, 1990). Fundamental differences in walleye pollock early life ecology exist between the GOA and SEBS (Bailey, 1989; Duffy-Anderson et al., 2003; Kendall et al., 1994), and it is likely that there are differences in vertical position as well. These differences may be critical, especially in efforts to model transport and habitat use in the SEBS.

The purposes of the present study were: (1) to describe the stage-specific vertical distribution patterns of the early life stages of walleye pollock in the SEBS and (2) to examine potential drivers of differences in distribution such as physical forcing, ontogeny, and trade-offs for survival. To this end, we examined the vertical distribution among life stages for evidence of ontogenetic vertical migration, we compared vertical distributions of each stage among time of day to test for diel vertical migration, and we assessed the interactions between the physical water column and habitat and vertical distribution patterns.

2. Materials and methods

2.1. Study area

The SEBS is bordered to the east by Alaska, to the south by the Alaska Peninsula and eastern Aleutian Islands, to the west by the Aleutian Basin, and to the north by Nunivak Island. Walleye pollock spawning areas included in this study were north of Unimak Island (Bering Canyon), the Alaska Peninsula and near the Pribilof Islands and Pribilof Canyon (Fig. 1). Shelf domains include the coastal domain (<50 m), the middle domain (50–100 m), the outer shelf domain (100–200 m), and the slope domain (depths >200 m, Fig. 1, Coachman, 1986; Stabeno et al., 2001).

2.2. Sampling for Ichthyoplankton vertical distributions

Vertical distributions were determined from depth-specific densities (number per 1000 m^3 of water sampled) derived from sampling with a 1 m^{-2} Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS, 333 or 505 μm mesh equipped with a flow meter to estimate volume filtered by each net). The larger mesh size was used when large phytoplankton blooms were present and clogged the smaller mesh. In a comparative study, Wiebe et al. (1976) found no difference in catchability for walleye pollock early life stages between the two mesh sizes so samples were pooled across mesh size. Walleye

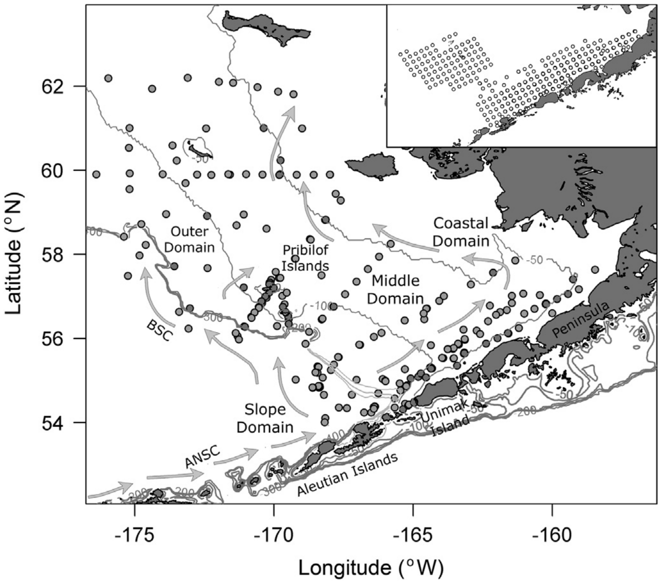

Fig. 1. Vertical distribution tows collected by MOCNESS (gray circles) from 1992 to 2009. Major currents (gray arrows) in this area include the Bering Slope Current (BSC) and the Aleutian North Slope Current (ANSC). Gray lines indicate the 50, 100, 200, and 1000 m isobaths. Walleye pollock spawning areas include the Alaska Peninsula, Bering Canyon (west of Unimak Island), and Pribilof Canyon (south of the Pribilof Islands). Hydrographic domains include three shelf domains (outer, middle, and coastal) and one off-shelf domain (slope). Inset: neuston samples (open circles) collected in 2003 and 2005–2009.

Table 1
Sampling for vertical distribution of walleye pollock (*Theragra chalcogramma*) in the southeastern Bering Sea 1992–2009.

Year	Cruise	Date range (month/day)	MOCNESS tows	CWMD tows	High-resolution tows	Neuston tows
1992	2MF92	4/16–4/22	20	6	0	0
1993	3MF93	4/17–4/28	17	4	0	0
1994	4MF94	4/16–4/27	9	5	0	0
1995	6MF95	4/23–4/30	5	2	2	0
	7MF95	5/5–5/16	9	3	3	0
1996	10MF96	9/7–9/15	21	19	18	0
1997	9MF97	9/11–9/17	13	2	2	0
1999	1MF99	4/17–4/18	6	6	6	0
2003	4MF03	5/18–5/24	9	9	9	53
2005	5MF05	5/10–5/18	20	20	20	71
2006	3MF06	5/9–5/18	12	12	10	90
	6MF06	9/11–9/22	9	9	6	86
2007	4MF07	5/8–5/17	2	2	2	83
2008	1MF08	2/19–2/26	8	8	8	0
	3DY08	5/12–5/21	7	7	7	64
	2HE08	7/3–7/17	44	44	0	0
2009	3DY09	5/8–5/17	2	2	2	77
	1KN09	6/13–7/10	91	91	0	0

1–3 cruises each year conducted MOCNESS tows with a wide range of depth intervals (MOCNESS tows), tows with depth intervals less than 20 m used for catch-weighted mean depths (CWMD tows), tows with depth intervals of 10 m (high-resolution tows), and/or neuston tows.

pollock early life stages were collected in MOCNESS tows in 13 years between 1992 and 2009 (Table 1) by NOAA's Fisheries-Oceanography Coordinated Investigations (FOCI) program. A tow is defined as the unit of sampling with multiple nets within a given tow. Concentration records were divided into stages based on standard length and developmental attributes outlined in the Ichthyoplankton Information System (http://access.afsc.noaa.gov/ichthyo/index.cfm). Catches were divided into five life stages: eggs, yolksac larvae (<4.5 mm SL), preflexion larvae (4.5–9.9 mm SL), postflexion larvae (10.0–24.9 mm SL), and early juveniles (25.0–64.9 mm SL). MOCNESS tows are not ideal for sampling the very surface of the water column, which can contain buoyant eggs. To supplement the information derived from MOCNESS tows, egg densities from Sameoto neuston tows ($30{\times}50\ \text{cm}^2$ mouth opening, 333 or 505 μm mesh), which fished the upper 25 cm of the water column, also were examined in 2003 and 2005–2009.

Temperature and density data were derived from vertical CTD (Sea Bird 19 or 25, Sea-Bird Electronics, Bellevue, Washington, USA) profiles collected concurrently with ichthyoplankton samples from 2002 to 2009. Prior to 2002, CTD vertical profiles matching ichthyoplankton tows in space and time were obtained from the EPIC data archive maintained by the Pacific Marine Environmental Laboratory (http://www.epic.noaa.gov/epic/). Thermo- and pycnocline depths were extracted from CTD casts for each MOCNESS tow. The thermo- and pycnocline depths were defined as the depth at which the greatest rate of change in temperature or density occurred (Coyle and Pinchuk, 2005). Only thermocline depth was examined because pycnocline depth was correlated with thermocline depth. Years were assigned to either cold or warm temperature categories based on May sea surface temperature anomalies (see Smart et al., 2012, for details) to test for differences in vertical distribution with prevailing annual conditions in the study area.

2.3. Ontogenetic vertical migration

Net depth intervals of MOCNESS tows were inconsistent across years and cruises, ranging from 10-m to 100-m intervals. Tows with net depth intervals greater than 20-m in the upper 50 m of the water column were removed from analysis. For the remaining tows, we converted depth-specific concentrations of each stage to catch-weighted-mean depths (CWMD) to provide a comprehensive view of vertical distribution. CWMD was calculated by the following equation:

$$\text{CWMD} = \sum_{i=1}^{n} x_i d_i \Big/ \sum_{i=1}^{n} xi \tag{1}$$

where x_i is the concentration of each stage at each depth interval i, d_i is the midpoint of each depth interval, and n is the total number of depth intervals in each tow. CWMDs were compared by a two-way analysis of covariance (ANCOVA) with stage and temperature category as fixed factors and day of year (DOY), thermocline depth (m), and bottom depth (m) as covariates (Sokal and Rohlf, 1995). The concentration of eggs in neuston tows was compared by one-way ANCOVA with temperature category as a fixed factor and thermocline depth and bottom depth as covariates. Neuston samples were collected primarily during two weeks in May, so we did not examine DOY as a covariate.

2.4. Diel vertical migration

Tows that sampled in 10-m net depth intervals in the upper 50 m of the water column (high-resolution tows) were used to examine diel vertical migration behavior of early life stages. Depth strata of high-resolution tows were 0–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m, 50–100 m, 100–200 m, and 200–300 m. Concentrations collected at each depth strata varied widely among samples and tows. Depth-specific concentrations from high-resolution tows were standardized among tows by conversion to the proportion of the total concentration in each tow collected at each depth stratum to remove any effect of differences in concentration among domains, years, or times of day. Each tow was assigned to either day time or night time (time of day, TOD) based on time and date of collection (Brodeur and Rugen, 1994). Tows collected in February between 0900 and 1900 were considered day time tows and tows collected between 1900 and 0900 were considered night time tows, in April and May, day time was 0630–2130 and night time was 2130–0630, and in September day time was 0700–2100 and night time was 2100–0700. Dusk and dawn categories were not used because there was no replication available for these time periods. Each tow also was assigned to a shelf domain to compare distributions among habitats.

The effects of depth stratum, TOD, and domain on proportion of each stage were examined using generalized additive mixed models (GAMMs) with TOD as a fixed factor, depth stratum and domain as continuous covariates, and tow as a random variable (Zuur et al., 2009). Temperature and bottom depth were initially examined as continuous covariates but were not chosen during the model fitting process. Models were fitted by comparing Akaike's Information Criterion values and removing non-significant variables until the best fit model was selected (Akaike, 1974). The negative binomial error distribution was a better fit to the data compared to other alternates, such as the Poisson, Gaussian, and lognormal distributions. Interactions between depth stratum and TOD were included to test for diel vertical migration. Interactions between depth stratum and domain were included to test for differences in vertical distributions among areas or habitats.

3. Results

3.1. Sampling for ichthyoplankton vertical distributions

Catches ranged from no early life stages collected to depth-specific concentrations of up to 540,000 individuals $1000\ \text{m}^{-3}$. Over 200,000 walleye pollock eggs, 34,000 larvae, and 125 early juveniles were collected by MOCNESS sampling since 1992.

3.2. Ontogenetic vertical migration

Walleye pollock CWMD and variability in CWMD decreased with ontogeny (Tables 2 and 3). CWMD was influenced by DOY, bottom depth, and thermocline depth. CWMD of all stages decreased with DOY (Table 3). CWMD of all stages except postflexion larvae increased with bottom depth (Table 3). CWMD of all stages except early juveniles increased with thermocline depth (Table 3). There was no difference in stage-specific CWMD or overall CWMD with temperature category. Eggs were collected at higher densities in surface neuston tows in cold years than in warm years (Table 4).

3.3. Diel vertical migration

There was no evidence of DVM in walleye pollock eggs (Table 5, Fig. 2), but the domain in which they were collected interacted with the depth stratum in which proportion of total egg concentration was highest (Table 5, Fig. 3). Eggs were found ≤ 30 m in all three shelf domains but ≥ 100 m over the slope. Walleye pollock eggs occurred throughout the water column, but proportion of concentration was higher in the upper 20 m or below 100 m relative to the middle of the water column. There was no difference in yolksac larval depth distribution between TODs (Table 5, Fig. 4). There were not enough replicate samples in multiple domains to assess for yolksac larvae. Yolksac larvae occurred at depths less than 100 m, and proportion of concentration was highest from 10–40 m relative to other depth strata.

For the two feeding larval stages, differences evidence for DVM were found. Preflexion larval depth distribution differed between TODs although the level of significance was marginal (Table 5, Fig. 5). Overall, preflexion larvae were shallower and more concentrated in the day time than at night time. Preflexion larvae were shallower over the shelf (10–20 m) than over the slope (20–30 m, Fig. 6). The interactions between depth strata and TOD were significant for postflexion larvae (Table 5). Postflexion larvae exhibited regular DVM; deeper during the day (10–40 m) than at night (0–20 m, Fig. 7). Domain did not interact with depth stratum for postflexion larvae (Fig. 8). Proportion of postflexion larval concentration was highest above 30 m and lowest below 30 m relative to other strata.

Table 2
Ontogenetic vertical distributions.

	Eggs	Yolksac larvae	Preflexion larvae	Postflexion larvae	Early juveniles
Mean	33.1	29.3	21.5	20	18.5
Std. Dev.	46.7	15.4	11.4	10.1	8.9

Summary of catch-weighted-mean depths (m; mean and standard deviations [Std. Dev.]) of walleye pollock (*Theragra chalcogramma*) early life stages in the Southeastern Bering Sea.

Table 3
Ontogenetic vertical distribution analyses.

Factor	df	SS	MS	*F*	*p*
Stage	4	1.05×10^{4}	2.60×10^{3}	2.743	**0.029**
Temperature	1	3.00×10^{2}	3.00×10^{2}	0.314	0.575
Stage×Temperature	4	1.14×10^{3}	2.84×10^{2}	0.299	0.878
DOY	1	1.76×10^{4}	1.76×10^{4}	18.592	< **0.001**
Bottom depth	1	1.14×10^{4}	1.14×10^{4}	11.991	**0.001**
Thermocline depth	1	9.09×10^{3}	9.09×10^{3}	9.577	**0.002**
Error	340	3.23×10^{5}	9.49×10^{2}		

Comparisons of catch-weighted-mean depths of walleye pollock (*Theragra chalcogramma*) early life stages and the physical characteristics that influence them. Degrees of freedom (df), sum of squares (SS), mean squares (MS), and f-ratios (*F*) are shown for all stages. *P*-values (*p*) in bold were significant at $\alpha=0.05$.

Table 4
Ontogenetic vertical migration.

Factor	df	SS	MS	*F*	*p*
Temperature	1	4.03×10^{9}	4.03×10^{9}	5.745	**0.017**
Bottom depth	1	1.04×10^{9}	1.04×10^{9}	1.481	0.224
TC depth	1	1.12×10^{9}	1.12×10^{9}	1.598	0.207
Error	513	3.60×10^{11}	7.02×10^{8}		

Comparisons of walleye pollock (*Theragra chalcogramma*) egg densities in the surface neuston layer and the physical characteristics that influence them. Degrees of freedom (df), sum of squares (SS), mean squares (MS), and f-ratios (*F*) are shown. *P*-values (*p*) in bold were significant at $\alpha=0.05$.

Table 5
Diel vertical distributions.

Stage	Factor	df	*F*	*p*
Eggs	Depth	2.85	19.3	< **0.001**
	TOD	1	0.6	0.439
	Domain	1	9.65	**0.002**
	Depth×TOD	3.91	3.88	0.1
	Depth×Domain	8	8.25	**0.001**
Yolksac larvae	Depth	2.72	8.08	**0.001**
	TOD	1	0.11	0.738
	Depth×TOD	4.1	2.48	0.349
Preflexion larvae	Depth	2.84	23.4	**<0.001**
	TOD	1	0.34	0.561
	Domain	1	0.17	0.678
	Depth×TOD	3.26	7.12	**0.034**
	Depth×Domain	4.21	3.89	**0.046**
Postflexion larvae	Depth	2.42	6.67	**0.001**
	TOD	1	0.04	0.847
	Domain	1	0.56	0.455
	Depth×TOD	2.78	4.48	**0.014**
	Depth×Domain	2.65	2.01	**0.131**
Early juvenile	Depth	2.49	3.39	0.03
	TOD	1	0.01	0.951
	Domain	1	0.01	0.963
	Depth×TOD	2.83	2.44	0.144
	Depth×Domain	2.63	0.65	0.616

Generalized additive mixed models for differences in proportion of total density of walleye pollock (*Theragra chalcogramma*) early life stages among depth strata (Depth), times of day (TOD), and domains. Degrees of freedom (df) or estimated degrees of freedom, *f*-ratios (*F*), and *p*-values (*p*). *P*-values in bold were significant at $\alpha=0.05$.

Sample sizes for early juveniles were low relative to the other stages. Early juveniles tended to occur deeper at night than during the day, but the interaction between TOD and depth strata was not significant (Table 5, Fig. 9). Early juvenile vertical distribution was not affected by domain (Fig. 10). Early juveniles occurred at depths less than 100 m with greatest concentration from 0 to 20 m.

4. Discussion

Ontogenetic and diel vertical migrations have adaptive significance for planktonic organisms, including optimal transport, energy conservation, access to prey, and avoidance of predators (Fortier and Leggett, 1983; Hare and Govoni, 2005; Hunter and Sanchez, 1976). For walleye pollock in the SEBS, spawning occurs in either deep-water canyons or over the shelf, eggs are buoyant, and juveniles are abundant over the shelf. Here, prey concentrations are highest in the upper water column and visual predators occur in the water column and near the benthos. Based on these

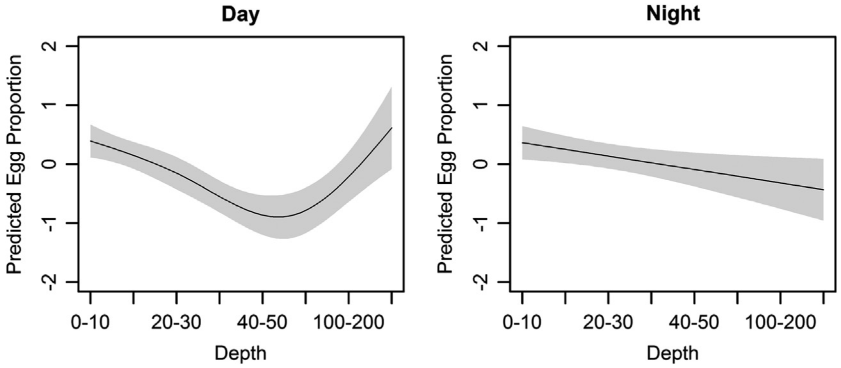

Fig. 2. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) eggs during day and night from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

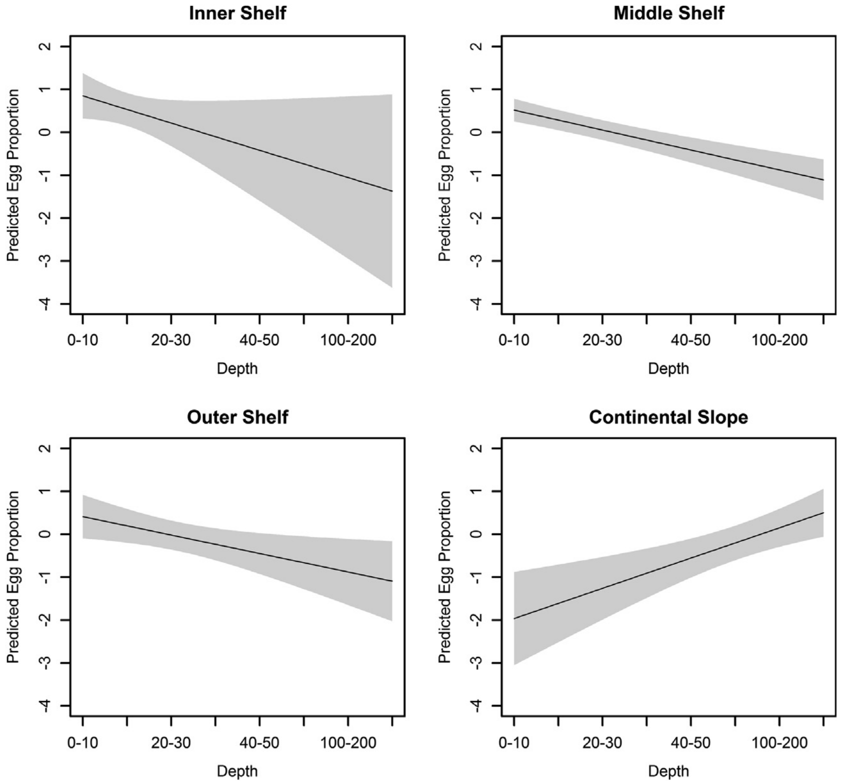

Fig. 3. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) eggs among domains from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

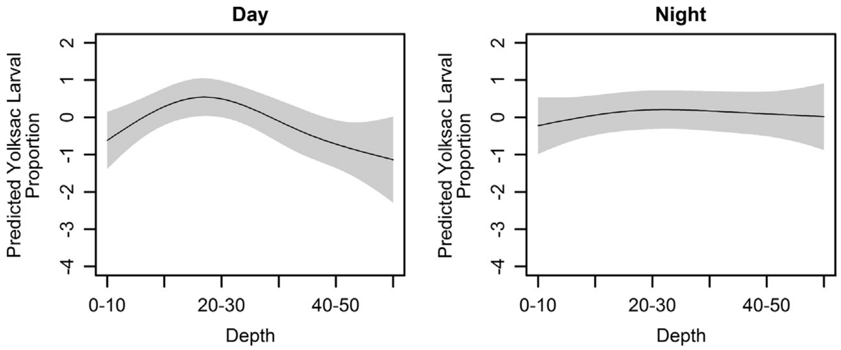

Fig. 4. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) yolksac larvae during day and night from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

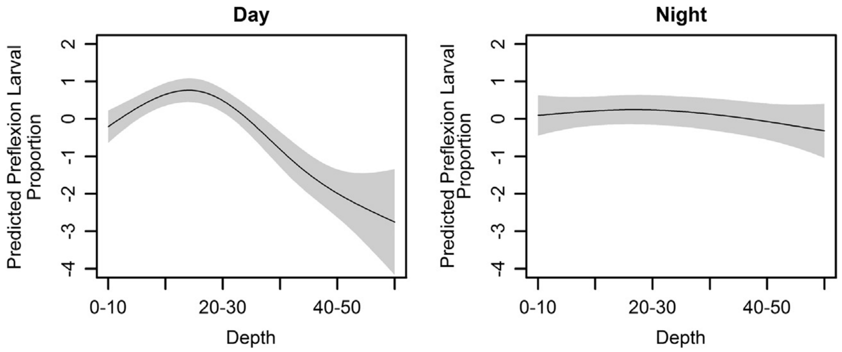

Fig. 5. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) preflexion larvae during day and night from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

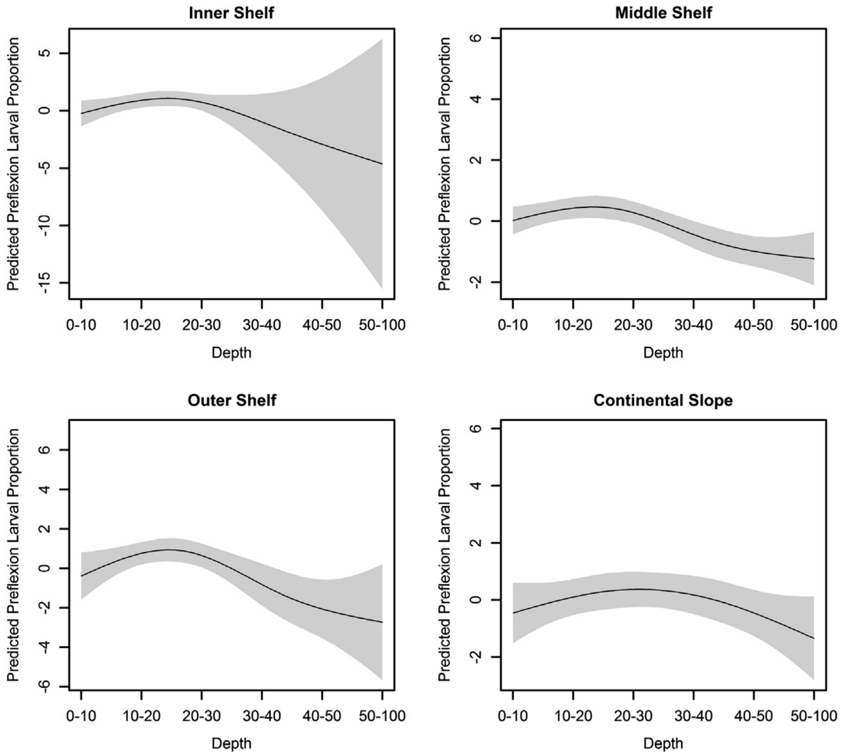

Fig. 6. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) preflexion larvae among domains from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

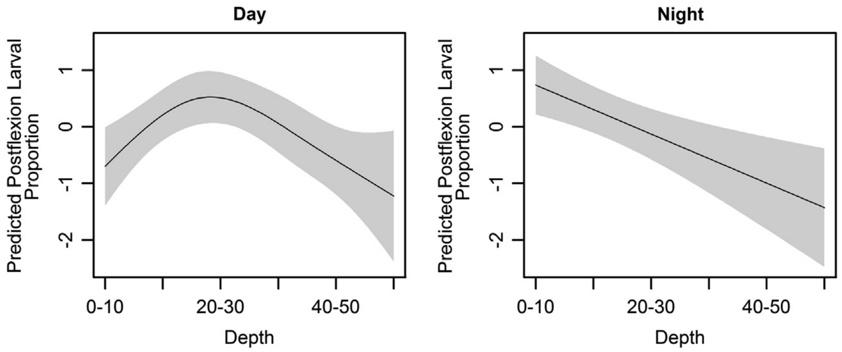

Fig. 7. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) postflexion larvae during day and night from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

characteristics, we would expect vertical migration strategies that maximize on-shelf transport from spawning grounds over the basin or retention over the shelf, such as a decrease in depth of occurrence to provide access to prey and minimize predation risk, such as OVM and regular DVM (Kerfoot, 1985). For walleye pollock early life stages in the SEBS, depth distribution became shallower and variability in depth distributions decreased with ontogeny supporting OVM, similar to the GOA but unlike Funka Bay.

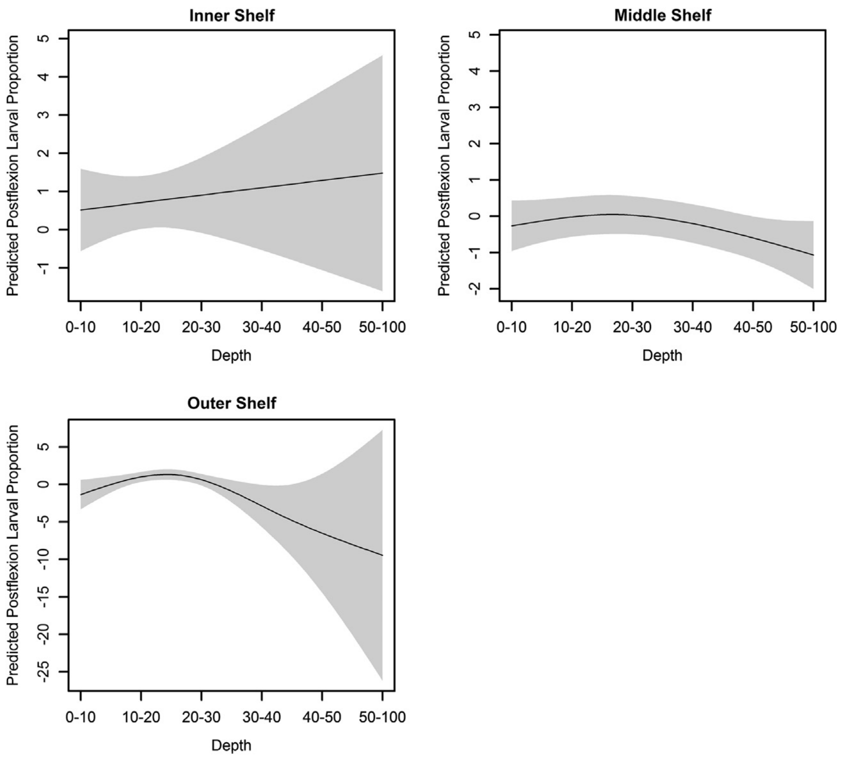

Fig. 8. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) postflexion larvae among domains from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

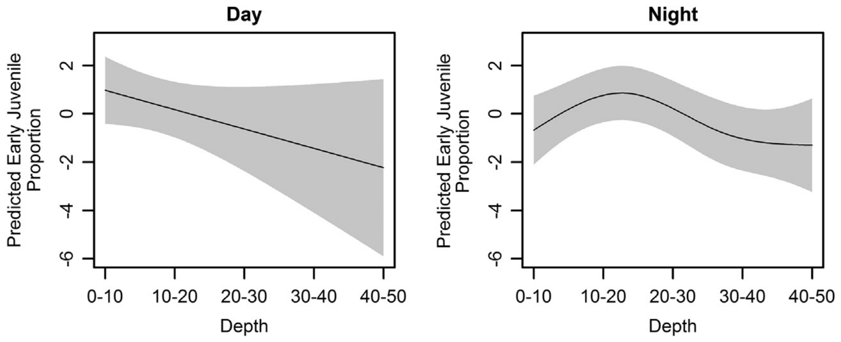

Fig. 9. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) early juveniles during day and night from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

Weighted mean depths decreased with the progression of summer as stratification tended to increase. Weighted mean depths also decreased as bottom depth decreased and as the thermocline depth decreased (except juveniles), suggesting that distributions mirror the breadth of the available water column. Two of the five early life stages examined exhibited evidence of DVM: reverse in preflexion larvae and regular in postflexion larvae. These two stages are active feeders, while eggs and yolksac larvae are nonmotile or weak swimmers and would not be expected to exhibit distribution patterns typically associated with active behaviors. Sample sizes for early juveniles were too small to assess DVM adequately.

OVM in walleye pollock provides several advantages for the early life stages. First, the majority of eggs over the slope were found deeper than 40 m, where they are exposed to the deep water Aleutian North Slope Current through Bering Canyon or the Bering Slope Current through Pribilof Canyon. Eggs spawned offshore, therefore, can be transported onto the shelf by these currents rather than advected further over the Aleutian Basin by cyclonic flow above these currents (Reed and Stabeno, 1999). Second, high egg densities were observed in the neuston layer over the shelf in cold years when surface temperatures were comparable to temperatures below in deep water in warm years (Stabeno et al., 2012), allowing for extended development times and, by extension, the potential for increased time for on-shelf transport in cold years, regardless of the vertical position. High egg densities in the surface layer in cold years could be the result of a passive rise to the surface in the absence of a distinct density structure in the water column or the result of delayed hatching at low temperatures. Third, yolksac larvae in the cooler waters below 20 or 30 m depth will conserve energy and extend the period of time before yolk reserves are exhausted and exogenous feeding must begin, which can be advantageous if larvae have not been transported far enough over the shelf to where prey are available. Fourth, following the rise to the upper 20 m of the water column, feeding larvae have access to prey in the upper water column (Coyle and Pinchuk, 2005) and warmer water, both of which reduce development time.

DVM typically is exhibited by feeding stages reacting to changes in time of day and light intensity, and walleye pollock conform to this pattern. As expected, neither eggs nor yolksac

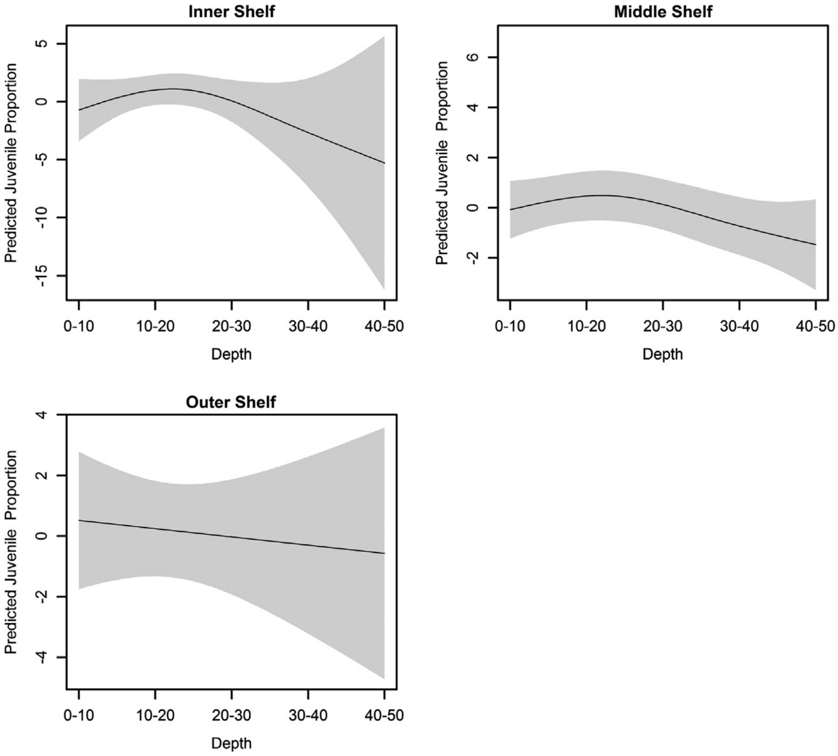

Fig. 10. Vertical distribution of southeastern Bering Sea walleye pollock (*Theragra chalcogramma*) early juveniles among domains from high-resolution MOCNESS tows. Line represents predicted proportions for each depth interval with 95% confidence intervals (shaded area).

larvae exhibited a pattern consistent with DVM. Vertical distributions of nonmotile or nonfeeding stages are driven generally by physics such as buoyancy or passive mixing. These two early stages displayed passive patterns which also suggests that diel differences in vertical distribution exhibited by feeding stages was driven by behavior rather than by diel changes in the physical water column. In preliminary analyses, we found no differences in the thermocline depth between day and night. Surprisingly, we were unable to conclude that early juvenile walleye pollock undergo DVM, although they tended to be deeper at night in the few tows in which they were collected. There is evidence from both laboratory (Sogard and Olla, 1996) and field (Bailey, 1989) studies that vertical migration in shorter juveniles (<60 mm) in the GOA is weak and the migration to deeper layers intensifies as the fish gain locomotory and sensory capabilities. Schabetsberger et al. (2000) documented DVM in juvenile walleye pollock between 30 and 92 mm SL near the Pribilof Islands. The juveniles in the present study were all shorter than 65 mm SL, supporting that DVM in these shorter fish is weak in the SEBS and consistent with the previous findings in the GOA. However, we were unable to address any impacts of predator presence or net avoidance in the current study.

Walleye pollock feeding larvae appear to take advantage of surface food concentrations, as they primarily occurred shallower than 30 or 40 m at the onset of feeding. We did not have samples to determine directly the vertical distributions of the preferred prey items, copepod eggs and nauplii. Walleye pollock undergo a transition from predominantly day time feeding as larvae (Canino and Bailey, 1995) to nocturnal feeding as juveniles (Brodeur et al., 2000). This is allowed by increased visual acuity and sensitivity to light with ontogeny (Carvalho et al., 2004; Miller et al., 1993). Preflexion larval distributions were consistent with reverse DVM (up during the day, down at night) and postflexion larvae underwent regular DVM (down and variable during the day, up at night), suggesting that different trade-offs between prey access, predator avoidance, and perhaps physical forces could be acting on the two stages. Other studies have found that copepod nauplii do not undergo diel vertical migrations (Haldorson et al., 1993; Irigoien et al., 2004). By moving into surface waters during the day when light levels are high and where their preferred prey likely occur (Brase, 1996; Hillgruber et al., 1995), preflexion larvae could have higher success capturing prey since visual acuity is low relative to later stages. Postflexion larvae would have higher capture success in surface waters at night at reduced light levels than preflexion larvae because of their improved visual acuity. Postflexion larvae are large enough to be of interest to visual predators such older age class walleye pollock (Juanes, 2003), which could lead to the pattern of avoiding surface waters during the day. Alternately, postflexion larvae in surface waters during the day may have been better able to avoid our collection gears due to their visual acuity and swimming abilities.

Walleye pollock vertical distributions vary among habitats both in the SEBS and the GOA. Forward et al. (1996) found three different patterns of vertical distribution for Atlantic menhaden (*Brevoortia tyrannus*) in three separate studies and suggested that vertical behaviors are flexible in order to incorporate necessary trade-offs that vary between ecosystems or habitats. Eggs in the SEBS were concentrated either below 100 m (slope) or in the upper 30 m (shelf domains), indicative of where they were spawned and probably their buoyancy (Kendall and Nakatani, 1992). SEBS yolksac larvae were concentrated around 30 m. In the GOA, eggs are spawned at or below 150 m, followed by an increase in depth prior to hatching (Kendall et al., 1994). GOA yolksac larvae remain at depths >150 m for several more days. One obvious difference between these systems is the depth of the water column and depth of spawning activity. Olla et al. (1996) proposed that remaining at the spawning depth in the GOA provided a predator refuge for eggs and yolksac larvae, an option that is not available in most of the SEBS habitats due to their relatively shallow water column. SEBS preflexion larvae underwent reverse DVM in most habitats and no DVM in the coastal domain. DVM is either regular or absent for preflexion larvae in the GOA (Davis and Olla, 1994; Olla and Davis, 1990a). In the shallow-water coastal domain, the stimulus to move up during the day (e.g. sufficient light for hunting) may not be in place for SEBS preflexion larvae because sufficient light levels are available throughout the shallow (≤ 50 m) water column (Kendall and Nakatani, 1992). Similar to larvae in the GOA, coastal domain SEBS preflexion larvae also could respond to very high light levels at the surface during the day with negative phototaxis (Olla and Davis, 1990a). Postflexion larvae in the SEBS undergo regular DVM, in accordance with behavior observed near Auke Bay, Alaska, GOA (Haldorson et al., 1993). In Auke Bay, larvae migrated in response to the trade-off between the vertical distribution of nauplii and avoidance of predators. For postflexion larvae, visual predators occur in all areas in which this stage was collected and the same potential predators occur in the SEBS, suggesting that the trade-off between feeding and predation risk could be a common factor across habitats and ecosystems for this stage. We did not find support for DVM in SEBS early juveniles most likely due to small sample sizes, but juveniles undergo regular DVM in the GOA (Brodeur and Rugen, 1994; Olla and Davis, 1990b) and larger juveniles near the Pribilof Islands in the SEBS undergo regular DVM in response to prey movement (Schabetsberger et al., 2000).

Smart et al. (2012) found shifts in the spatial distributions of walleye pollock larvae and juveniles between cold years and warm years. The authors hypothesized that spatial shifts were driven by changes in area-specific mortality or transport. Satellite-tracked drifters and hydrographic models show high variation in on- and off-shore transport among years (Danielson et al., 2011; Stabeno et al., 2012), which could be linked to temperature conditions (Sohn et al., 2010) and might explain the differences in spatial distribution. Annual differences in vertical distributions could impact the amount of transport off-shore if larvae respond to variations in conditions with adjustments in their vertical distributions (Napp et al., 2000). We found no support for differences in vertical distributions related to categorizing years as either cold or warm.

5. Conclusions

Current speeds in the SEBS middle shelf tend to be slow relative to other spawning areas for walleye pollock (<5 cm s^{-1}, Napp et al., 2000). Because of these slow speeds, the probability of retention over the spawning grounds is high. Some off-shelf spawning grounds such as Bering Canyon may not have the highest growth potential, thus selection for an ontogenetic migration toward the surface where transport onto the shelf would be enhanced is likely in the SEBS. Walleye pollock early life stages underwent ontogenetic vertical migration and feeding stages were found in the upper portion of the water column where prey availability is high typically. Feeding larvae also exhibited diel vertical migrations that suggest trade-offs occurred between access to prey and exposure to predators. Characteristics of the habitat and ecology of each stage suggested that some determinants of vertical distribution are common between the SEBS and GOA (i.e. prey, light levels, predators) while others are not (i.e. depth refuges, spawning depth). Several hypotheses developed for the SEBS have linked variation in recruitment to the level of overlap between juveniles and their predators or juveniles and their prey, which in turn may be related to the extent and direction of transport. For example, Wespestad et al. (2000) found that strong year classes were linked to high spatial segregation of juveniles and cannibalistic older age classes. The authors proposed that juvenile distribution was closely tied to the transport and distribution of eggs and larvae. One way to address the connection between these various life stages is to model transport. Our results clearly demonstrated that pollock larvae are not passive particles, early life stages are not distributed randomly throughout the water column, and vertical distributions from the GOA are not comparable to all stages in the SEBS. Accurate modeling needs to account for variation in vertical distribution and behavior among stages and habitats, and these data are now available for the SEBS.

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