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Juvenile walleye pollock (*Theragra chalcogramma*) are one of the primary prey items for bird and mammal predators in the Bering Sea and support a large commercial fishery. An understanding of the environmental factors that determine the horizontal and vertical distribution of juvenile pollock is needed to estimate the effects that environmental variation may have on pollock and their predators. During the summers of 2008 and 2009, surveys were conducted in three topographic zones (Middle Shelf, Outer Shelf, and Slope) near the Pribilof Islands in the southeastern Bering Sea. Environmental data collected for each transect included temperature, salinity, depth, dissolved oxygen, and chlorophyll a fluorescence. Additionally, each transect consisted of 10 km of multi-frequency acoustic sampling, a vertically integrated zooplankton net tow, and a targeted oblique fish tow. In 2008, juvenile pollock were found primarily in the Middle Shelf zone and were dominated by small young of the year individuals. In 2009, juvenile pollock were significantly less abundant, young of the year were larger, and vertical distributions were much deeper. In both years, juvenile pollock horizontal distribution was highly variable and not well explained by the physical environment. Temperature structure (thermocline depth, mean temperature at pollock depth, and mean temperature above the thermocline) explained 70% of the variability in the vertical distribution of age-0 pollock which also varied with time of day and topographic zone. These differences in horizontal and vertical distribution are likely to affect the use of habitat by predators and may have implications for future sampling.

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Horizontal and Vertical Distribution of Juvenile Pollock (*Theragra chalcogramma*) in the Southeastern Bering Sea

by
Neal E. McIntosh

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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Neal E. McIntosh, Author

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CONTRIBUTION OF AUTHORS

Dr. Kelly Benoit-Bird assisted with data collection and processing, and was involved in the design and writing of all chapters. Dr. Scott Heppell collected and provided some of the data used in Chapter 2.

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Chapter 1 – Introduction

The Bering Sea ecosystem supports vast numbers of fish, seabirds, and marine mammals, and supplies most of the seafood consumed in the United States (Hiatt et al. 2004). Climate change has been shown to cause changes within physical and biological aspects of the Bering Sea ecosystem (Grebmeier et al. 2006). The Intergovernmental Panel on Climate Change (2007) estimated that the ocean has absorbed more than 80% of the heat added to the climate system, and that global water temperature has increased to depths of at least 3000 meters. This could have serious impacts on marine species, particularly on cold water species such as those that live in the Bering Sea. Impacts could include changes in abundances or northward expansions of distribution range.

On a regional scale, the timing of the ice retreat in the Bering Sea may affect distributions and abundances of potential prey for seabirds and pinnipeds. Hunt et al. (2002) predicted that years with late ice retreat, “cold years”, will have poor recruitment of fish, but that species that prefer cold water may be more accessible to central place foragers on the Pribilof Islands. In contrast, “warm years” should have stronger year classes of fish, but the distribution of cold water species may shift away from the islands (Hunt et al. 2002). Hunt et al. (2002) suggest that the mechanisms of control on the ecosystem shift between bottom-up in cold years to top-down in warm years.   If this hypothesis is correct, this could result in other significant, long term changes in ecosystem function with changing climate.

In order to better predict the effects that climate change may have on the Bering Sea ecosystem, the National Science Foundation and the North Pacific Research Board funded a large, interdisciplinary, ecosystem wide research project in the Bering Sea. The goal has been to better understand ecosystem processes such as physical oceanography, atmospheric interactions, human impacts, and trophic interactions in order to understand how climate change may impact those processes.

Top predators such as seabirds and marine mammals are a highly visible component of the Bering Sea ecosystem, making them prime indicator species for studies of climate change. The breeding success of seabirds on the Pribilof Islands has been shown to have been stable or on a steady decline over the past thirty years (Byrd et al. 2008).   Due to the low abundance of seabird nest predators on the Pribilof Islands, it has been hypothesized that breeding success depends on prey quality and availability (Byrd et al. 2008). Changes in climate are likely to alter the quality, abundance, and distribution of the prey on which seabird and fur seals depend. The Patch Dynamics Study, a part of the large ecosystem wide study, examined seabird and pinniped foraging in relation to the prey available.   Other researchers from the Patch Dynamics Study are investigating seabird foraging behavior and marine mammal, particularly Northern fur seal (*Callorhinus ursinus*), foraging behavior in the southeastern Bering Sea. This thesis and related contributions (e.g. (Benoit-Bird et al. in review)) address the availability, distribution, and behavior of prey near the Pribilof Islands and Bogoslof Island.

The Pribilof Islands and Bogoslof Island were chosen for study of predator-prey interactions in the Bering Sea since nearly three quarters of the world's Northern fur seal population spend the summer breeding season in rookeries on the Pribilof Islands (Angliss and Lodge 2004), and the islands have some of the largest seabird colonies in the Northern Hemisphere (Hickey and Craighead 1977). Additionally, the Pribilof Islands are geographically isolated, and typically mark the southern extent of the winter ice cover and the summer cold pool, suggesting that this area would be particularly sensitive to changes in climate. One goal of the Patch Dynamics Study was to investigate the distributions of potential prey for the central place foragers of the Pribilof Islands and Bogoslof Island and identifiy the factors that might be driving the distributions of prey species. The specific objective of this study was to determine the environmental factors that controlled the distribution of juvenile pollock patches, near the Pribilof Islands during the summers of two cold years.

Chapter 2 - Horizontal and Vertical Distribution of Juvenile Pollock (*Theragra chalcogramma*) in the Southeastern Bering Sea

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ABSTRACT

Juvenile walleye pollock (*Theragra chalcogramma*) are one of the primary prey items for bird and mammal predators in the Bering Sea and support a large commercial fishery. An understanding of the environmental factors that determine the horizontal and vertical distribution of juvenile pollock is needed to estimate the effects that environmental variation may have on pollock and their predators. During the summers of 2008 and 2009, surveys were conducted in three topographic zones (Middle Shelf, Outer Shelf, and Slope) near the Pribilof Islands in the southeastern Bering Sea. Environmental data collected for each transect included temperature, salinity, depth, dissolved oxygen, and chlorophyll a fluorescence. Additionally, each transect consisted of 10 km of multi-frequency acoustic sampling, a vertically integrated zooplankton net tow, and a targeted oblique fish tow. In 2008, juvenile pollock were found primarily in the Middle Shelf zone and were dominated by small young of the year individuals. In 2009, juvenile pollock were significantly less abundant, young of the year were larger, and vertical distributions were much deeper. In both years, juvenile pollock horizontal distribution was highly variable and not well explained by the physical environment. Temperature structure (thermocline depth, mean temperature at pollock depth, and mean temperature above the thermocline) explained 70% of the variability in the vertical distribution of age-0 pollock which also varied with time of day and topographic zone. These differences

in horizontal and vertical distribution are likely to affect the use of habitat by predators and may have implications for future sampling.

INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) is a generally demersal fish species native to the North Pacific Ocean. Juvenile walleye pollock are an important trophic link in the Bering Sea ecosystem as young of the year (age-0) pollock primarily prey on small zooplankton such as copepods (Brodeur et al. 2000). In turn juvenile pollock are prey for several demersal fish species, especially adult walleye pollock, sea birds such as common and thick-billed murres, and marine mammals such as Northern fur seals (Livingston 1993). At age 3, walleye pollock recruit to the largest commercial fishery in the United States (Livingston 1993).

Studies of age-0 walleye pollock in the Bering Sea have focused mostly on the Bering Sea Shelf and the frontal features near the Pribilof Islands (Brodeur et al. 2000; Ciannelli et al. 2002; Winter et al. 2005), an important predator breeding site. According to the Oscillating Control Hypothesis proposed by Hunt et al. (2002), warm years in the Bering Sea are expected to yield strong year classes of walleye pollock, and cold years are expected to result in poor year classes of pollock, suggesting that temperature may play an important role in determining the survival and distribution of juvenile pollock. Ciannelli et al. (2002) examined age-0 pollock distributions in relation to their prey near the Pribilof Islands, and found that age-0 pollock distributions were influenced by different mechanisms between their study years and locations with factors such as growth potential, prey availability, advection, and predator avoidance all potentially playing a role in the distribution of age-0 pollock. Winter et al. (2005) suggested that adult walleye pollock year class strength was determined by age-0 pollock feeding success, and they observed possible instances of prey depletion by age-0 walleye pollock near the Pribilof Islands. These studies have primarily found higher abundances of age-0 pollock on the Middle Shelf (<100 m depth) and lower abundances with more variability on the Outer Shelf (100-200 m depth) and into the Pribilof Canyon (>200 m) (Swartzman et al. 2002; Brodeur et al. 2002; Winter et al. 2005).

Studies that have focused on the vertical distribution of juvenile walleye pollock have primarily concentrated on diel vertical migration. Bailey (1989), Swartzman et al. (1999), and Schabetsberger et al. (2000) used acoustics to analyze the diel variability in the vertical distribution of juvenile pollock. Schabetsberger et al. (2000) showed that juvenile walleye pollock migrated vertically from deeper waters during the day to nearer the surface at night, likely following their vertically migrating zooplankton prey. Bailey (1989) found that juvenile pollock were ten times more abundant in surface waters during the night than during the day; he hypothesized that vertical migration of age-0 walleye pollock is based on food availability, with small vertical migrations when food is plentiful and large migrations out of the warm upper ocean layers when food is scarce. Swartzman et al. (1999)

observed diel vertical migration of juvenile pollock, but found that age-0 pollock were in close proximity to, and typically above, the thermocline regardless of time of day.

The distribution of juvenile walleye pollock in the horizontal and vertical spatial domain is important to predators searching for pollock as prey. For example, breeding seabirds and pinnipeds that rely on islands would expend less energy and spend less time away from their offspring on a 10 kilometer foraging trip than a 100 kilometer foraging trip. The vertical distribution of prey is also of great importance to air-breathing predators as depth of prey can also influence prey availability and foraging time underwater. If juvenile pollock are deeper than a predator's diving capacity, the predator will have to change its behavior accordingly by either finding shallower pollock, other prey, or waiting for pollock to vertically migrate. Additionally, physiological costs for these air-breathing predators are likely higher for deeper dives (Croll et al. 1992).

The objective of this study was to understand the physical and biological environmental drivers that influence the small scale vertical and horizontal distribution of juvenile walleye pollock in proximity to seabird and fur seal breeding colonies in the southeastern Bering Sea, as inaccessibility to juvenile pollock as a prey source might negatively impact the reproductive success of those predators. It is important to determine what conditions are driving those distributions at a scale that is comparable to the scale at which seabird and mammal predators are searching for prey. To that end, this study was conducted on a fine spatial scale, with many closely spaced, short transects, stratified across different topographic zones radiating around the Pribilof Islands, in order to examine the distributions of juvenile walleye pollock in a manner that approximates how a central place forager might search for prey.

METHODS

Study Site

The Pribilof Islands are an archipelago on the edge of the Bering Sea shelf, west of mainland Alaska and north of the Aleutian Island chain. The two largest islands, St. Paul and St. George, are located approximately 90 km apart, and make up 97% of the landmass of the archipelago (Stabeno et al. 1999). There is a tidally driven front separating the well-mixed water close to each island from the highly stratified waters of the Bering Sea shelf (Stabeno et al. 1999). The islands and the surrounding waters are highly productive, and serve as a nursery area for juvenile walleye pollock (Swartzman et al. 1999). During the summer, the islands harbor some of the largest seabird colonies in the Northern hemisphere (Hickey and Craighead 1977), and have Northern fur seal (*Callorhinus ursinus*) rookeries that account for nearly three quarters of the worldwide population (Angliss and Lodge 2004). The large abundance of juvenile pollock predators relying on the Pribilof Islands and the highly productive, heterogeneous habitat in the nearby waters make it an ideal place to study small-scale distributions of age-0 walleye pollock.

Field Data

Data were collected using chartered fishing vessels from mid-July to mid-August of 2008 and 2009 in the southeastern Bering Sea near the Pribilof Islands, Alaska along a number of 10-km long transects. Each transect consisted of a CTD cast at the start of the transect to measure oceanographic characteristics, a vertical net tow for mesozooplankton, a targeted trawl for euphausiids and forage fish, 10 km of multi-frequency acoustics to estimate euphausiid and fish biomass and distribution, and a second CTD cast at the end of the transect.

In 2008, 110 transects were surveyed from the F/V Frosti from 13 July to 7 August. In 2009, 141 transects were completed with duties split between the F/V Frosti and the F/V Gold Rush from 18 July to 12 August (Fig. 1). In 2008, sixty transects were planned pre-cruise, and were distributed randomly within three topographic zones within 200 km of St. Paul, Alaska [57^{o}08’05” N, 170^{o}19’34” W]. Topographic zones were determined by depth following previous studies in this area; the Middle Shelf zone had depths from 50-100 m, the Outer Shelf zone from 100-200 m, and the Slope zone >200 m (Coachman 1986). Three of the 20 planned transects within each zone were designated as repeat transects and were visited multiple times throughout the cruise. In 2009, the study area was expanded to include waters near Bogoslof Island, Alaska [53^{o}56’09” N, 168^{o}02’20 W]. In addition to re-surveying transects that were randomly chosen in 2008, in 2009, 15 additional random transects were added to the outer shelf zone and 36 to the slope zone. Additional “adaptive” transects were added on an ad-hoc basis during the cruise based on several criteria, including: large patches of fish or euphausiids observed using acoustics, large aggregations of feeding birds or mammals seen on the water, or reports of telemetry-tagged birds or mammals from another study that were in the vicinity of vessel surveys. In 2008 five of the adaptive transects were used to sample near the Pribilof Islands; these five transects were re-sampled in 2009 as planned transects.

Multi-frequency acoustic data were collected using Simrad EK60 split-beam echosounders along all transects and for the majority of the time the vessels were in transit through the study area. Transducers were affixed approximately one meter below the surface to a rigid pole mount attached to the side of the vessel. The maximum vessel speed for acoustic surveys was 15 km h^{-1}. Acoustic frequencies used were 38 kHz, 70 kHz, 120 kHz, and 200 kHz. The 38 kHz system had a conical beam angle of 12^{o}; the 70, 120, and 200 kHz systems each had a conical beam angle of 7^{o}. The pulse length for all frequencies was 256 µs. Echosounders were calibrated, following the method described by Foote et al. (1987), with a 38.1 mm diameter tungsten carbide reference sphere. The 38 kHz echosounder had an effective range of 1200 m while the 70, 120, and 200 kHz echosounders had a range of 600 m, 350 m, and 200 m, respectively. Acoustical echograms of the four frequencies were viewed in real time so that the abundance and distribution of biological scatterers could guide in situ sampling.

A Sea Bird Electronics CTD (conductivity, temperature, depth) sensor package was used to profile water characteristics to a depth of 100 m or 10 m from the bottom, whichever was shallower, at the beginning and end of each transect. In addition to conductivity, temperature, and pressure, the CTD unit measured dissolved oxygen, fluorescence, and light transmission at 530 nm. In 2008 the F/V Frosti used a SBE 19 V.1 CTD with a Wet Labs ECO-FLNTURT combination fluorometer-turbidity sensor, a CSTAR green light transmissometer, and a Sea Bird Electronics 42 dissolved oxygen sensor. In 2009 the F/V Gold Rush used the same CTD package that was used on the F/V Frosti in 2008. In 2009 the F/V Frosti used a SBE 19 V.2 CTD with a Wet Labs Wet Star fluorometer, a CSTAR green light transmissometer, and a Sea Bird Electronics 42 O_2 sensor. Both CTDs were equipped with a remote depth sensor (Simrad PI32) that allowed depth of the package to be observed in real time.

A vertically integrated zooplankton net tow was performed at the beginning of each transect to a depth of 100 m or 10 m from the bottom, whichever was shallower. The net was kept as close to vertical as weather conditions would allow. Net depth was guided by a real-time remote depth sensor (Simrad PI32) affixed to the net. The zooplankton net had a 0.75 m diameter mouth, 333 µm mesh, and was equipped with a General Oceanics flowmeter modified to only operate on the upward cast. The net was towed at a rate of 1 m s^{-1}, and zooplankton captured in the net were immediately preserved in a solution of 5% buffered formalin in seawater for later analyses.

Following the zooplankton net tow, a 20-minute targeted trawl for fish and euphausiids was performed at a speed of approximately 2 to 4 km hr^{-1}. The nets used were modified Marinovich trawls which measured 10.5 m in length, with a 49 m^2 square opening, and with a cod end liner with 3 mm mesh. Real-time acoustic data were used to place the net at a depth within the upper 100 m of the water column where it would be most likely to encounter aggregations of fish or euphausiids. Real-time remote sensors placed at the mouth of the net were used to ensure proper net placement in the water column and to monitor vertical and horizontal spread. Immediately after capture, non-jellyfish contents of the net were identified, enumerated, and 20 randomly selected individuals of each species were measured for length before subsamples were frozen for further analysis.

Laboratory Analyses

All CTD data were aligned to account for instrument lags, data were filtered, edited for loops, and low-pass filtered before calibrations were applied to convert data to appropriate measures. Clines (e.g. thermocline, oxycline) were determined by finding the largest point-to-point difference in 0.5 m averaged downcast values; the calculated clines were visually compared to profiles for validation. Water column stratification ($d\sigma_t/dz$) was calculated by taking the difference in the densities at 1 meter below the surface and at the deepest point of the cast and dividing by the depth of the cast.

Zooplankton preserved wet weights were determined in the laboratory post-cruise. Each sample was washed with a solution of 5% buffered formalin and seawater onto a 15 cm diameter, 5 μm particle retention filter paper under vacuum pressure until excess fluid was removed. If samples were larger than approximately 500 mL, a Folsom plankton splitter was used to create a subsample prior to filtering. This procedure was then used to filter blank samples of 5% buffered formalin and seawater to determine the average weight of an empty wet filter; 4 volumes each of 100 mL, 200 mL, 300 mL, 400 mL, and 500 mL were filtered. The empty filter weights were not significantly different and did not vary with volume of fluid filtered. After samples were free of excess water, the contents of the filter were weighed on an analytical scale to the nearest 0.001 g with the average wet filter weight subtracted to yield the sample wet weight. To convert to biomass density, wet weights were divided by the volume of water sampled by the zooplankton net.

Ten samples from the Outer Shelf zone were selected from the 2009 zooplankton samples for further analysis. These samples were split with a Folsom plankton splitter and examined under a dissection microscope for analysis to species and length measurement. Zooplankton were identified to the lowest taxonomic group possible (copepods were identified to genus), enumerated, and a random subsample of each identified group was measured for length. Zooplankton were examined in a proportion of the sample that yielded a count of at least 100 individuals per identified group unless there were less than 100 individuals of that group in which case the count for the entire sample was determined. Zooplankton were classified by size into the following groups: <2 mm, 2-4 mm, 4-6 mm, and >6 mm for all zooplankton classes; copepods were grouped as small if prosome length was <2 mm, and large if prosome length was >2 mm

Acoustical data were analyzed using Echoview version 4.7 by Myriax. Volume scattering was averaged over cells of 5 m depth and 5 echo width from 5 m below the surface to 0.5 m from the sounder-detected bottom or to 200 m depth, whichever was shallower. The binned volume scattering at 38 kHz was subtracted from that at 120 kHz to categorize data as either swimbladdered fish or euphausiids based on the observed frequency response (Kang et al. 2002; Korneliussen and Ona 2002). Cells designated as fish had a S_{v120}-S_{v38} in the range of -9.3 to 9.3 dB; cells categorized as euphausiids were within the range of 9.3 to 30 dB (De Robertis et al. 2010). Comparisons of area scattering over the volume sampled by individual net tows and the estimated biomass in the net tows had significant relationships for fish sampled at 38 kHz ($R^2 = 0.74$, $p < 0.05$) and euphausiids sampled at 120 kHz ($R^2 = 0.57$, $p < 0.05$), suggesting that these acoustic measures can be used as proxies for euphausiid and fish abundances (Benoit-Bird et al. in review).

The nautical area scattering coefficient (NASC in m^2 nmi^{-2}) was found for each transect by integrating each category over the entire transect to a depth of 100 m using a -85 dB S_v integration threshold; fish were integrated at 38 kHz, euphausiids were integrated at 120 kHz. The NASC for each transect can be considered an index of total abundance of all fish (38 kHz) which were >95% juvenile pollock by number and weight as verified by trawl sampling, or euphausiids (120 kHz) within the top 100 m of the water column.

When the acoustical layers targeted with the trawl included numerous small fish schools (Fig. 2), the trawls were overwhelmingly dominated (>95 % of catch) by juvenile walleye pollock. In both years most of the juvenile walleye pollock caught were a size (<66 mm) consistent with age-0 pollock. In 2008, age-1 pollock were caught on one transect (<1% of total transects), and in 2009, age-1 or older pollock were caught on three of the planned transects (<5% of total transects).

Post-cruise, juvenile pollock patches were visually identified in the acoustical data, and the minimum, maximum, and median pollock depths for each transect were determined. The pollock median depth is the depth at which 50% of the pollock observed on that transect were above and 50% of the pollock were below. The depth interval inhabited by age-0 pollock was determined by subtracting the minimum pollock depth from the maximum pollock depth. Age-0 pollock density was estimated by dividing the 38 kHz NASC by the pollock range. The difference between the thermocline depth and the median pollock depth was used to assess age-0 pollock vertical distribution in relation to the thermocline.

Statistical analyses

All statistical analyses were performed using data collected at the transect scale. To analyze the effects of environmental variation on juvenile pollock distribution, best subsets multiple linear regression model selections were performed using a randomly selected 50% subset of the 2008 transects with acoustically identified pollock. For the vertical distribution of age-0 pollock the response variable was median pollock depth. Possible explanatory variables for the vertical distribution were: topographic zone; time of day; thermocline depth; mean temperature above and below the thermocline; temperature at pollock minimum, maximum, and median depth; mean standard length of pollock; water column stratification; oxycline depth; and chlorophyll maximum depth. For the horizontal distribution of pollock, the response variable was the 38 kHz NASC value and possible explanatory variables were: topographic zone, time of day, Julian date, surface temperature, thermocline depth, mean temperature to 100 m depth, surface salinity, total chlorophyll concentration integrated over the upper 100 m, maximum chlorophyll concentration within the upper 100 m, oxycline depth, minimum oxygen saturation, water column stratification, euphausiid abundance (120 kHz NASC), zooplankton total biomass, and distance from nearest colony. The model selection procedure was repeated on a randomly selected 50% subset of the 2009 transects with acoustically identified pollock and a randomly selected 50% subset of the combined 2008-09 transects with acoustically identified pollock (App. 1). The best models were selected with two methods: 1) the models with the highest adjusted R^2 were chosen, 2) the models with the Cp statistic, an estimate of the total mean square prediction error, less than or equal to the number of parameters in the model were chosen. Once the best models were identified using the adjusted R^2 and the Cp method, they were run on all of the 2008 transects with acoustically identified pollock, all of the 2009 transects with acoustically identified pollock, and all of the combined data set with acoustically identified pollock. Since several of the adaptive transects were placed due to large aggregations of fish as indicated by acoustics output, the analysis of the horizontal distribution of age-0 pollock was performed only on the planned transects with acoustically identified pollock within 200 km of St. Paul including the transects that were added near the Pribilof Islands since these were planned transects for 2009.

Analysis of Variance (ANOVA) was used to compare differences in the environmental variables used in the horizontal and vertical model selections between sample years and zones. Paired t-tests were used to compare interannual differences in the environmental variables for transects that were repeated in both 2008 and 2009. All interannual comparisons were made using only transects within 200 km of St. Paul Island. ANOVA was also used to compare differences in juvenile pollock distributions between years, among zones, and to make day versus night comparisons. Tukey's Honestly Significant Difference (Tukey HSD) tests were performed on a post-hoc basis to significant ANOVA results, and 95% confidence intervals (CI) around the difference in the means were determined.

In 2009, juvenile pollock abundances within the Outer Shelf zone were highly variable. Within this zone five transect pairs were selected to include one transect with a high abundance of acoustically identified juvenile pollock (38kHz NASC >150 m^2nmi^{-2}) and one transect with a low abundance of pollock (38kHz NASC <50 m^2nmi^{-2}). Transects chosen for paired analysis were geographically close, were sampled within a few days of each other, and were sampled at a similar time of day or night. Paired t-tests were performed to determine whether differences in oceanographic parameters might account for the difference in pollock abundance. There were no significant differences in oceanographic parameters between the pairs so these samples were deemed appropriate to use as paired samples to compare transects with high and low abundance of age-0 pollock in terms of zooplankton community structure. To determine if age-0 pollock distribution was related to zooplankton community structure, Multiple Analysis of Variance (MANOVA) and paired t-tests were performed on species composition, zooplankton and copepod size classes, and species diversity and evenness indices from these samples using a factor classification for high or low age-0 pollock abundance and taking into account the paired nature of the samples.

RESULTS

Environmental Variation

Sea surface temperature was not significantly different between 2008 and 2009 for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.1). Sea surface temperature was significantly higher in the Outer Shelf zone than in the Middle Shelf zone (95% Tukey HSD CI of 1.05-2.14 ^{o}C, $p < 0.0001$), and significantly higher in the Slope than in the Middle Shelf (95% Tukey HSD CI of 1.47-2.55 ^{o}C, $p < 0.0001$), there was no significant difference in sea surface temperature between the Slope and Outer Shelf (Tukey HSD, $p > 0.05$). For transects sampled in both 2008 and 2009, sea surface temperature was significantly higher in 2009 than in 2008 (95% paired-t test CI of 0.01-0.69 ^{o}C, $p < 0.05$).

Depth averaged temperature was significantly higher in 2009 than in 2008 for transects within 200 km of St. Paul (95% Tukey HSD CI of 0.18-0.58, $p < 0.001$, App. 2.2). There was no interaction between zone and year for depth averaged temperature. Depth averaged temperature was significantly higher in the Outer Shelf zone than in the Middle Shelf zone (95% Tukey HSD CI of 0.58-1.14 ^{o}C, $p < 0.0001$), significantly higher in the Slope than in the Middle Shelf (95% Tukey HSD CI of 1.31-1.87 ^{o}C, $p < 0.0001$), and significantly higher in the Slope than in the Outer Shelf (95% Tukey HSD CI of 0.43-1.02, $p < 0.0001$). For transects sampled in both 2008 and 2009, depth averaged temperature was significantly higher in 2009 than in 2008 (95% paired-t test CI of 0.23-0.71 ^{o}C, $p < 0.001$).

Mean temperature above the thermocline was not significantly different between 2008 and 2009 for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.3). Mean temperature above the thermocline was significantly higher in the Outer Shelf zone than in the Middle Shelf zone (95% Tukey HSD CI of 0.73-1.74 ^{o}C, p <

0.0001), significantly higher in the Slope than in the Middle Shelf (95% Tukey HSD CI of 1.37-2.38 ^{o}C, $p < 0.0001$), and significantly higher in the Slope than in the Outer Shelf (95% Tukey HSD CI of 0.12-1.16 ^{o}C, $p < 0.05$). For transects sampled in both 2008 and 2009, mean temperature above the thermocline was not significantly different between 2009 and 2008 (paired-t test, $p > 0.05$).

Mean temperature below the thermocline was not significantly different between 2008 and 2009 for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.4). Mean temperature below the thermocline was significantly higher in the Outer Shelf zone than in the Middle Shelf zone (95% Tukey HSD CI of 0.59-1.36 ^{o}C, $p < 0.0001$), significantly higher in the Slope than in the Middle Shelf (95% Tukey HSD CI of 1.47-2.23 ^{o}C, $p < 0.0001$), and significantly higher in the Slope than in the Outer Shelf (95% Tukey HSD CI of 0.48-1.28 ^{o}C, $p < 0.0001$). For transects sampled in both 2008 and 2009, mean temperature below the thermocline was significantly higher in 2009 than in 2008 (95% paired-t test CI of 0.07-0.50 ^{o}C, $p < 0.01$).

Thermocline depth was not significantly different between 2008 and 2009 for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.5). Thermocline depth was significantly deeper in the Outer Shelf zone than in the Middle Shelf zone (95% Tukey HSD CI of 3.74-12.90 m, $p < 0.0001$), and significantly deeper in the Slope than in the Middle Shelf (95% Tukey HSD CI of 1.46-10.53 m, $p < 0.0001$), there was no significant difference in thermocline depth between the Slope and Outer Shelf (Tukey

HSD, $p > 0.05$). For transects sampled in both 2008 and 2009, thermocline depth was not significantly different between 2009 and 2008 (paired-t test, $p > 0.05$).

Surface salinity was significantly higher in 2009 than in 2008 for transects within 200 km of St. Paul (95% Tukey HSD CI of 13.80-15.60 PSU, $p < 0.0001$, ANOVA, $p < 0.0001$, App. 2.6). Surface salinity was significantly higher in the Middle Shelf zone than in the Slope zone (95% Tukey HSD CI of 1.14, 4.18 PSU, $p < 0.0001$), surface salinity was not significantly different between the Outer Shelf and the Middle Shelf (Tukey HSD, $p > 0.05$) or between the Slope and the Outer Shelf (Tukey HSD, $p > 0.05$). For transects sampled in both 2008 and 2009, surface salinity was significantly higher in 2009 than in 2008 (95% paired-t test CI of 13.31-16.13 PSU, $p < 0.0001$).

Total chlorophyll was significantly higher in 2009 than in 2008 for transects within 200 km of St. Paul (95% Tukey HSD CI of 230.00-295.80 mg m^{-3}, $p < 0.0001$, ANOVA, $p < 0.0001$, App. 2.7). There was no interaction between year and zone. Total chlorophyll was significantly higher in the Slope zone than in the Middle Shelf zone (95% Tukey HSD CI of 16.17-108.87 mg m^{-3}, $p < 0.005$), total chlorophyll was not significantly different between the Outer Shelf and the Middle Shelf (Tukey HSD, $p > 0.05$) or between the Slope and the Outer Shelf (Tukey HSD, $p > 0.05$). For transects sampled in both 2008 and 2009, total chlorophyll was significantly higher in 2009 than in 2008 (95% paired-t test CI of 234.32-335.09 mg m^{-3}, $p < 0.0001$).

Maximum chlorophyll was significantly higher in 2009 than in 2008 for transects within 200 km of St. Paul (95% Tukey HSD CI of 15.06-21.31 mg m^{-3}, p <

0.0001, ANOVA, $p < 0.0001$, App. 2.8). Maximum chlorophyll did not significantly vary by zone (ANOVA, $p > 0.05$). For transects sampled in both 2008 and 2009, maximum chlorophyll was significantly higher in 2009 than in 2008 (95% paired-t test CI of 14.67-24.24 mg m^{-3}, $p < 0.0001$).

The maximum chlorophyll depth was significantly deeper in 2008 than in 2009 for transects within 200 km of St. Paul (95% Tukey HSD CI of 5.13-11.70 m, $p < 0.0001$, ANOVA, $p < 0.0001$). Maximum chlorophyll depth did not significantly vary by zone (ANOVA, $p > 0.05$). For transects sampled in both 2008 and 2009, maximum chlorophyll depth was significantly deeper in 2008 than in 2009 (95% paired-t test CI of 6.42-13.54 m, $p < 0.0001$).

Depth of the oxycline did not vary by year for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.9) or by zone (ANOVA $p > 0.05$). For transects sampled in both 2008 and 2009, depth of the oxycline was not significantly different between 2009 and 2008 (paired-t test, $p > 0.05$). Minimum percent oxygen saturation was significantly higher in 2009 than in 2008 for transects within 200 km of St. Paul (95% Tukey HSD CI of 5.39-13.30%, $p < 0.0001$, ANOVA, $p < 0.0001$, App. 2.10). Minimum percent oxygen saturation did not vary by zone (ANOVA $p > 0.05$). For transects sampled in both 2008 and 2009, minimum percent oxygen saturation was significantly higher in 2009 than in 2008 (95% paired-t test CI of 3.72-16.66%, $p < 0.01$).

Water column stratification did not vary by year for transects within 200 km of St. Paul (ANOVA $p > 0.05$, App. 2.11). Water column stratification was significantly greater in the Middle Shelf zone than in the Outer Shelf zone (95% Tukey HSD CI of 0.08-0.15 $d\sigma_t/dz$, $p < 0.0001$), and significantly higher in the Middle Shelf than in the Slope (95% Tukey HSD CI of 0.10-0.18 $d\sigma_t/dz$, $p < 0.0001$), there was no significant difference in water column stratification between the Slope and Outer Shelf (Tukey HSD, $p > 0.05$). For transects sampled in both 2008 and 2009, water column stratification was not significantly different between 2009 and 2008 (paired-t test, $p > 0.05$).

Horizontal Distribution

The acoustically determined abundance of age-0 pollock varied significantly by year and by zone, with a significant interaction between zone and year (ANOVA $p < 0.05$; Fig. 3). Age-0 pollock abundance was significantly higher in 2008 than in 2009 for the planned transects within 200 km of St. Paul (95% Tukey HSD CI of 200.05-808.13 $m^2\ nmi^{-2}$, $p < 0.01$, ANOVA, $p < 0.01$; Fig. 3, App. 2.12, App. 2.13). Age-0 pollock abundance was significantly greater in the Middle Shelf zone than in the Outer Shelf zone (95% Tukey HSD CI of 99.47-914.76 $m^2\ nmi^{-2}$, $p < 0.05$), and significantly greater in the Middle Shelf zone than in the Slope zone (95% Tukey HSD CI of 345.45-1338.62 $m^2\ nmi^{-2}$, $p < 0.001$), there was no significant difference in age-0 pollock abundance between the Outer Shelf and Slope (Tukey HSD, $p > 0.05$; Fig. 3). For transects sampled in both 2008 and 2009, acoustically determined abundance of age-0 pollock was significantly higher in 2008 than in 2009 (95% paired-t test CI of 56.03-529.37 m^2 nmi^{-2}, $p < 0.05$).

Walleye pollock caught in the trawls had a mean standard length of 41.4 mm with a standard deviation of 41.5. The frequency distribution of sampled pollock lengths was bimodal with the strongest peak at 35 mm and a secondary distribution centered around 130 mm. No pollock were observed to have a standard length between 67-91 mm, indicating a break in cohorts which we used to define age-0 and age-1 pollock. This was supported by findings presented by Nishimura and Yamada (1988) and Brown and Bailey (1992). Further details on walleye pollock length and age classes for this study can be found in (Whitman 2010). Age-0 pollock caught in the trawls were significantly larger in 2009 (36.8 mm) than in 2008 (28.3 mm) within 200 km of St. Paul (95% Tukey HSD CI of 5.90-11.09 mm, $p < 0.05$; ANOVA, $p < 0.0001$). Additionally, age-0 pollock were significantly larger in the Outer Shelf zone than in the Middle Shelf (95% Tukey HSD CI of 1.50, 9.05 mm, $p < 0.05$; ANOVA, $p < 0.01$), and significantly larger in the Slope zone than in the Middle Shelf zone (95% Tukey HSD CI of 0.63-10.71 mm, $p < 0.05$; ANOVA, $p < 0.05$), age-0 pollock length was not significantly different between the Outer Shelf and the Slope. For transects sampled in both 2008 and 2009, age-0 pollock were significantly larger in 2009 than in 2008 (95% paired-t test CI of 5.52-9.42 mm, $p < 0.0001$).

Age-0 pollock were more widely distributed in the two years (App. 2.12, App. 2.13); acoustically identified pollock were found in 39 of the 62 random, non-repeated transects (63%) in 2008 and in 47 of the 54 random, non-repeated transects within 200 km of St. Paul (87%) in 2009. No significant relationship was found between the 38 kHz NASC and any of the explanatory variables used in the multiple linear regression model selection.

Zooplankton biomass (wet weight) ranged from $2.13 \cdot 10^{-2}$ to 14.49 g m^{-3} across all transects sampled. Within 200 km of St. Paul Island, the mean abundance of zooplankton was significantly higher in 2009 than in 2008 (95% CI of 0.95-2.40 g m^{-3}, ANOVA, $p < 0.0001$; t-test, $p < 0.0001$, App. 2.14). There was no significant relationship between total zooplankton biomass and the horizontal distribution of age-0 pollock (linear regression, $p > 0.05$), nor was there a significant relationship between acoustically determined euphausiid abundance (120 kHz NASC, App. 2.15), and the abundance of acoustically identified age-0 pollock (38 kHz NASC) for the planned transects within 200 km of St. Paul (linear regression, $p > 0.05$, Fig. 5). For transects sampled in both 2008 and 2009, zooplankton biomass was significantly higher in 2009 than in 2008 (95% paired-t test CI of 0.85-1.29 g m^{-3}, $p < 0.0001$).

Isopods and large copepods (>2 mm) were the only taxa (App. 3) that had significantly different abundances on transects with low acoustically determined pollock abundance than on those with a high abundance of pollock. The mean abundance of isopods was significantly higher for transects with high abundances of age-0 pollock than for transects with low abundances of pollock (95% Tukey HSD CI of $2.3 \cdot 10^{-2}$-$6.8 \cdot 10^{-2}$ indiv. m^{-3}, $p < 0.01$, ANOVA, pollock abundance $p < 0.01$, pair p >

0.05). The abundance of large copepods (>2 mm) was significantly higher for transects with high abundances of age-0 pollock (95% Tukey HSD CI of 67.6-328.7 indiv. m^{-3}, $p < 0.05$, ANOVA, pollock abundance $p < 0.05$, pair $p < 0.05$).

Vertical Distribution

In addition to the difference in overall age-0 pollock biomass between the two years, there were also significant differences in their vertical distribution in the water column (Fig. 6). The pollock median depth, the depth at which 50% of the pollock were shallower and 50% were deeper, was significantly deeper in 2009 (29.96 m) than in 2008 (19.95 m) in the area within 200 km of St. Paul Island (Fig. 7, App. 2.16) (ANOVA, $p < 0.001$; t-test, $p < 0.001$). For transects sampled in both 2008 and 2009, age-0 pollock were significantly deeper in 2009 than in 2008 (95% paired-t test CI of 5.15-17.23 m, $p < 0.001$). A multiple linear regression model showed that pollock median depth is affected by the temperature structure within the water column:

$$\text{Pollock median depth} = \beta_0 - \beta_1(\text{temperature at the pollock median depth}) + \beta_2(\text{mean temperature above the thermocline}) + \beta_3(\text{thermocline depth}), \qquad \text{(Equation. 1)}$$

where β_0 is the model intercept and β_1, β_2, and β_3 are the slopes. Model coefficients for the area within 200 km of St. Paul Island are summarized in Table 1. The pollock median depth (App. 2.17) had a negative relationship with the temperature at the pollock median depth, and a positive relationship with the mean temperature above the thermocline and the thermocline depth. The additive linear model explained 62% (adj. R^2) of the variability in the 2008 median pollock depth ($p < 0.0001$) and 56% (adj. R^2) of the variability in the 2009 median pollock depth for the entire sample area ($p < 0.0001$), and 71% (adj. R^2) of the variability in the 2009 median pollock depth within 200 km of St. Paul ($p < 0.0001$). Within 200 km of St. Paul, the additive linear model explained 70% (adj. R^2) of the variability in the pollock median depth for both years, with sample year added into the model ($p < 0.0001$). The temperature at the pollock median depth did not vary significantly with year or zone (ANOVA, $p > 0.05$), probably because there was substantial variation in temperature at the pollock median depth within each year and zone.

Age-0 pollock median depth varied with sampling zone and time of day (ANOVA, zone $p < 0.0001$, time of day $p < 0.001$; Fig. 8). Age-0 pollock median depth was significantly deeper in the Outer Shelf zone than in the Middle Shelf zone (Tukey HSD 95% CI of 4.11-16.77 m, $p < 0.001$), and significantly deeper in the Slope zone than in the Middle Shelf zone (Tukey HSD 95% CI of 7.77-23.32 m, $p < 0.0001$), there was no significant difference in pollock median depth between the Outer Shelf and Slope (Tukey HSD, $p > 0.05$). Diel vertical migration of age-0 pollock was seen in both years (Fig. 6) as determined by the age-0 pollock median depth being significantly deeper during the day than at night (95% Tukey HSD CI of 3.18-15.03 m, $p < 0.01$, ANOVA, $p < 0.01$). Time of day and zone were tested as factors in the multiple linear regression model. Time of day was not significant in the model for 2008, 2009 within

200 km of St. Paul, or both years combined within 200 km of St. Paul (MLR $p > 0.05$). Zone was not significant in the model for both years combined within 200 km of St. Paul or for 2009 within 200 km of St. Paul (MLR $p > 0.05$). Zone was significant in the model when 2008 was evaluated separately ($p < 0.0001$); with age-0 pollock median depth following the same trends with zone in the linear model as in the ANOVA for zone (Appendix 4).

Age-0 pollock occurred over a larger average depth range (pollock maximum depth – pollock minimum depth) in 2009 than in 2008 (95% Tukey HSD CI of 3.77-15.61 m, $p < 0.01$, ANOVA, $p < 0.01$). For transects sampled in both 2008 and 2009, the depth range was significantly larger in 2009 than in 2008 (95% paired-t test CI of 4.61-17.21 m, $p < 0.01$). Additionally, the mean age-0 pollock density as determined by dividing the 38 kHz NASC by the vertical range was significantly higher in 2008 than in 2009 (95% Tukey HSD CI of 31.88-107.59 m nmi^{-2}, $p < 0.001$, ANOVA, $p < 0.001$). For transects sampled in both 2008 and 2009, pollock density was significantly higher in 2008 than in 2009 (95% paired-t test CI of 26.38-143.86 m nmi^{-2}, $p < 0.01$).

Age-0 pollock median depth in relation to the thermocline depth also varied with year and time of day (ANOVA, year $p < 0.01$; time of day $p < 0.001$, Fig. 9 shows an example). After accounting for time of day, juvenile pollock median depth was above the thermocline in 2008 (mean difference = 4.0 m) and below the thermocline in 2009 (mean difference = -3.73 m) (95% Tukey HSD CI of 1.88-13.56 m (2009 minus

2008), $p < 0.01$). After accounting for interannual differences, age-0 pollock were found below the thermocline during the day (mean difference = -2.68 m) and above the thermocline at night (mean difference = 9.15 m) (95% Tukey HSD CI of 5.17-18.5 m (day minus night), $p < 0.001$). There was no significant difference in thermocline depths between the two sample years for all transects within 200 km of St. Paul (ANOVA, $p > 0.05$), but for those transects with acoustically identified age-0 pollock the thermocline was deeper in 2009 (mean = 27.7 m) than in 2008 (mean = 22.8) (ANOVA, $p < 0.05$).

DISCUSSION

We sought to determine what environmental factors control the small-scale horizontal and vertical distribution of age-0 pollock in the Bering Sea near the Pribilof Islands. Both 2008 and 2009 were considered cold years in the Bering Sea (Hunt et al. 2011). Overall the physical characteristics in the sampling area were fairly similar between 2008 and 2009, though there were significant differences in the depth averaged temperature, surface salinity, and minimum percent oxygen saturation. Additionally, there were significant differences between transects sampled in both years for sea surface temperature, depth averaged temperature, mean temperature below the thermocline, sea surface salinity, and minimum percent oxygen saturation. Though, these differences were significantly different most of them were likely not significant to organisms (e.g. less than 1°C difference between the two years). There were large differences in measured biological parameters such as total chlorophyll, zooplankton abundance, and juvenile pollock abundance, distribution, and individual size. The cruises occurred over the same time period in both years, however, it is possible that the timing of the spring bloom in the Bering Sea or the hatch dates for pollock occurred at different times during the two years. This could account for the differences in zooplankton abundance and the average age-0 pollock size, which may in turn be some of the drivers for the small-scale horizontal and vertical distribution of pollock.

We found higher abundances of age-0 pollock in 2008 than in 2009 for the planned transects within 200 km of St. Paul. Age-0 pollock were found in all three topographic zones, including the Slope (>200 m depth), with significant differences in abundances between the Middle Shelf and both the Outer Shelf and Slope zones, but not between the Outer Shelf and Slope zones. Approximately 5% of the juvenile pollock biomass (38 kHz NASC) was encountered on planned transects in the Slope zone in both years, indicating that there is a significant amount of juvenile pollock biomass in the Slope zone.

In both years, the environmental variables we evaluated were not able to explain the variations in the horizontal distribution of age-0 pollock. The best linear models had many factors (>5) and explained very little (<40%) of the age-0 pollock horizontal distribution variability. This agrees with Brodeur et al. (2002) who found that age-0 pollock did not seem to aggregate in any particular habitat, and with Ciannelli et al. (2002) who suggested that age-0 pollock distributions may be affected by different factors in different geographical areas (i.e. frontal region, shelf) and that these factors might vary in importance in different years. Additionally, all of our parameters except distance from nearest colony measured bottom up controls, so it is possible that top down controls that we did not measure, e.g. predation by fish, may be affecting the horizontal distribution of juvenile walleye pollock.

The interannual difference in juvenile pollock distribution and abundance could be due to differences in spawning success at different locations in the southeastern Bering Sea. Bacheler et al. (2010) showed that walleye pollock spawning varies greatly over space and time and centers on three main areas in the southeastern Bering Sea: near Bogoslof Island, near Unimak Island, and near the Pribilof Islands. Variations in the relative success of these spawning locations or in the currents near these areas may have led to the variations in the age-0 pollock abundance and distribution. Perhaps the Pribilof Island spawning location was particularly successful in 2008, or perhaps currents in 2008 permitted greater retention of eggs and larvae near the Pribilof Islands.

Age-0 pollock caught in the trawl within 200 km of St. Paul were longer in 2009 than in 2008. This could be due to a difference in hatch date between the two years or a difference in the growth rate. Age analysis of otoliths was not possible for this study due to the use of the fish collected for other analyses. Support for the difference in hatch date hypothesis was presented by Whitman (2010); he reported a close relationship between age-0 pollock length and energy density in our study area that was consistent for both study years, suggesting that the difference in individual size between the two years is related to a difference in hatch date and not a difference in growth rate.

We found a higher abundance of age-0 pollock in our study area in 2008 than in 2009; however, mesozooplankton biomass was higher in 2009 than in 2008, and was not related to the horizontal distribution of age-0 pollock. Similar to other studies in this area (Swartzman et al. 2002; Brodeur et al. 2002; Ciannelli et al. 2002; Winter et al. 2005) we found that age-0 pollock distributions were most variable in the Outer Shelf zone, which is the reason that this zone was chosen for further analysis of the 2009 zooplankton samples. The paired samples from the Outer Shelf zone in 2009 suggest that juvenile pollock may have been responding to large Calanoid copepods. Our findings agree with Coyle et al. (2008) who found that large copepods were more abundant and were consumed by age-0 pollock during the cold year they sampled, but smaller copepods were more abundant and were consumed by age-0 pollock during a warm year. The paired Outer Shelf samples also showed a significant relationship between areas with a high abundance of age-0 pollock and high isopod abundances. Isopods were not very abundant compared to other zooplankton in the samples, and it is not very likely that age-0 pollock were cuing in on isopod abundances. However, it is possible that isopods and large copepods were both responding to something similar and so were found in areas with high juvenile pollock abundances. It is likely that the species or size of zooplankton prey might be the most important predictor of where age-0 pollock were found, but our limited examination of zooplankton species composition makes it difficult to extrapolate our results from the Outer Shelf to the entire study area.

Unlike the horizontal distributions of age-0 pollock, we found significant relationships between environmental parameters and vertical distributions of age-0 pollock. We found that the median depth of age-0 pollock was not related to typical temperature metrics such as sea surface temperature or depth averaged temperature as might have been expected from the Oscillating Control Hypothesis (Hunt Jr. et al. 2002), but rather depended on the vertical temperature structure (thermocline depth, mean temperature above the thermocline, and the temperature at the median pollock depth). This finding is consistent with the behavior of age-0 pollock in the laboratory and previous field observations of the vertical distribution of age-0 pollock. Sogard and Olla (1993) found that vertical distribution of age-0 pollock was impacted most by thermal stratification. Swartzman et al. (1999) observed that juvenile pollock were typically near and often above the thermocline. We found that age-0 pollock were near the thermocline in both years, but in 2008 most of the age-0 pollock were above and in 2009 they were a similar distance below the thermocline despite the thermocline depth not being significantly different between the two years. Our results indicate that the drivers of vertical distribution of juvenile pollock are more complicated than merely an association with the thermocline.

We found that age-0 pollock in our study area had a much deeper vertical distribution and larger vertical range in 2009 than in 2008. Additionally, diel vertical migrations were larger in 2009 than in 2008. This may be due in part to the difference in fish size between the two years. Bailey (1989) found that larger juvenile pollock exhibited larger vertical migrations. Sogard and Olla (1993) saw ontogenetic shifts in age-0 pollock behavior in the laboratory with smaller pollock avoiding cold water and spending less time below the thermocline than larger fish. Sogard and Olla (1993) suggest that as age-0 pollock get larger they may become more tolerant to cold water, and the risks associated with descending below the thermocline may be outweighed by the benefits such as increased accessibility to prey. If age-0 pollock depth and length are related it is a complicated relationship since we did not find a clear relationship between pollock length and pollock median depth in the model selection.

During both years, we observed that age-0 pollock were found deeper during the day and shallower at night, consistent with diel vertical migration behavior. Bailey (1989) observed similar variations in juvenile pollock depth distributions on a diel cycle in autumn. Schabetsberger et al. (2000) also observed diel variations in age-0 pollock distributions in late summer, with pollock staying deeper in the water column during the day and coming into shallower water at night. It is unclear whether age-0 pollock are vertically migrating in order to follow their zooplankton prey or if it is in response to changes in light levels. Age-0 pollock in the laboratory have been shown to alter their vertical position in response to both food availability and high light intensity (Olla and Davis 1990; Sogard and Olla 1993). Our results show that small age-0 pollock (average length <40 mm) in our study area were exhibiting diel vertical migration behavior in mid-summer of 2008 and 2009.

Bailey (1989) suggested that age-0 pollock diel vertical migration depends on food availability, and he hypothesized that larger vertical migrations occur when food is scarce. We found a greater abundance of mesozooplankton in 2009 than in 2008, but vertical migrations were larger in 2009 than in 2008. While the biomass of mesozooplankton encountered was higher in 2009 than in 2008, it is possible that the species composition may have been such that it was not suitable food for age-0 pollock. Additionally, zooplankton may have been exhibiting a different vertical distribution between the two years. Ciannelli et al. (1998) suggest that juvenile pollock may migrate vertically to attain an energy advantage since food is more plentiful in warmer, shallower waters, but respiration rate is lower in deeper, cooler waters. So, if food was not adequate for age-0 pollock in 2009 they may have gone below the thermocline and deeper in the water column to either search for better food or to reduce their respiration rate.

The findings from this study have implications for sampling age-0 pollock in the southeastern Bering Sea. Several ongoing surveys of age-0 pollock distribution in the Bering Sea have not consistently sampled the Slope zone since it was thought that age-0 pollock avoided deep water. We found that in terms of age-0 pollock distributions, the Outer Shelf zone and Slope zone were not significantly different. Additionally, some ongoing surveys of age-0 pollock in the Bering Sea have primarily used surface trawls to sample juvenile pollock. These surveys may be undersampling age-0 pollock since we found extremely deep aggregations of age-0 pollock in 2009, including one transect having a median pollock depth of 100 m.

The differences in age-0 pollock abundance and vertical distribution between the two years of this study could have had potential impacts on pollock predators. Not only were there fewer age-0 pollock in 2009 than in 2008, they were also deeper and less densely aggregated. A seabird or marine mammal predator would potentially have needed to dive longer and deeper in the area around the Pribilof Islands in 2009 to consume the same amount of age-0 pollock prey in 2008, and would have obtained fewer (but larger) pollock per dive because of reduced density. This represents a higher energetic cost to air breathing predators in 2009 due to longer search times and longer, deeper dives with lower potential prey encounter rates. Murres in our study area were found to make more dives in areas that had shallow, dense prey patches (Benoit-Bird et al. in review), suggesting that the conditions observed in 2008 were more suitable for murre foraging. Murres in our study area also may be responding to diel patterns in the juvenile pollock distribution as murre foraging dives were found to be deeper during the day and shallower at night (Benoit-Bird et al. in review). However, due to the deeper vertical distribution of age-0 pollock in 2009, bottom associated piscivorous fish, such as older walleye pollock, may have had greater access to age-0 pollock as a prey source.

We observed a high degree of variability in juvenile pollock abundances between geographically close transects and, though we did not examine it here, we saw high levels of variability within individual transects. The high degree of local spatial (1-10 km) variability in age-0 pollock distributions, and our coarser scale environmental metrics might be why we were unable to explain the small-scale pollock horizontal distributions using environmental variation. We suspect based on our zooplankton taxonomic studies in the Outer Shelf zone in 2009 that the type or size of zooplankton prey available might be important. Our results show further evidence that the area around the Pribilof Islands has high environmental heterogeneity and that processes that affect age-0 pollock distributions may be occurring on a scale smaller than our 10 km transects (Ciannelli 2002), and certainly at scales smaller than the surveys that are used to assess abundance of older pollock.

Slow-swimming animals such as age-0 pollock may experience more environmental variation by moving vertically in the water column than horizontally, so while they have little control over their horizontal location they may be able to find better conditions by changing their vertical position. This may be why we were better able to explain vertical distribution patterns than horizontal distribution patterns. The patterns we found in the vertical distribution were consistent between our study years and across topographic zones, despite inherent oceanographic differences among zones. Our results also suggest that the factors controlling the vertical distribution of age-0 pollock would not be sampled properly without targeted sampling; remotely sensed data such as satellite derived sea surface temperature would not accurately predict juvenile pollock distributions. In summary, we found that during cold years in the Bering Sea, there was a high degree of variability in the horizontal distribution of age-0 pollock, but the age-0 pollock were following clear patterns in their vertical distribution.

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Table 1. Model coefficients for the multiple linear regression model: Pollock median depth = $\beta_0 - \beta_1$(temperature at the pollock median depth) + β_2(mean temperature above the thermocline) + β_3(thermocline depth). When both years were combined a factor for study year was also added into the model.

	Model Intercept (β_0)		Temperature at the Pollock Median Depth (β_1)		Mean Temparture Above the Thermocline (β_2)		Thermocline Depth (β_3)		Factor Variable for Year = 2009 (β_4)		Adjusted R^2	p-Value
	Value	p-Value	Value	p-Value	Value	p-Value	Value	p-Value	Value	p-Value		
2008	11.70	< 0.001	-6.06	< 0.00001	4.94	< 0.00001	0.46	< 0.00001	•••	•••	0.62	< 0.00001
2009 (within 200 km of St. Paul)	18.19	< 0.05	-10.06	< 0.00001	8.05	< 0.00001	0.43	< 0.0001	•••	•••	0.71	< 0.00001
2008 & 2009 (within 200 km of St. Paul)	12.82	< 0.01	-8.89	< 0.00001	7.37	< 0.00001	0.49	< 0.00001	•••	•••	0.68	< 0.00001
2008 & 2009 with year included in model (within 200 km of St. Paul)	12.48	< 0.01	-8.60	< 0.00001	7.07	< 0.00001	0.44	< 0.00001	3.98	< 0.05	0.70	< 0.00001

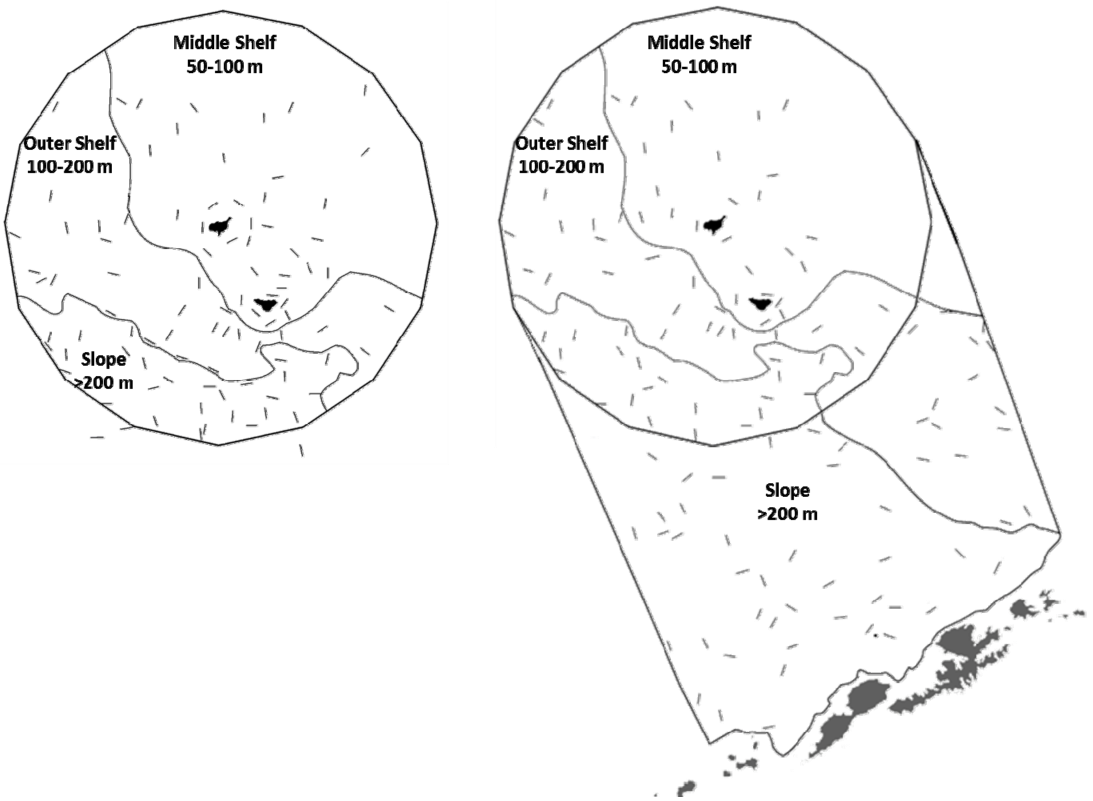

Figure 1. Study area for 2008 (left) and 2009 (right). Gray lines separate topographic zones, Middle Shelf 50-100 m, Outer Shelf 100-200 m, Slope >200 m. Short gray lines are 10 km transect lines.

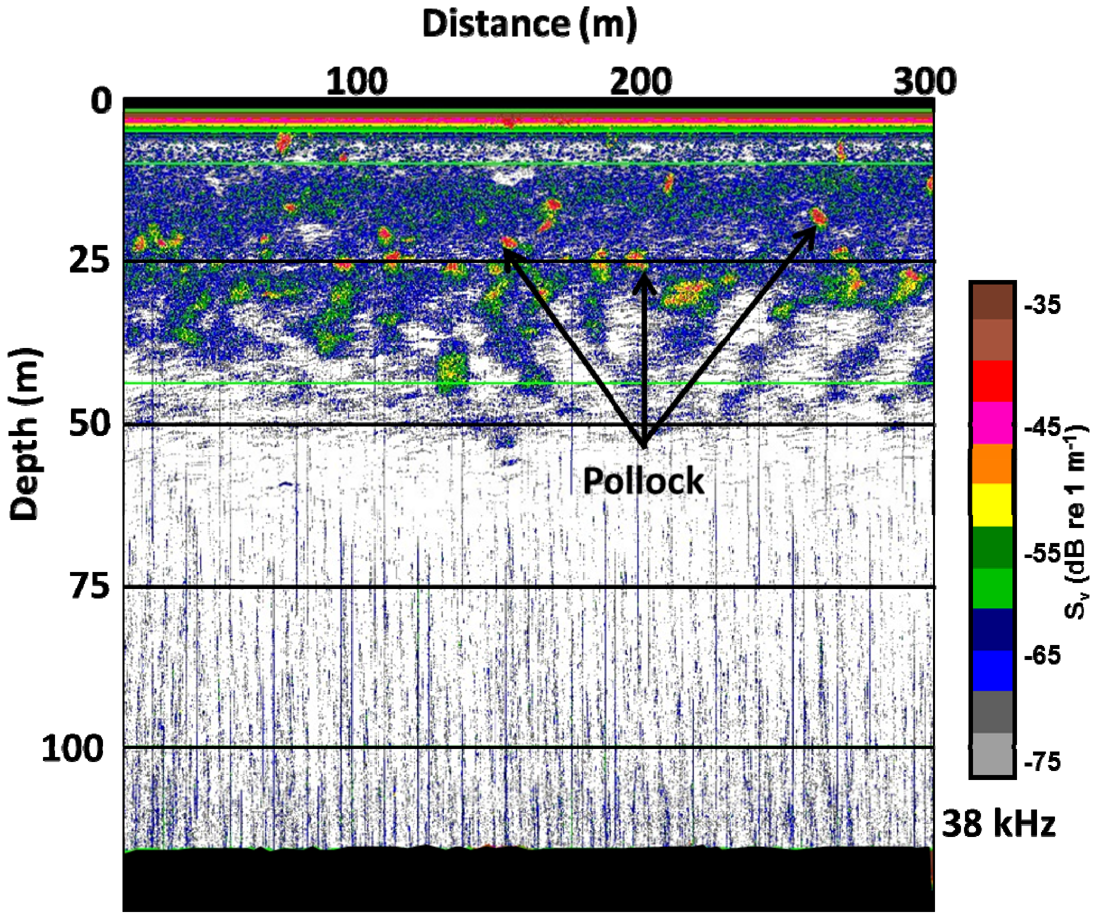

Figure 2. Representative 38 kHz echogram from a 300 m section of an Outer Shelf transect showing the leopard spot appearance of juvenile walleye pollock (*Theragra chalcogramma*) schools.

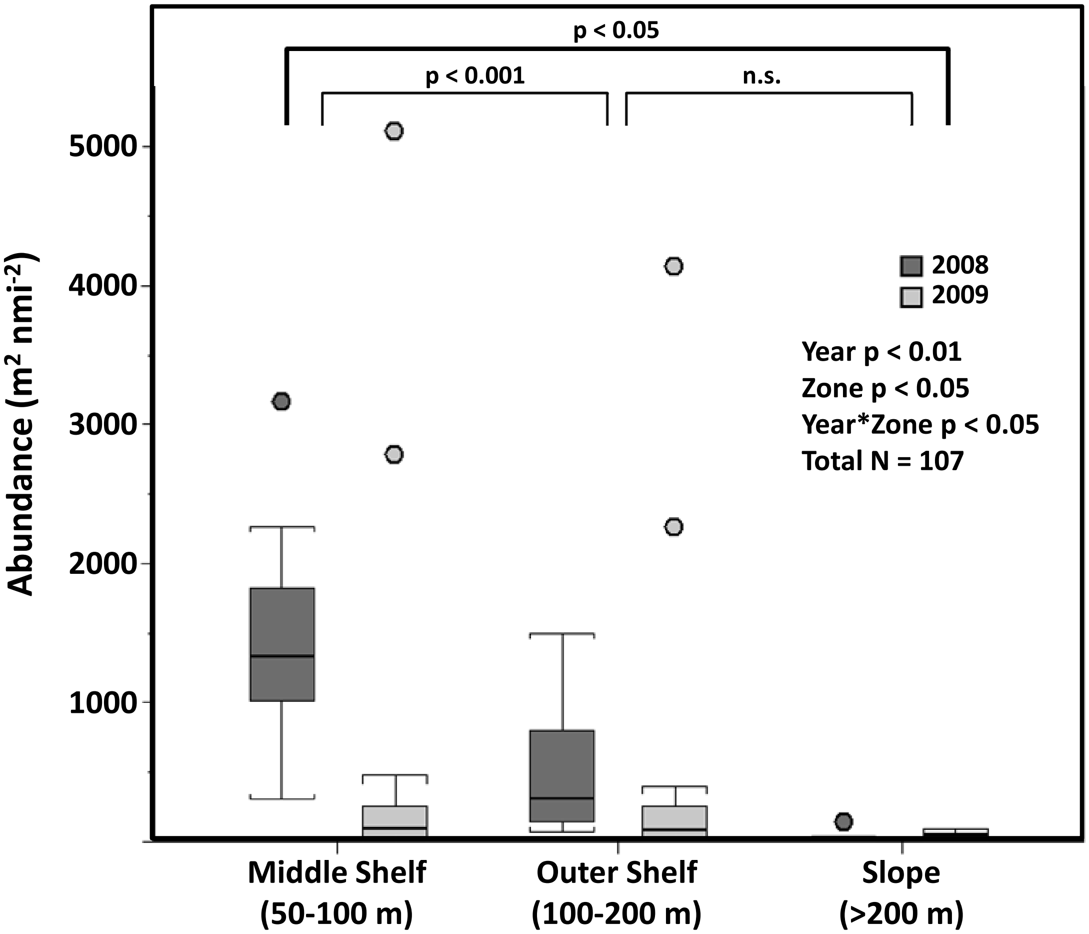

Figure 3. Age-0 walleye pollock (*T. chalcogramma*) abundance within 200 km of St. Paul, Alaska by year and zone. For all box plots: box edges indicate the interquartile range (IQR), the dark line indicates the median, the upper cap is drawn at the largest observation that is less than or equal to the 75th percentile + 1.5*IQR, the lower cap is drawn at the smallest observation that is greater than or equal to the 25th percentile - 1.5*IQR, dots indicate outliers.

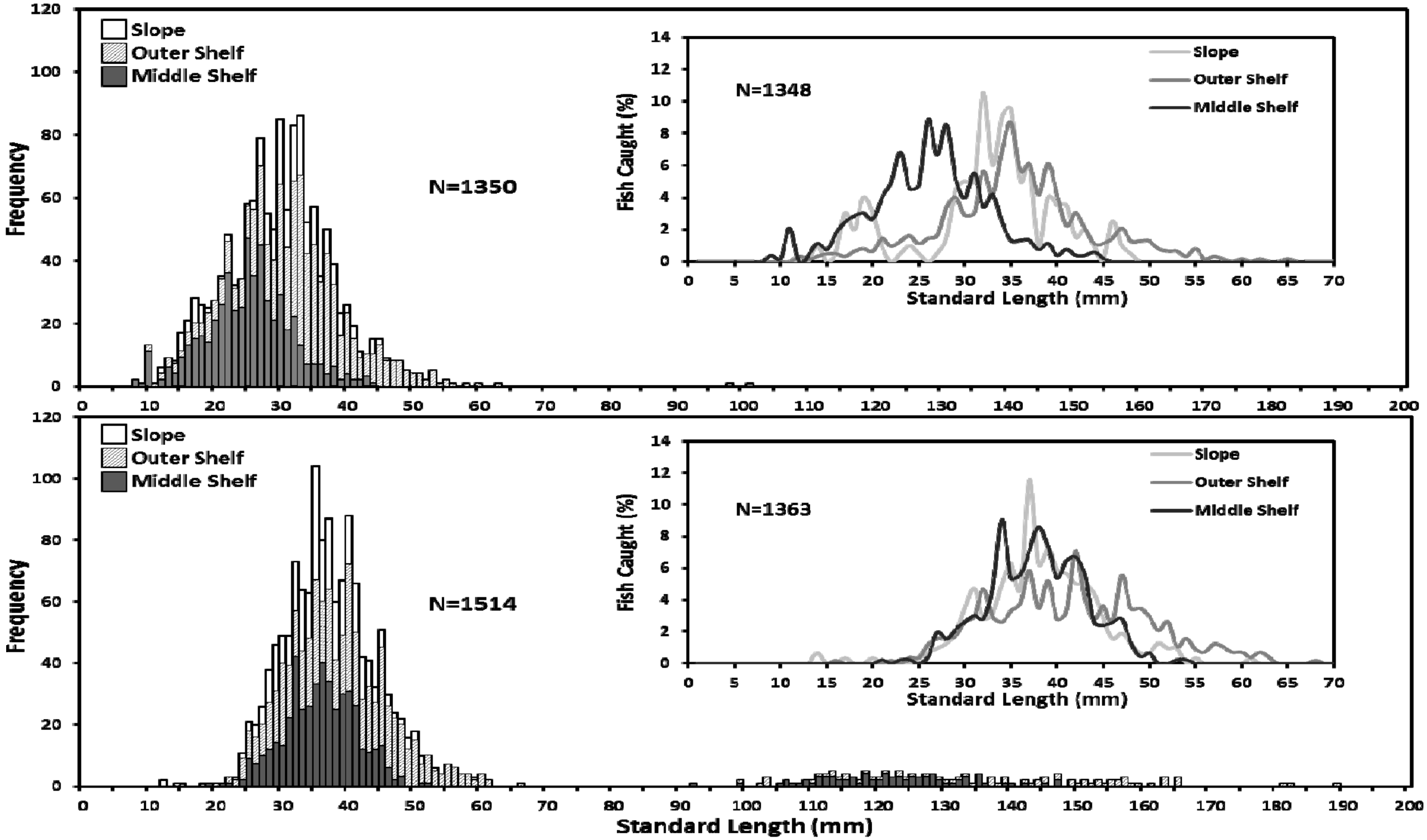

Figure 4. Stacked length frequency distribution by zone of all walleye pollock (*T. chalcogramma*) measured from trawl in 2008 (top panel) and 2009 (bottom panel) with standard length (SL) <200 mm. Pollock with SL >200 mm not shown (2008 N=1, 2009 N=27). Inset shows fish caught per zone versus standard length for age-0 walleye pollock (SL <70 mm).

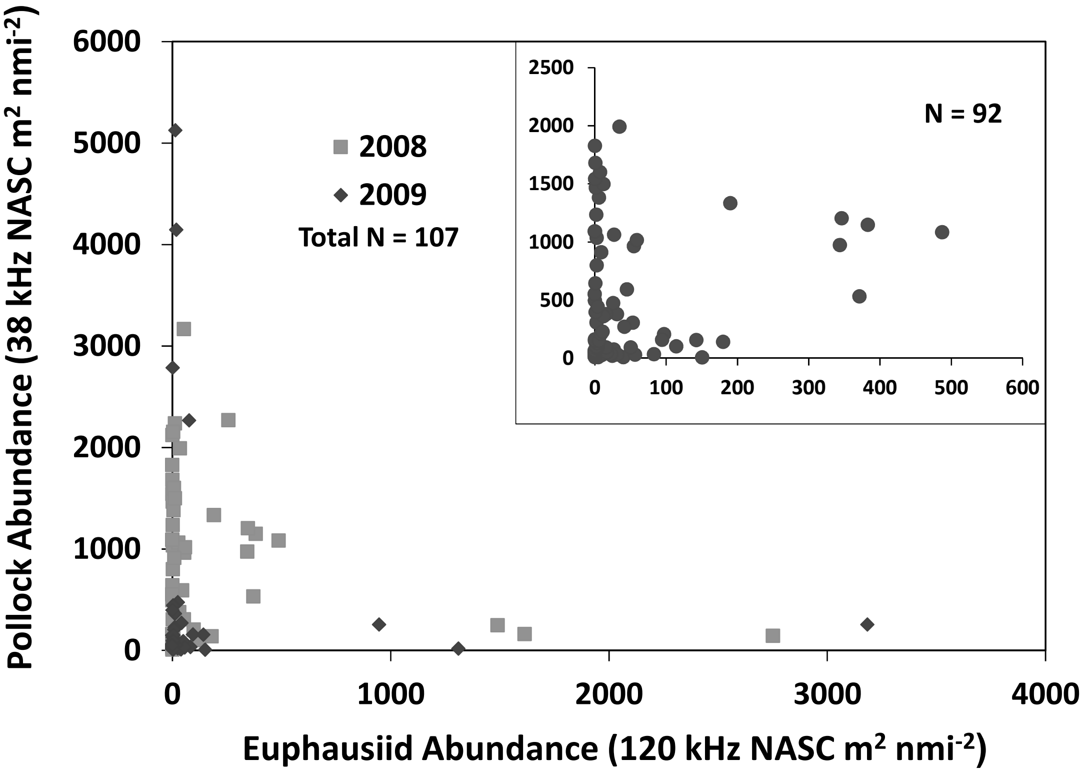

Figure 5. Acoustically identified euphausiid abundance (120 kHz NASC) versus acoustically determined pollock (38 kHz NASC) for random transects within 200 km of St. Paul, Alaska. Squares denote samples from 2008, diamonds denote samples from 2009. The inset has the same units for the axes and shows data from both years combined excluding samples with 120 kHz NASC values > 500 m^2 nmi^{-2} and 38 kHz NASC values > 2000 m^2 nmi^{-2}.

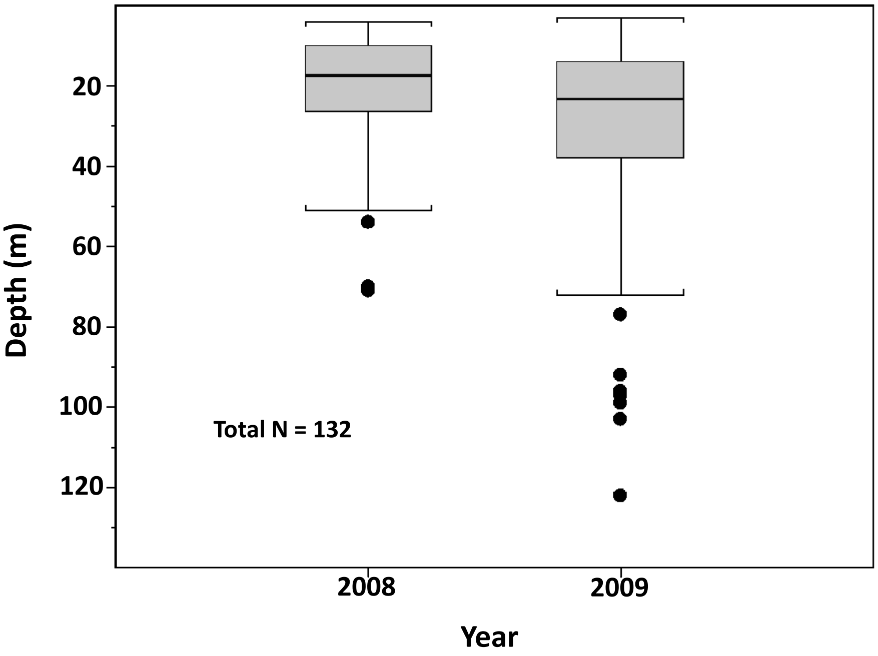

Figure 6. Juvenile walleye pollock (*T. chalcogramma*) vertical distribution within 200 km of St. Paul, Alaska.

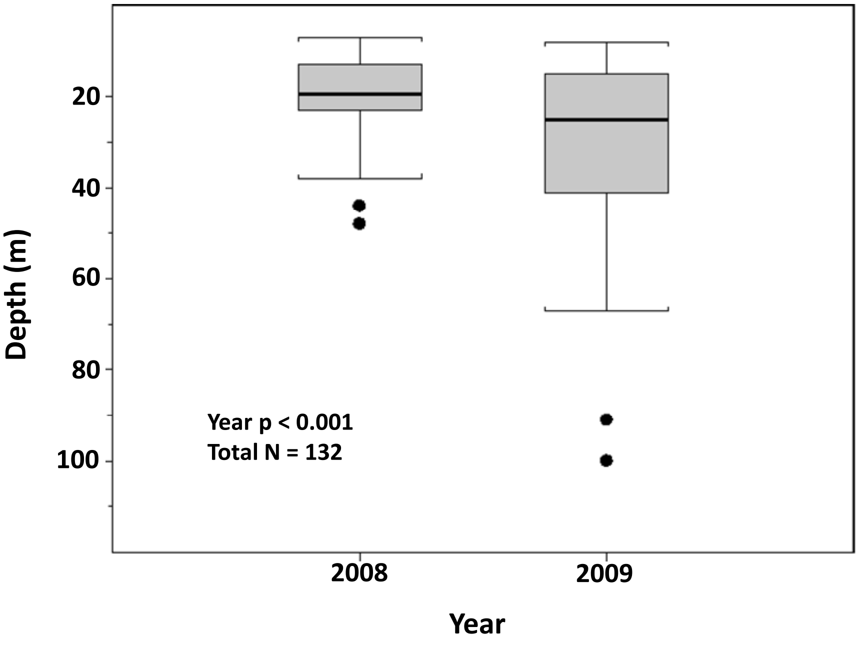

Figure 7. Age-0 walleye pollock (*T. chalcogramma*) median depth versus study year within 200 km of St. Paul, Alaska.

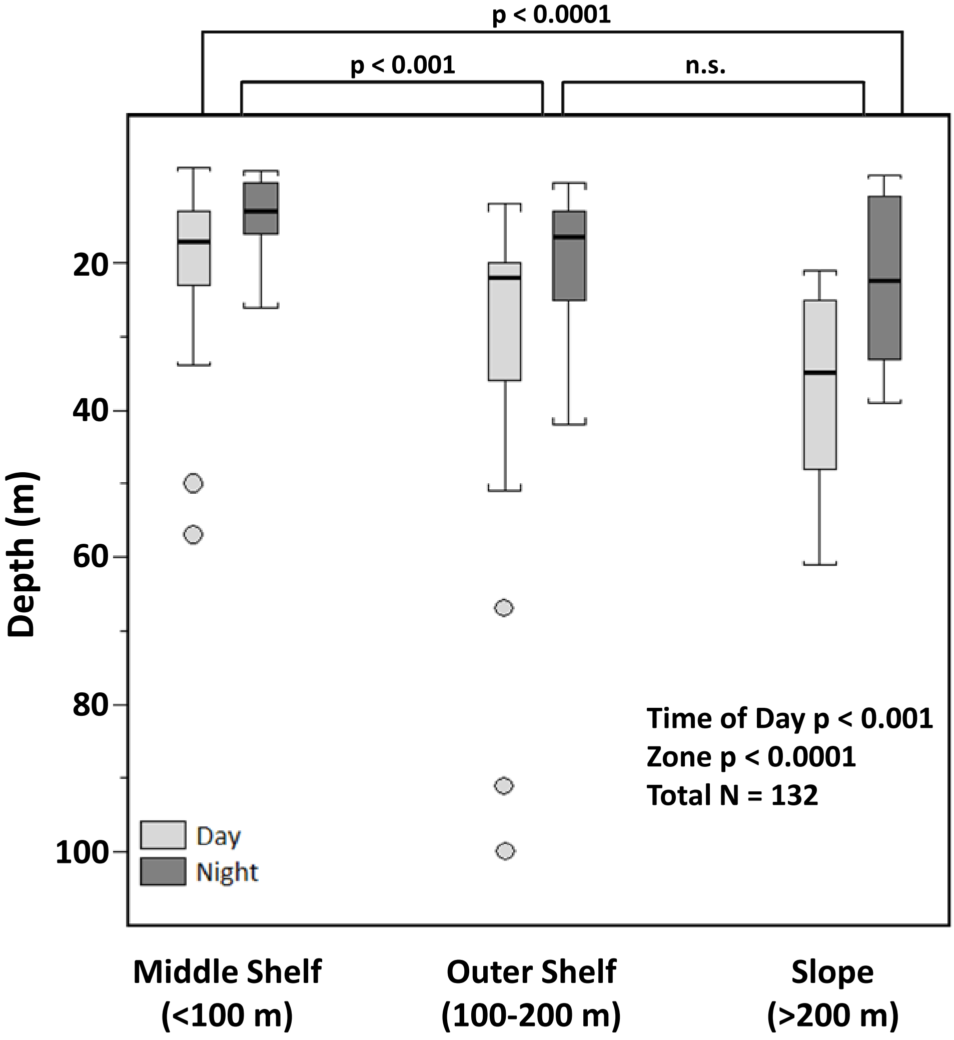

Figure 8. Age-0 walleye pollock (*T. chalcogramma*) median depth versus time of day and zone.

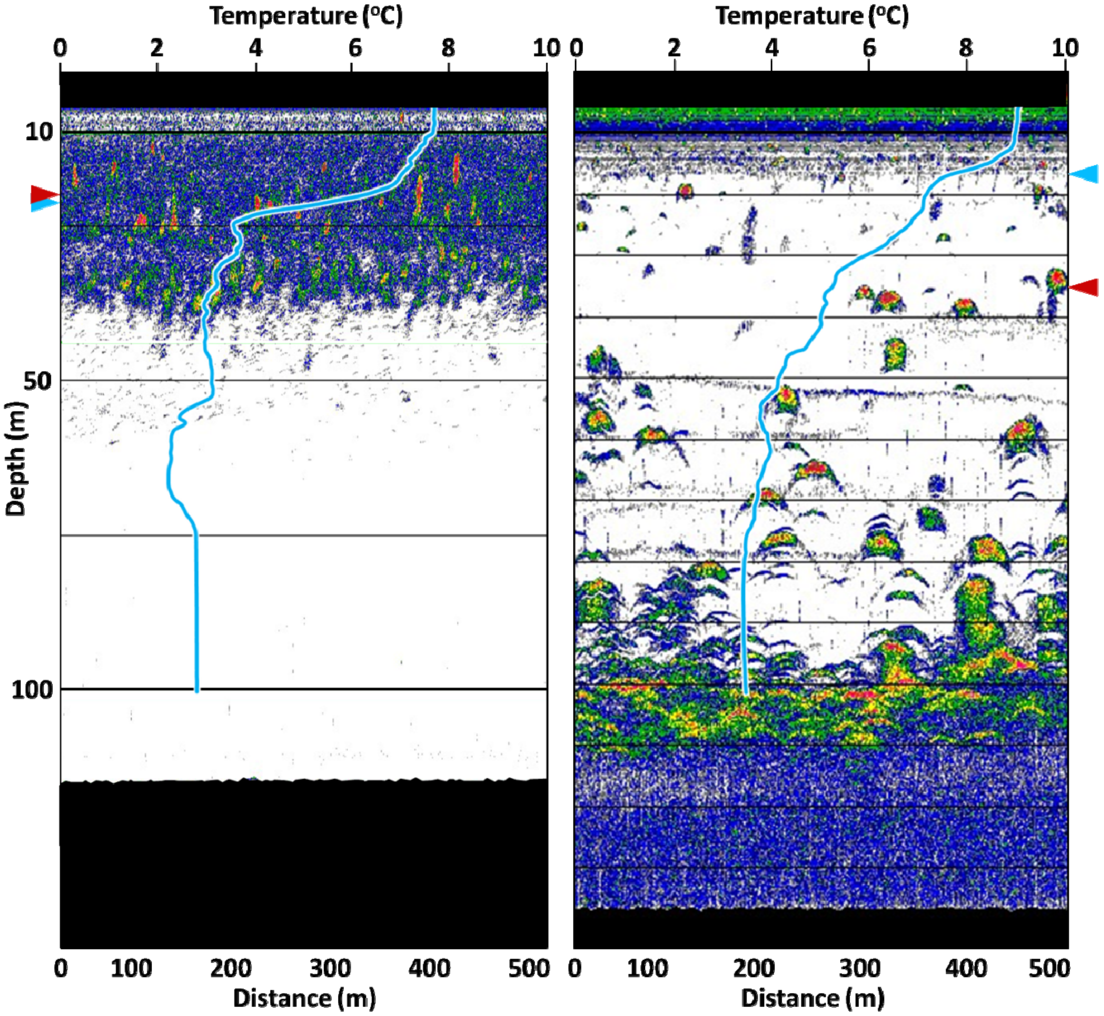

Figure 9. Two representative 38 kHz echograms from daytime Outer Shelf transects with temperature profiles from the transect overlaid. Blue triangle pointers (▶) denote thermocline depth, red triangle pointers (▶) denote pollock median depth. On the left is a 500 m section of a transect from 2008 showing aggregations of juvenile pollock schools near the thermocline (20.7 m). On the right is a 500 m section of a transect from 2009 showing much deeper juvenile pollock schools that are below the thermocline (16.5 m). Median pollock depth was 20 m for the 2008 transect (left), and 35 m for the 2009 transect (right).

Chapter 3 – Conclusion

We sought to determine what environmental factors were controlling the distribution of juvenile walleye pollock (*Theragra chalcogramma*) patches near the Pribilof Islands during the summers of two cold years. The physical environment was similar within the study area, but the distribution and abundance of juvenile pollock (primarily age-0s) varied greatly. We found that juvenile pollock were smaller in length, more abundant, shallower, and more densely aggregated in the water column in 2008 than in 2009. Juvenile pollock horizontal distribution was highly variable in both years and not well explained by the measured characteristics of the physical environment. Temperature structure (thermocline depth, mean temperature at pollock depth, and mean temperature above the thermocline) explained two-thirds of the variability in the vertical distribution of age-0 pollock which also varied with time of day and topographic zone. These differences in horizontal and vertical distribution are likely to affect the use of habitat by predators and have implications for future sampling.

We observed diel vertical migration of age-0 pollock in both study years with pollock found on average 3 to 15 m deeper during the day than at night. Pollock predators appear to be cuing in on the diel vertical migrations of age-0 pollock, since murres in our study area dove deeper during the day and shallower at night (Benoit-Bird et al. in review). Pinnipeds also showed diel patterns in their foraging behavior.

Tagged Northern fur seals in our study area made the majority of their forage dives in relatively shallow water (~25 m) at night (Trites, Battaile, and Nordstrom unpublished data). The mean pollock median depth at night was 18 m which suggests that fur seals were likely encountering age-0 pollock on their nighttime foraging dives. All predators and prey that have been examined thoroughly in the Patch Dynamics Study have been shown to exhibit strong diel patterns of behavior.

Age-0 pollock are often an important prey item for fur seals (Sinclair et al. 2011), black and red-legged kittiwakes, and thick-billed and common murres (Hunt et al. 1996). However, differences in the diets of fur seals and seabirds between the Pribilof and Bogoslof Island breeding colonies (Renner, Paredes, Trites, unpublished data) suggest that, fur seals and other predators are exhibiting high reproductive success on Bogoslof Island without relying on age-0 pollock.

Based on the results presented here, we suggest changes in sampling that would permit further analysis of predator-prey interactions in the study area. Two years of survey data allowed interannual comparisons to be made near the Pribilof Islands, however we were unable to make interannual comparisons near Bogoslof Island due to only sampling there in 2009. Near the Pribilof Islands, the two study years were strikingly different biologically despite having fairly similar physical characteristics. It would be interesting to see if the interannual patterns we observed near the Pribilof Islands also were present near Bogoslof Island. In 2009, juvenile pollock were less abundant and deeper within 200 km of Bogoslof Island than within 200 km of St. Paul, but age-0 pollock were deeper in the entire study area in 2009 and age-0 pollock in both years were deepest in the entire Slope zone, not just near Bogoslof. It is particularly important to better understand how Bogoslof Island compares to the Pribilof Islands because of differences between predator behavior and reproductive success between the two breeding sites. Central place foragers on Bogoslof Island made shorter foraging trips than those on the Pribilof Islands, and seabirds and fur seals have recently been more successful on Bogoslof Island than on the Pribilof Islands (Trites, Battaile, Renner, and Roby, unpublished data). Fur seals on Bogoslof Island stayed relatively close to the island (usually <100 km) with an average trip length of about 2.5 days, while fur seals on the Pribilof Islands made longer foraging trips (200-400 km) that were 5-13 days in duration (Trites, Battaile, and Nordstrom, unpublished data). Additionally, tagged seabirds on Bogoslof Island made shorter trips than their counterparts on the Pribilof Islands (Paredes, personal communication). This suggests that there are differences in prey accessibility and perhaps quality between the Pribilof Islands and Bogoslof Island.

In addition to a second year of sampling near Bogoslof Island, other changes to sampling may have provided useful results. It has been suggested that age-0 pollock exhibit larger vertical migrations when food is scarce (Bailey 1989), but we observed larger vertical migrations in 2009 when biomass of mesozooplankton was greater. It is possible that the preferred prey of age-0 pollock were distributed differently vertically in the water. Vertically stratified sampling of the zooplankton would have allowed us to better characterize the type of zooplankton prey at the depths of juvenile walleye pollock. However, not only would vertically stratified sampling of zooplankton have required additional, more cumbersome sampling equipment; it is also a fairly difficult and time consuming undertaking.

Our description of diel vertical migration was arrived upon by comparing all the median pollock depths during the day to all the median pollock depths at night. This produced a highly significant result, and we are confident in the result, but remaining at a single station or transect for an entire diel cycle in several locations may have given us the opportunity to examine directly the diel vertical migration of juvenile pollock and their zooplankton prey, perhaps allowing us to directly test hypotheses about the drivers of vertical migration of juvenile pollock.

Despite the fact that both 2008 and 2009 were considered cold years in the Bering Sea, and that the cruise dates covered the same time period, we observed large interannual variations in the distribution of age-0 pollock. It is possible that the timing of the spring bloom in the Bering Sea or the hatch dates for pollock occurred at different times during the two years. This could account for the differences in zooplankton abundance and the average age-0 pollock size, which may be related to the small-scale horizontal and vertical distribution of pollock. The original research plan for the large Bering Sea ecosystem study hoped that the study years would encompass both a cold and a warm year. Given our findings, it seems serendipitous that sampling occurred over two cold years because the large differences in the biological data we described near the Pribilof Islands between 2008 and 2009 might have been attributed to inherent differences between the temperature regimes had the two years not both been cold years.

Our study showed that age-0 pollock were sometimes found much deeper in the water column than previously thought. This conclusion was also independently reached by a research group that performs ongoing studies of pollock abundance in the Bering Sea. Historically, assessments of juvenile pollock abundance have used only surface trawls; the recent addition of acoustic sampling to their protocol allowed them to observe deep aggregations of previously undersampled age-0 pollock (Parker-Stetter et al. 2011). Our results also showed that the interannual variability in the distribution and abundance of age-0 pollock and other biological characteristics can be extreme between two cold years in the southeastern Bering Sea. These differences likely account for differences in the foraging behavior observed in the focal predator species in the Southeastern Bering Sea, indicating the importance of age-0 pollock in this ecosystem.

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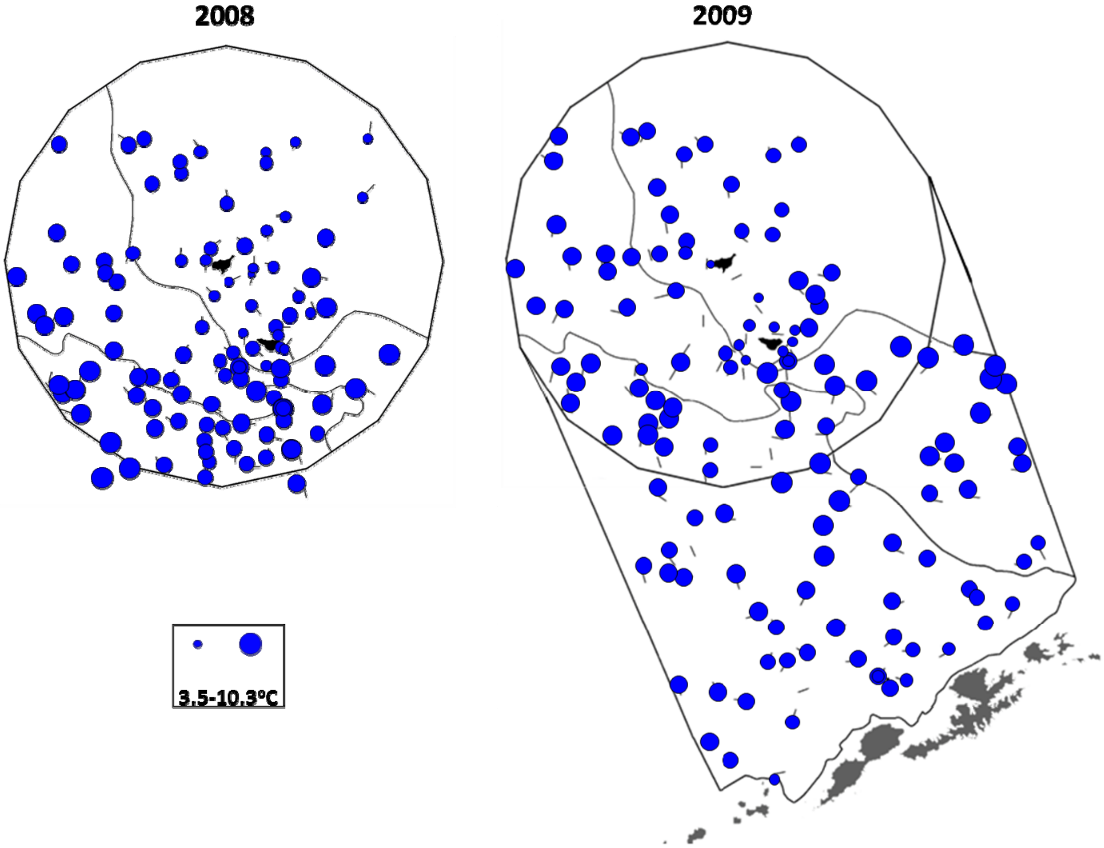
APPENDICES

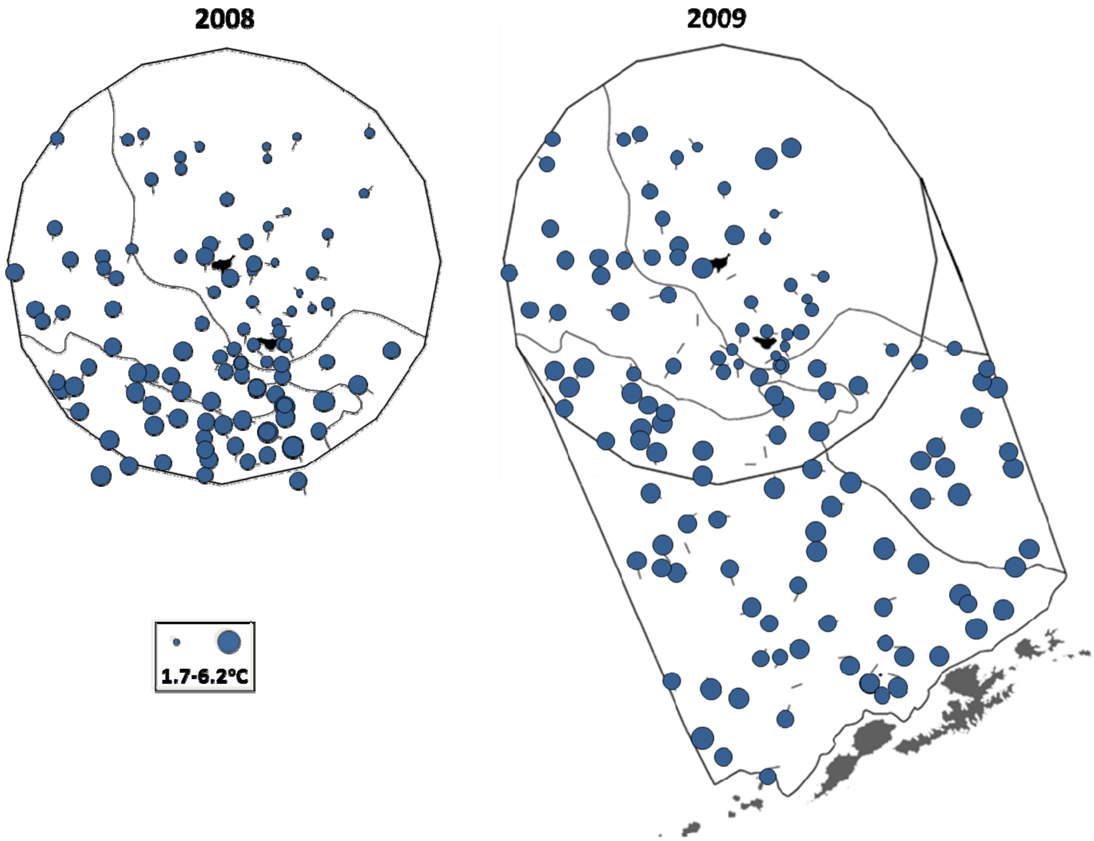
APPENDIX 1. Number of transects per zone put into model selection and number of transects per zone with acoustically identified pollock.

	2008		2009	
ZONE	**# Transects in Model Selection**	**# Transects with Acoustically Identified Pollock**	**# Transects in Model Selection**	**# Transects with Acoustically Identified Pollock**
Middle Shelf (<100 m)	18	37	14	27
Outer Shelf (100 -200 m)	14	28	20	39
Slope (>200 m)	5	9	8	26

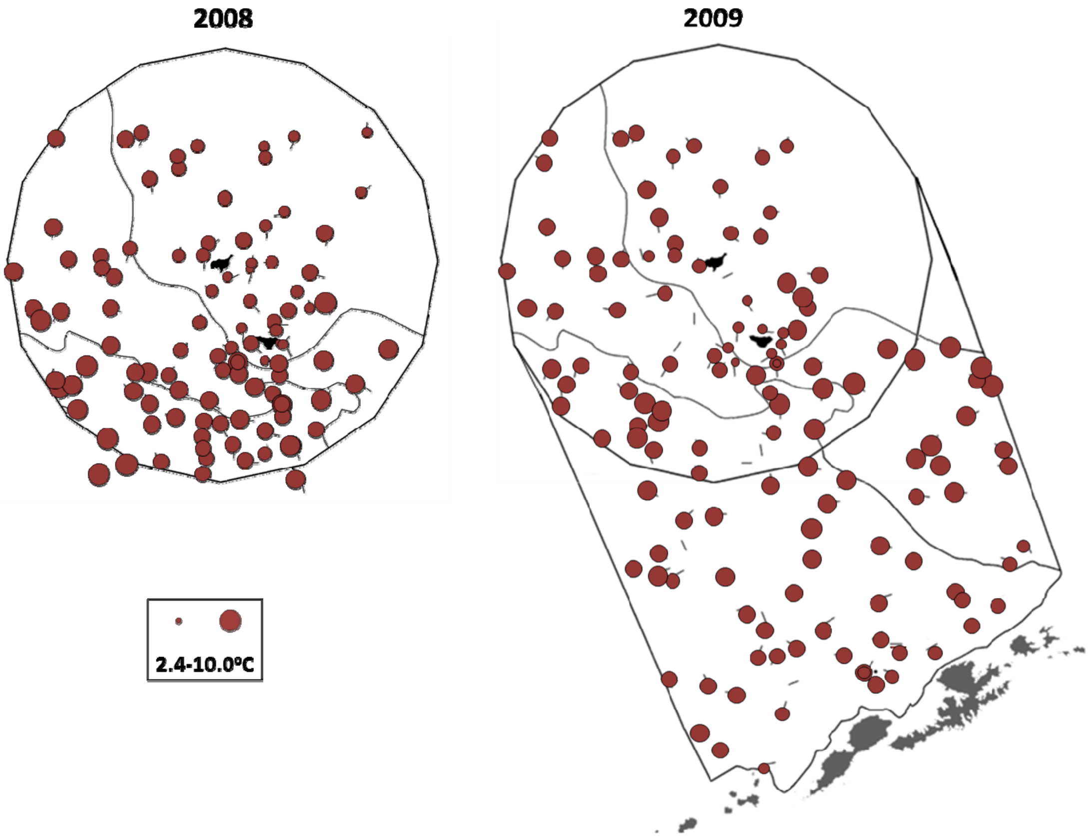
Appendix 2. Bubble plots of environmental variables. Short gray lines indicate transect lines.



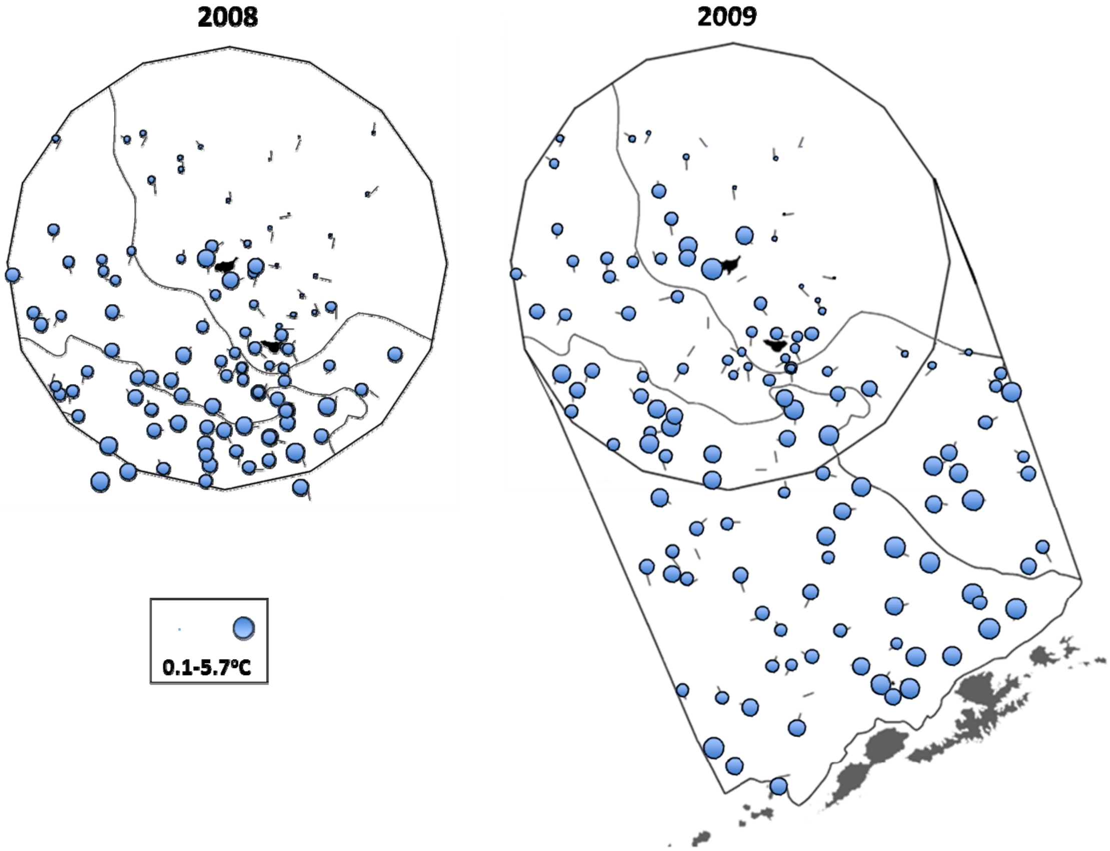
App. 2.1. Sea surface temperature. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



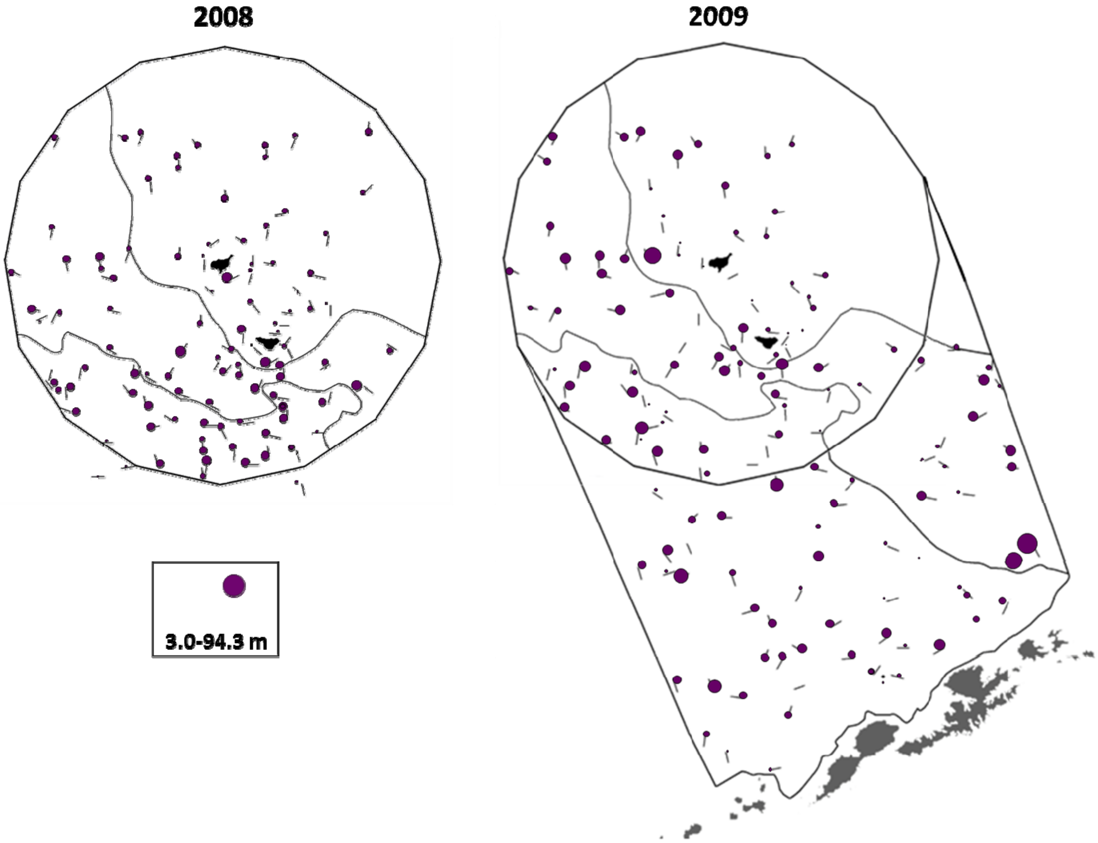
App. 2.2 Mean temperature to 100 m depth. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



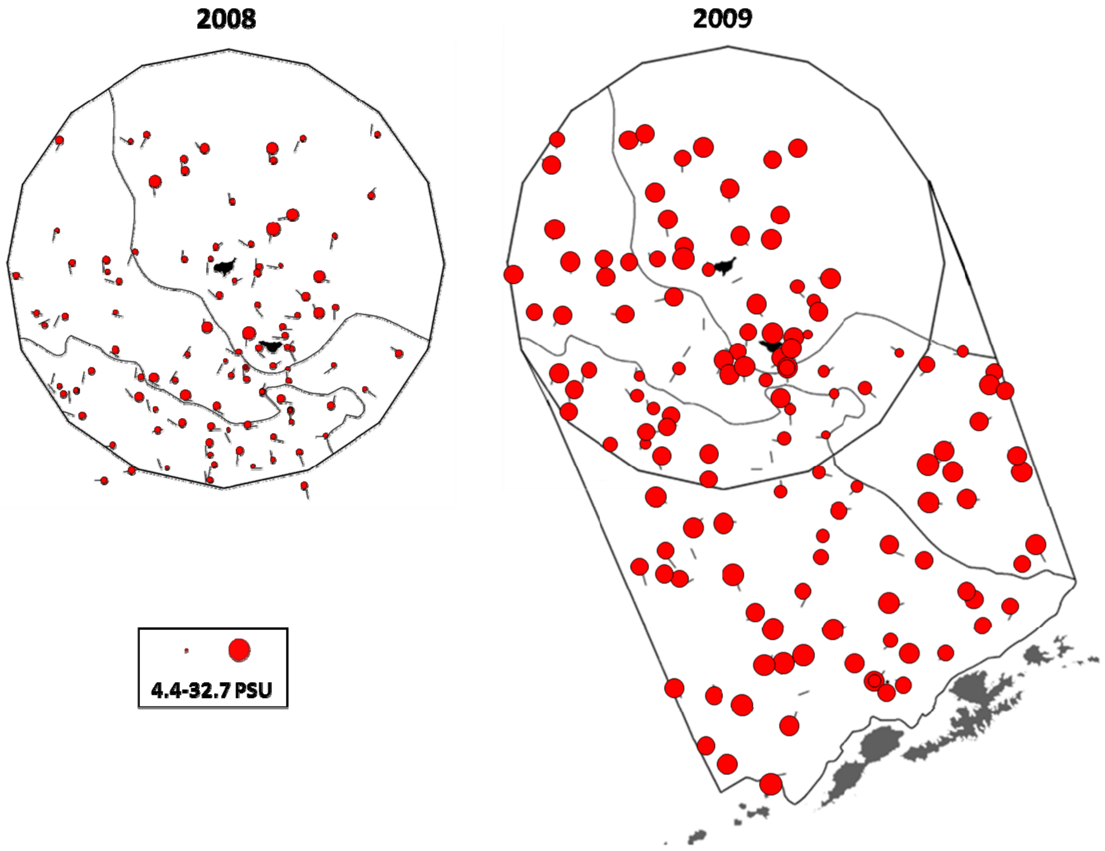
App. 2.3. Mean temperature above the thermocline. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



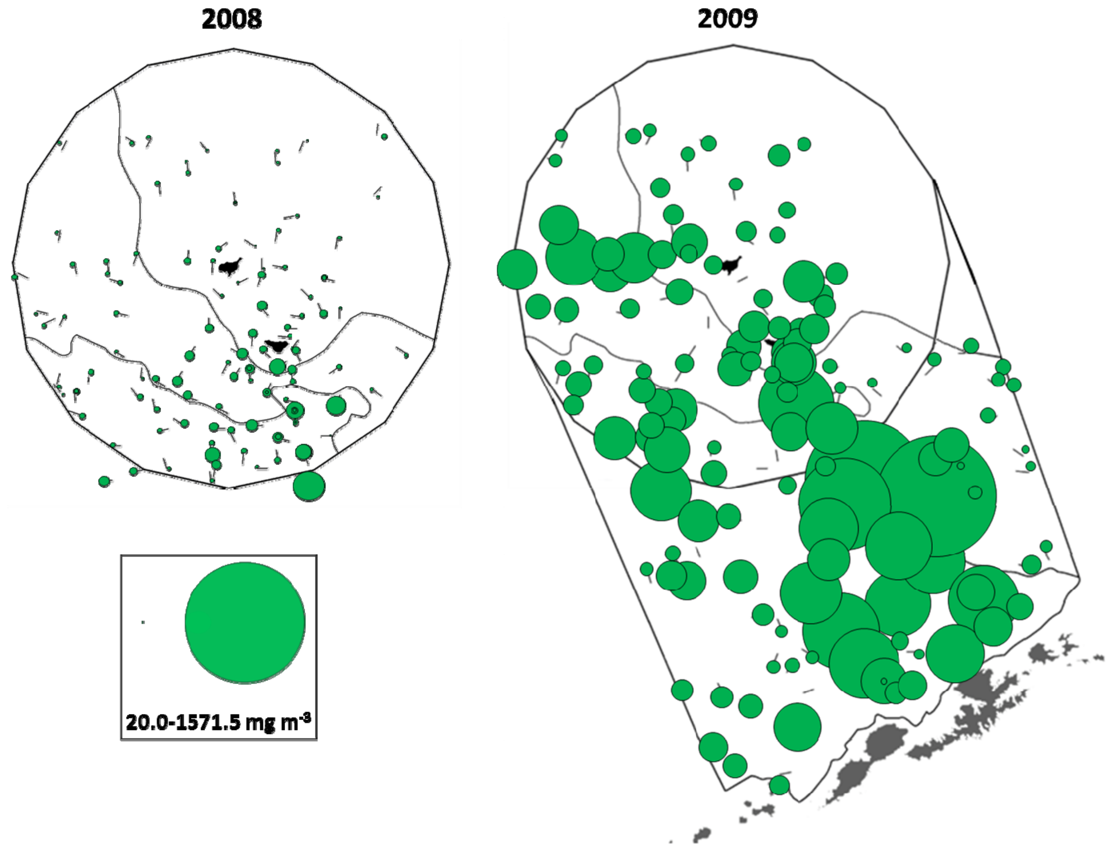
App. 2.4. Mean temperature below the thermocline. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



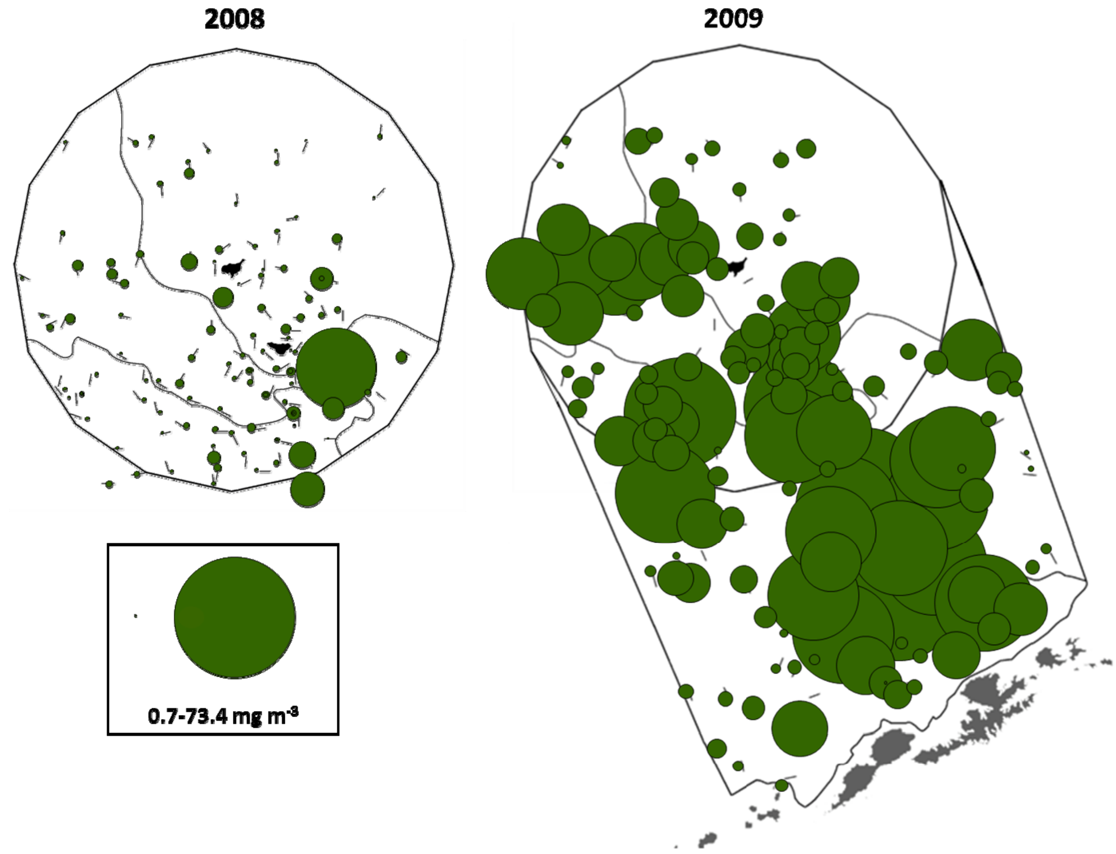
App. 2.5. Thermocline depth. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



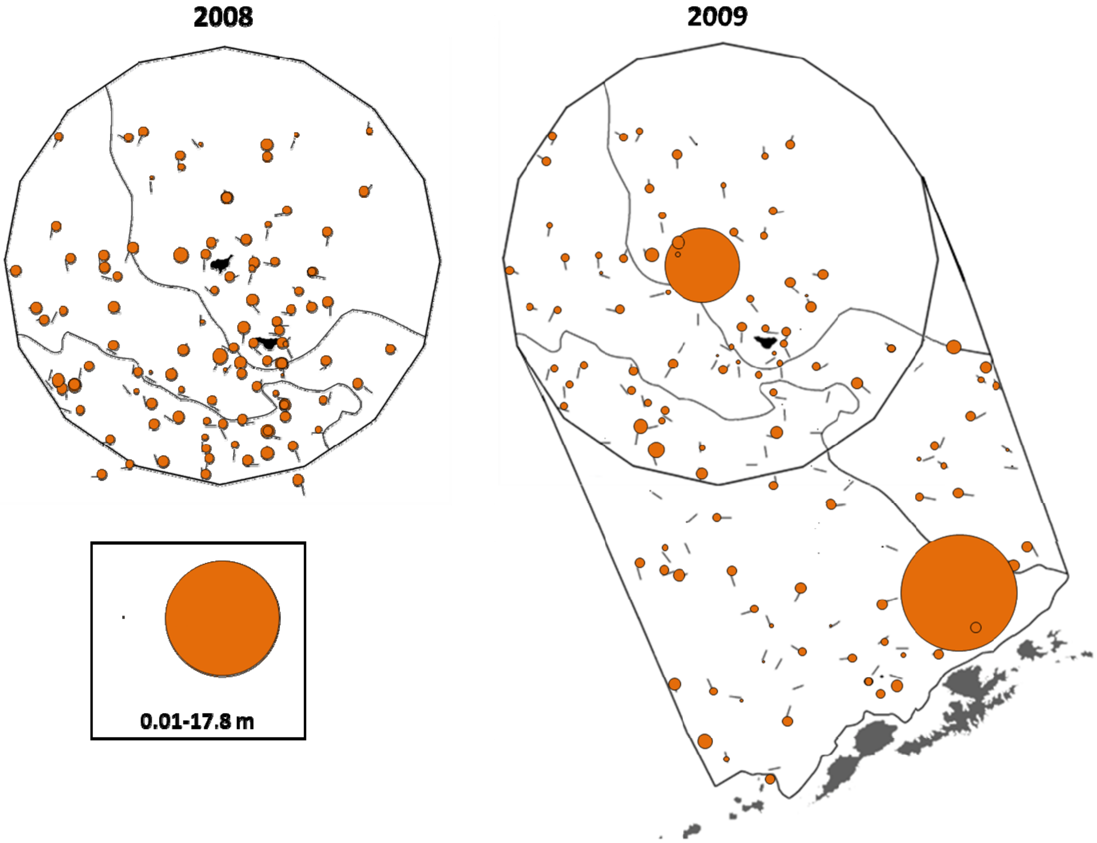
App. 2.6. Sea surface salinity. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



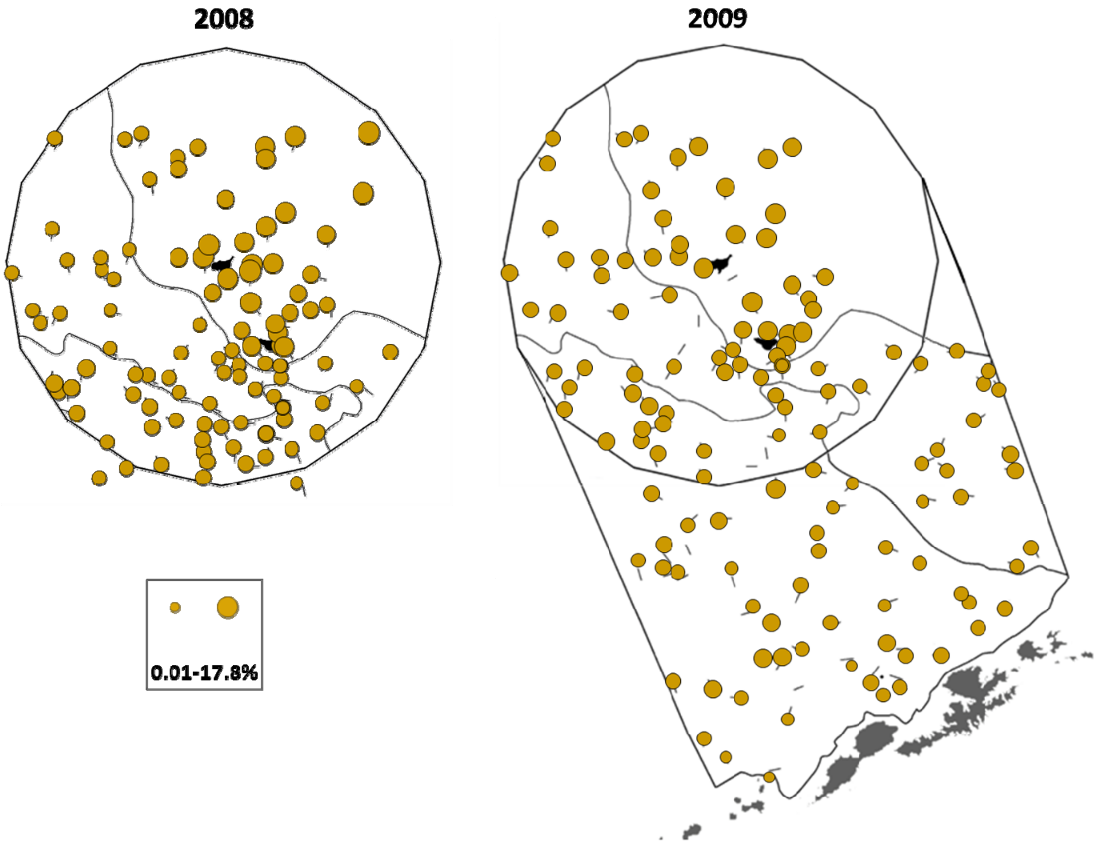
App. 2.7. Total chlorophyll. Bubbles scaled to 50% of width. Empty transects indicate transects where CTD data was lost.



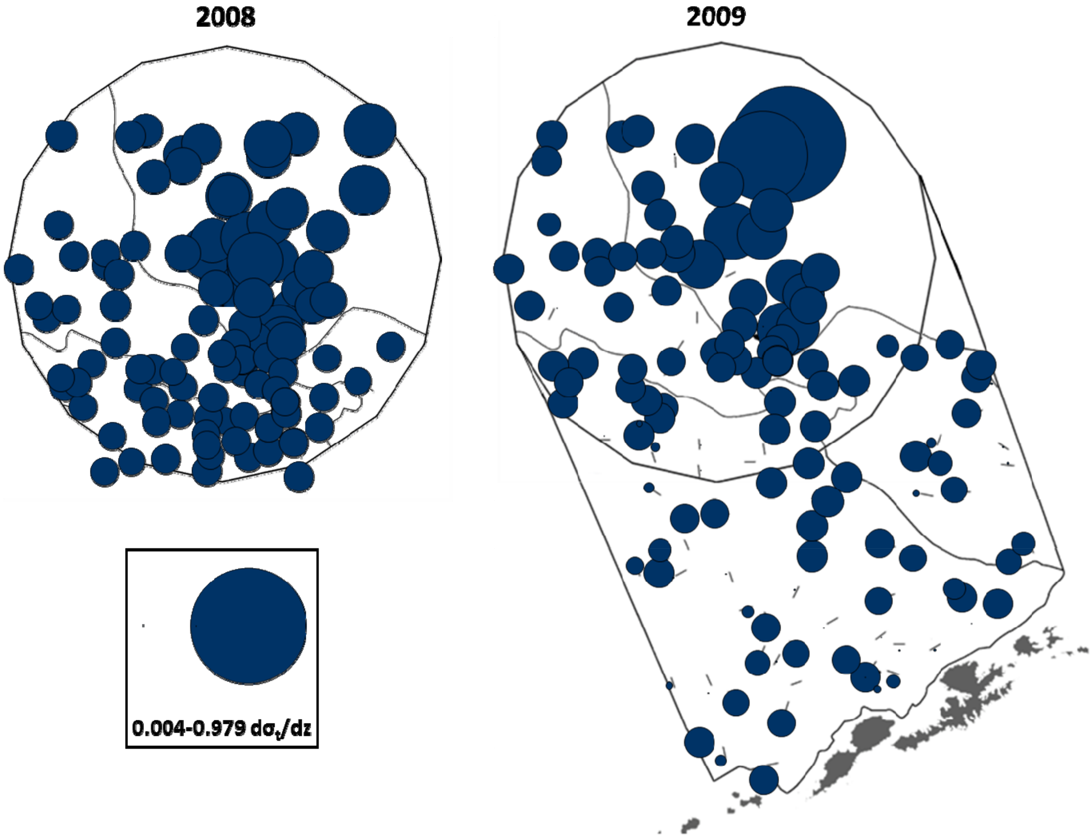
App. 2.8. Chlorophyll maximum. Bubbles scaled to 50% of width. Empty transects indicate transects where CTD data was lost.



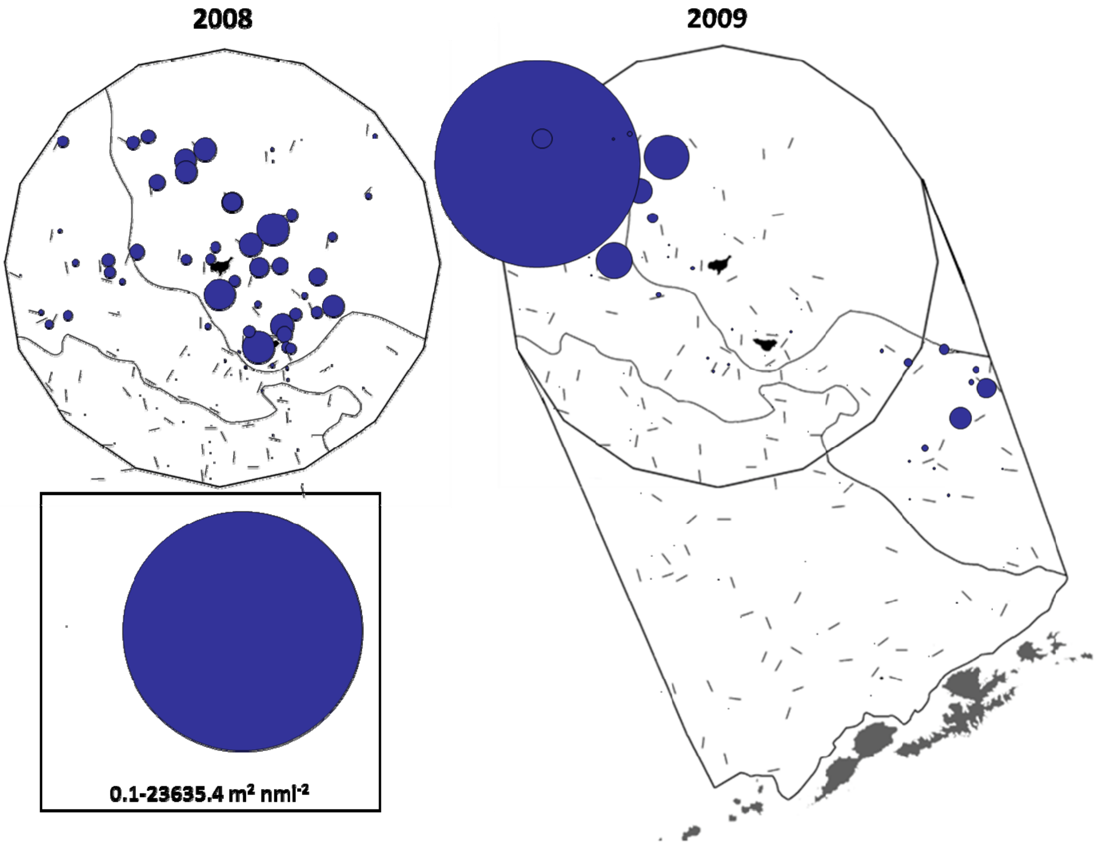
App. 2.9. Oxycline depth. Bubbles scaled to 50% of width. Empty transects indicate transects where CTD data was lost.



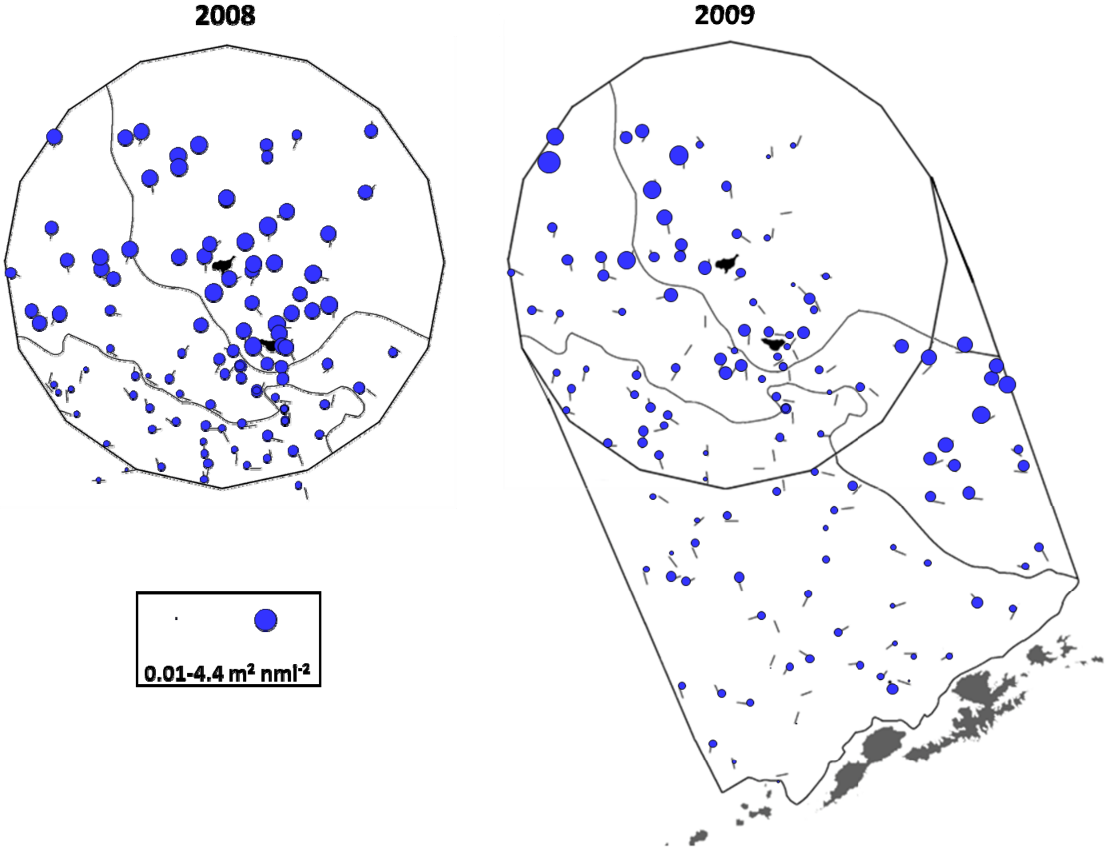
App. 2.10. Minimum percent oxygen saturation. Bubbles scaled to 10% of width. Empty transects indicate transects where CTD data was lost.



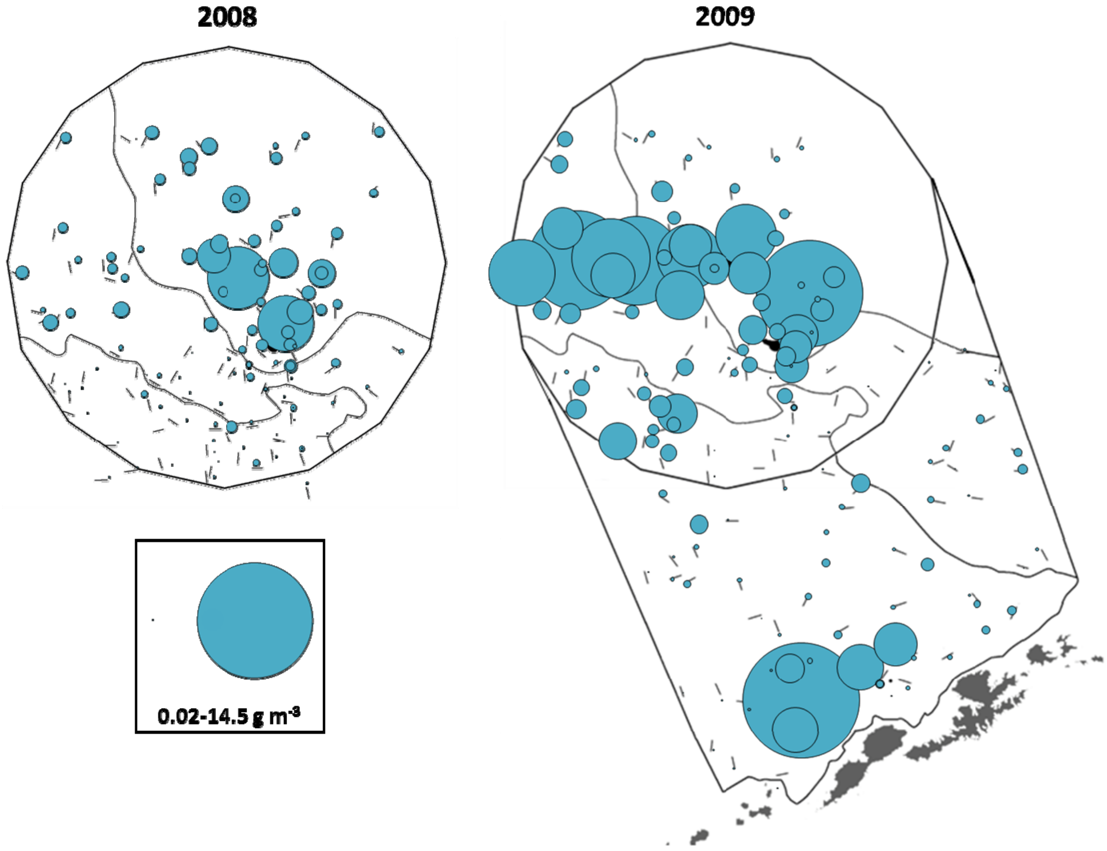
App. 2.11. Water column stratification. Bubbles scaled to 50% of width. Empty transects indicate transects where CTD data was lost.



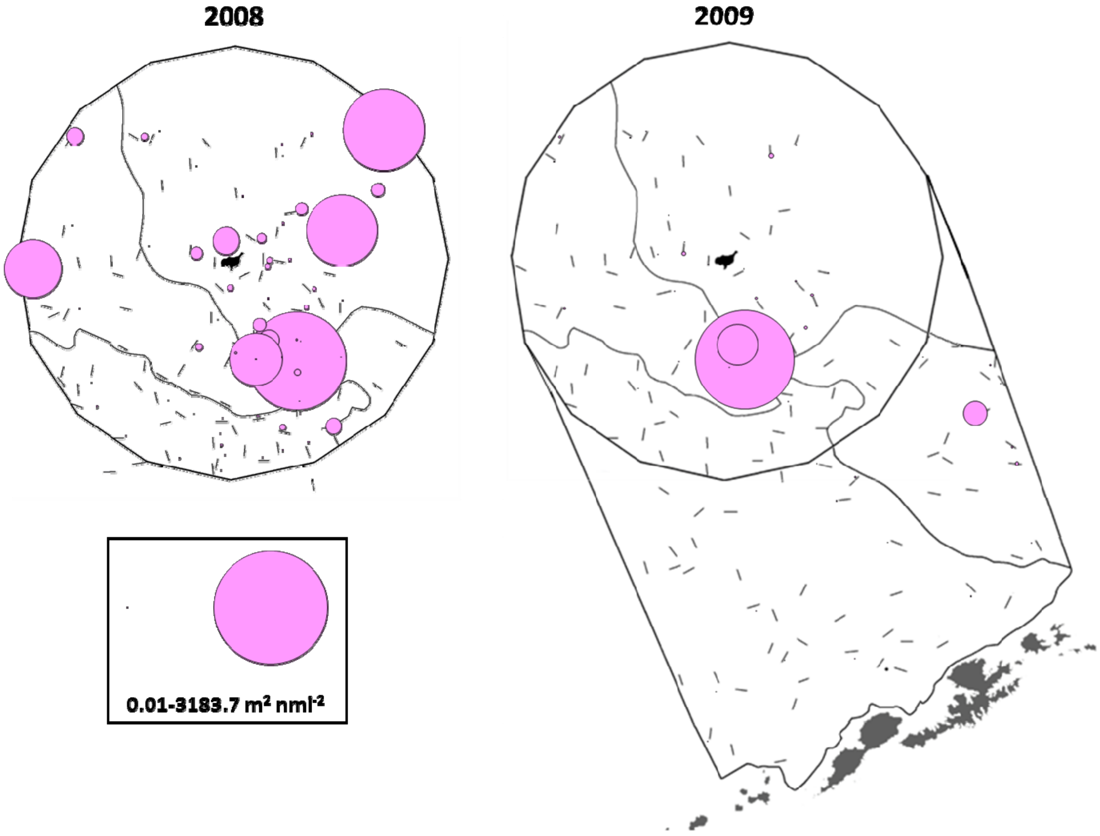
App. 2.12. Acoustic fish abundance (38 kHz NASC). Bubbles scaled to 100% of width.



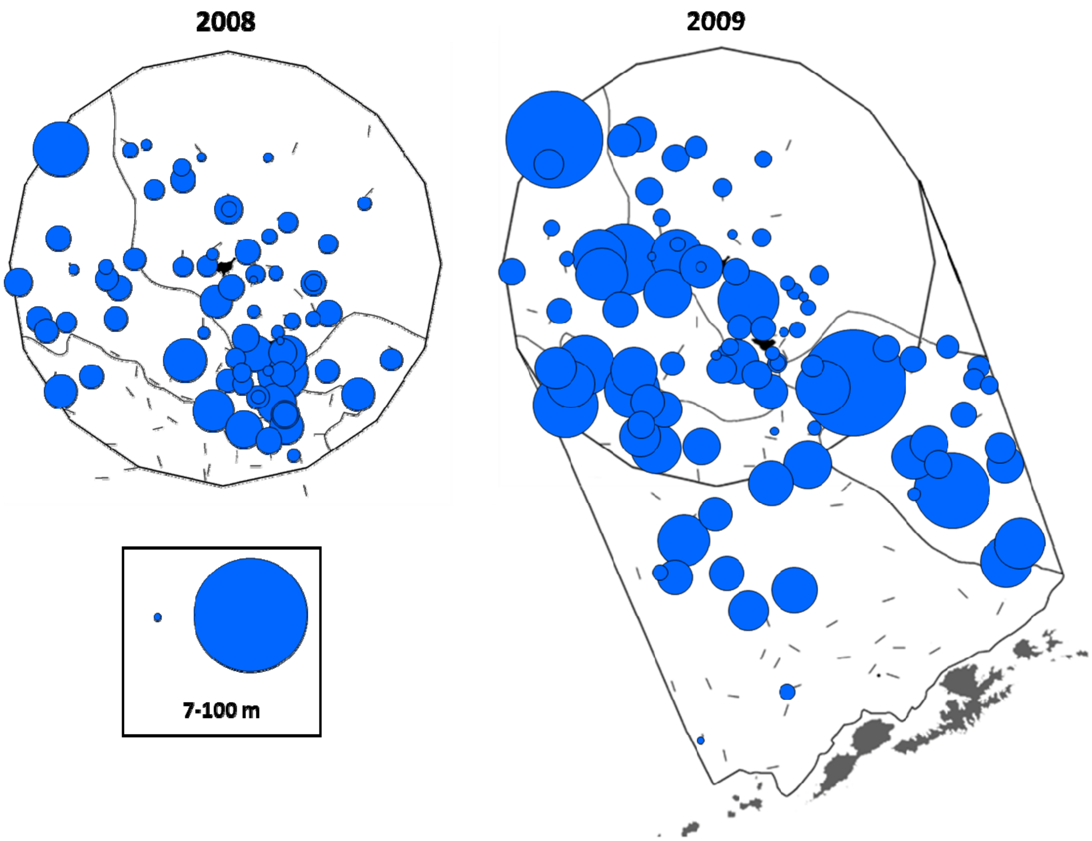
App. 2.13. Acoustic fish abundance (log(38 kHz NASC)). Bubbles scaled to 10% of width.



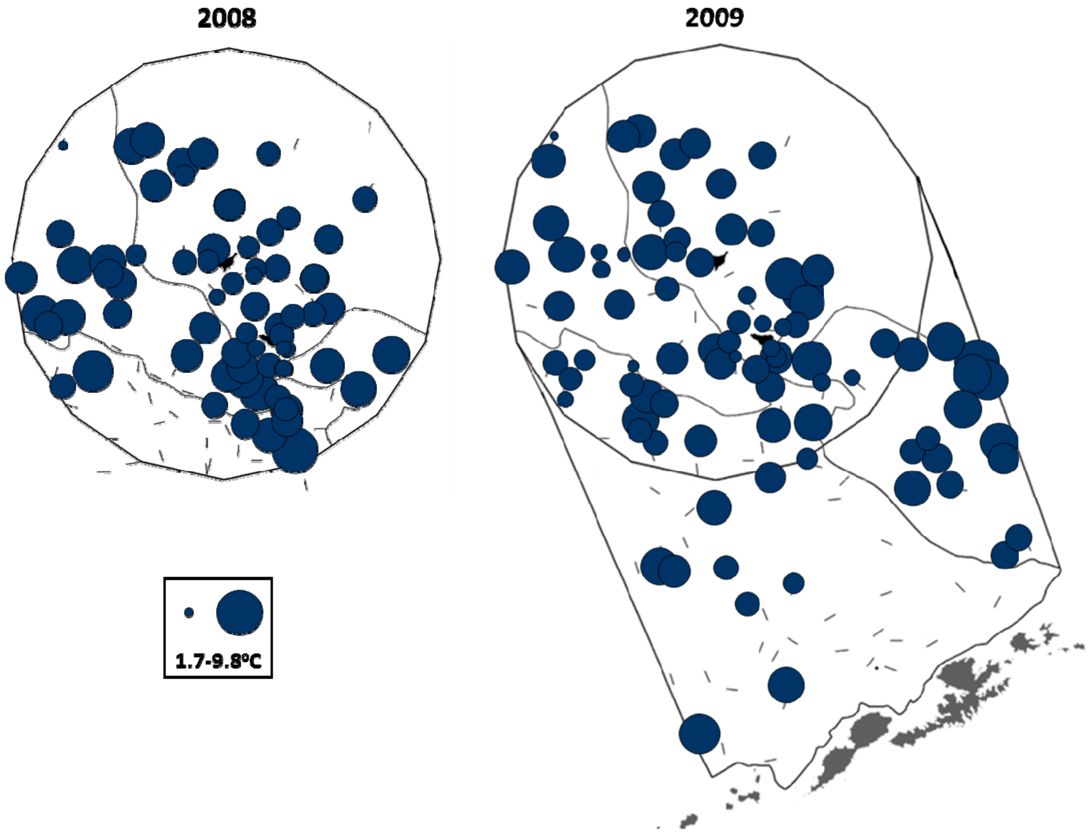
App. 2.14. Zooplankton biomass. Bubbles scaled to 50% of width.



App. 2.15. Acoustic euphausiid abundance (120 kHz NASC). Bubbles scaled to 50% of width. Empty transects indicate values of 0.



App. 2.16. Pollock median depth. Bubbles scaled to 50% of width. Empty transects indicate areas that were sampled, but where pollock were not acoustically identified.



App. 2.17. Temperature at pollock median depth. Bubbles scaled to 20% of width. Empty transects indicate areas that were sampled, but where pollock were not acoustically identified.

Appendix 3. List of taxa from 2009 Outer Shelf zooplankton samples.

		Mean (SD)
Copepod, Calanoida		
	Eucalanus spp. **	75.15 (±81.90)
	Calanus spp. **	185.97 (±270.57)
	Acartia spp.*	77.65 (±71.46)
	Metridia spp. *	34.84 (±42.09)
	Pseudocalanus spp. *	98.55 (±81.32)
	Neocalanus spp. **	14.40 (±14.84)
	Candacia spp. **	0.00 (±0.01)
	Total Calanoid Copepods	486.55 (±363.56)
Copepod, Cyclopoida		
	Oithona spp. *	104.01 (±174.89)
	Oncaea spp. *	0.01 (±0.05)
	Copepod, unid. *	0.01 (±0.02)
	Total Cyclopoida Copepods	104.03 (±174.88)
Total Copepods		590.58 (±393.79)
Euphausidae		
	Adult and large juveniles	0.55 (±0.49)
	Protozoea	0.13 (±0.32)
	Zoea	0.05 (±0.11)
Other Crustaceans		
	Amphipod	0.68 (±0.46)
	Isopod	0.03 (±0.03)
	Ostracod	0.04 (±0.03)
	Cumacea	0.05 (±0.13)
	Crab, zoea	0.07 (±0.11)
	Crab, megalopa	0.01 (±0.02)
	Caridean shrimp	0.01 (±0.01)
	Shrimp, unid.	0.01 (±0.02)
	Barnacle, larvae	0.00 (±0.01)

Appendix 3 (continued)

Mollusca		**Mean (SD)**
	Pteropod	4.81 (±4.97)
	Gastropod, unid.	0.00 (±0.01)
	Bivalve, unid.	0.00 (±0.01)
Echinoderm		
	Larvae, unid.	0.30 (±0.46)
	Brittle star	0.00 (±0.01)
Fish		
	Juvenile, unid.	0.01 (±0.02)
	Fish larvae, unid.	0.00 (±0.01)
Larvacea		86.78 (±154.06)
Chaetognatha		11.28 (±10.04)
Foraminifera		11.68 (±15.77)
Radiolaria		0.00 (±0.01)
Egg, unid.		3.90 (±7.56)
Nauplius, unid.		21.87 (±56.70)
Larvae, unid.		0.01 (±0.03)
Polychaete, unid.		0.34 (±0.74)
Ctenophora		0.09 (±0.29)
Hydrozoa		0.07 (±0.10)
Sipunculida		0.00 (±0.01)
Worm, unid.		0.02 (±0.06)

Appendix 3 (continued)

Zooplankton Size Classes		**Mean (SD)**
	Zooplankton < 2 mm	358.94 (±282.77)
	Zooplankton 2-4 mm	363.19 (±248.03)
	Zooplankton 4-6 mm	0.09 (±0.13)
	Zooplankton > 6 mm	11.95 (±10.09)
Copepod Size Classes	**Small (>2mm PL) Copepods (*)**	336.93 (±272.37)
	Large (<2mm PL) Copepods (**)	275.52 (±261.74)

Appendix 4. Model coefficients for the 2008 multiple linear regression model. Pollock median depth = model intercept (β_0) – temperature at the pollock median depth (β_1) + mean temperature above the thermocline (β_2) + thermocline depth (β_3) + zone (β_4, β_5, β_6). Bolded values show significant differences between zones.

	Model Intercept (β_0)		**Temperature at the Pollock Median Depth (β_1)**		**Mean Temparture Above the Thermocline (β_2)**		**Thermocline Depth (β_3)**		**Factor Variable for Zone = MS (β_4)**		**Factor Variable for Zone = OS (β_5)**		**Factor Variable for Zone = SL (β_6)**		**Adjusted R^2**	**p-Value**
	Value	**p-Value**	**Value**	**p-Value**	**Value**	**p-Value**	**Value**	**p-Value**	**Value**	**p-Value**	**Value**	**p-Value**	**Value**	**p-Value**		
2008 (reference zone = Middle Shelf (MS))	17.67	< 0.00001	-5.93	< 0.00001	3.84	< 0.00001	0.39	< 0.00001	***	***	**4.11**	< 0.05	**7.09**	< 0.01	0.67	< 0.00001
2008 (reference zone = Outer Shelf (OS))	21.78	< 0.00001	-5.93	< 0.00001	3.84	< 0.00001	0.39	< 0.00001	**-4.11**	< 0.05	***	***	2.99	> 0.05	0.67	< 0.00001
2008 (reference zone = Slope (SL))	24.76	< 0.00001	-5.93	< 0.00001	3.84	< 0.00001	0.39	< 0.00001	**-7.09**	< 0.01	-2.99	> 0.05	***	***	0.67	< 0.00001