Distribution of age-1 and age-2 walleye pollock in the Gulf of Alaska and eastern Bering Sea: sources of variation and implications for higher trophic levels

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Abstract

Walleye pollock (*Theragra chalcogramma*) is the predominant groundfish species in the North Pacific Ocean, and it is a focal point in the ecology of the region. However, there is only a limited knowledge of the distribution of the juveniles of this species (age-1 and age-2 individuals). We examine the horizontal and vertical distribution of age-1 and age-2 walleye pollock in the eastern Bering Sea and Gulf of Alaska and relate observed patterns to key physical (temperature, latitude, longitude, bathymetry) and biological (diet, physiology) characteristics. We used data collected from three sources: a field survey conducted in the Gulf of Alaska (2001), field data collected from echo integration trawl surveys in the eastern Bering Sea (1994, 1996, 1997, 1999), and laboratory experiments investigating the behavior and physiology of age-1 and age-2 individuals under various thermal conditions. Results indicate there is the potential for differences in the ecology of walleye pollock between the Bering Sea and the Gulf of Alaska. Data from 1996 and 1997 indicate that age-1 and age-2 walleye pollock in the Bering Sea are vertically separated in the water column

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(though they co occur in other years), with age-1 pollock located near bottom and age-2 pollock schooling higher in the water column. However, we did not find evidence of vertical separation among these cohorts in the Gulf of Alaska. Adult pollock (age-4+) appear to be demersal during the day in both systems. Diet analyses of pollock collected in the Bering Sea (1990-1997) indicate a high degree of cannibalism of age-0s by age-1 and age-2 individuals, though there is no evidence of inter-year class cannibalism in samples collected from the Gulf of Alaska (2001). Additionally, laboratory experiments show that the thermal range of pollock decreases with age, suggesting that younger fish may be able to exploit more of the vertical water column than older fish because they have greater thermal tolerances. Further work needs to be done to pursue the study of potential differences in spatial separation among cohorts between the Gulf of Alaska and the Bering Sea. However if the differences that we observed are reproduced, our laboratory results suggest that, in the Bering Sea, spatial separation could be related to a combination of temperature tolerance and intensive intraspecific predation pressure, while the lack of intraspecific predation pressure in the Gulf of Alaska might permit a greater co-mingling of age classes.

Introduction

The North Pacific Ocean is a highly productive ecosystem that supports a vast array of fishes, birds, and mammals. The dominant fish component of this ecosystem is the walleye pollock (*Theragra chalcogramma*), which sustains one of the world's largest commercial fisheries and provides a forage base for higher trophic level animals (Springer 1992). The immature stages of this species transfer energy from zooplankton to higher trophic levels (Brodeur and Wilson 1999), making them an important link in the food chain. Several recent studies have focused on the ecology of age-0 pollock (Brodeur 1998; Swartzman et al. 1999; Wespestad et al. 2000), but distribution patterns of later immature stages (age-1 and age-2s) remain uncertain. Bottom trawl surveys have been used to provide information on the dispersal of age-1 juveniles, but age-2 juveniles are infrequently collected in bottom trawls (Karp et al. 1989). Some information on the distribution of pollock juveniles has also been gathered from existing midwater trawl and hydroacoustic data (McKelvey 1996), but the overall spatial and temporal patterns of distribution between these two cohorts remain unclear. Studies that clarify where and when juvenile pollock are present can help to reduce concerns about bycatch of juveniles, and are important in understanding energy transfer to higher trophic levels.

Data from the National Marine Fisheries Service bottom trawl and echo integration trawl surveys suggests that, in the Eastern Bering Sea (EBS), age-1 and age-2 pollock schools may be vertically separated in the water column. These observations suggest that age-2s may be schooling higher in the water column, while age-1s are primarily located on-bottom. The factors that motivate this presumed stratification are unexplained, and it is also not known whether such a stratification exists in the Gulf of Alaska (GOA). Studies of young-of-the-year pollock suggest vertical distribution is influenced by predation pressure (Bailey 1989), bioenergetic criteria (Sogard and Olla 1994; Ciannelli et al. 1998), and prey availability. These factors and others probably contribute to the patterns of distribution of later immature stages as well, acting synergistically to affect re-

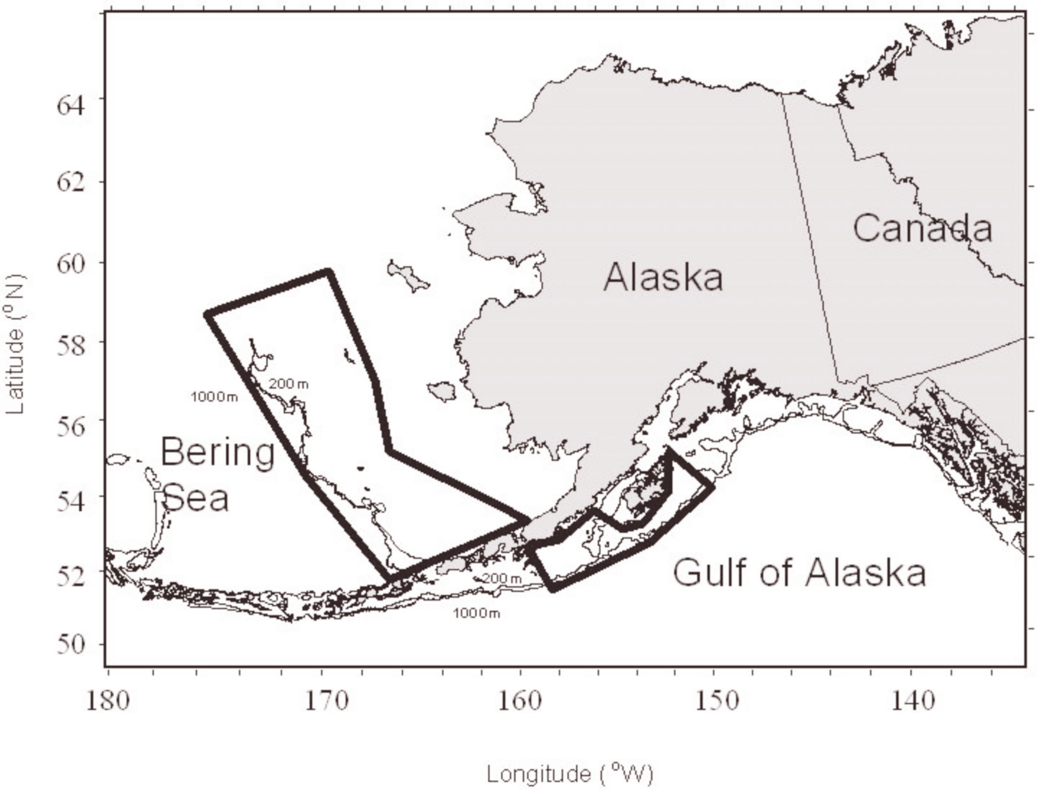

Figure 1. *Extent of field surveys (black boxes) in the eastern Bering Sea and Gulf of Alaska in 1994, 1996, 1997, 1999 (EBS) and 2001 (GOA).*

sponse. This paper: 1) examines the spatial distribution of age-1 and age-2 walleye pollock in the EBS and GOA, 2) relates observed patterns to predominant physical and biological characteristics to identify potential determinants for segregation, and 3) examines the implications of these results on upper trophic level organisms. Our multifaceted approach provides a preliminary analysis of the distribution of immature walleye pollock in the North Pacific Ocean, and examines some of the underlying physical and biological factors contributing to patterns in distribution and behavior.

Materials and methods

Gulf of Alaska – Field Surveys. Two field surveys were conducted in the GOA in August and September 2001, which assessed the vertical distribution of immature walleye pollock. Cruises were conducted on board the NOAA ship *Miller Freeman* in the vicinity of Kodiak Island, Alaska (Figure 1).

Age-1 and age-2 pollock were collected at discrete depths, either from bottom trawls (Poly Nor'easter bottom trawls (3.5 inch codend) or shrimp trawls (3.2 cm stretched mesh, 3mm mesh codend liner)) or from depth discrete mid-water trawls (anchovy trawls (3.2 cm stretched mesh, 3mm mesh codend liner) or Aleutian wing trawl (3.5 inch codend). A randomly selected subset of walleye pollock was taken from each trawl, frozen, and returned to the laboratory for stomach content analyses to provide data on diet. An analysis of variance (ANOVA) was used to test the hypothesis that there was no difference in the vertical distributions of age-1 and age-2 walleye pollock.

Bering Sea – Acoustic Surveys. Acoustic data on fish distribution in the EBS were collected between June and September (1994, 1996, 1997, 1999) with a Simrad EK500 scientific split beam echo sounding system. The transducer operated at 38 kHz and was mounted on the bottom of the NOAA ship *Miller Freeman*'s retractable centerboard. Echo integration and target strength data were collected simultaneously. Trawling was conducted opportunistically to sample echo sign observed on the echosounder display. Midwater sign was sampled with a large, commercial midwater trawl fitted with a 3.2 mm/1.25 in codend liner. Near bottom sign was sampled with a survey bottom trawl that was fitted with the same sized mesh. Estimates of pollock biomass and numerical abundance by length and age (Traynor 1996) were developed from the acoustic and trawl data.

Stomach Content Analyses. Fish collected from the field (GOA) were measured and weighed, and the stomachs excised. Stomach contents were visually evaluated for fullness (empty, trace prey, 25%, 50%, 75% 100%, distended). Upon dissection, individual taxa were enumerated and identified to the lowest possible taxon. Wet weights for each prey species were measured. Data were grouped into higher taxonomic categories for statistical analyses and an ANOVA (Zar 1984) was used to determine whether there were differences in composition of stomach contents with respect to age (size class) and location (EBS vs. GOA).

Stomach content data for pollock collected from the EBS was compiled from the Alaska Fisheries Science Center's fish food habits database that includes individuals of age-1+ captured throughout the eastern Bering Sea from 1990 to 1997. Methods for stomach content analyses for fishes collected in the EBS were similar to those used in the analyses of GOA-collected samples (but see Livingston and deReynier 1996 for a complete description).

Behavioral Experiments. Age-0 walleye pollock for laboratory experiments were collected near Port Townsend, Washington, in June 1999, and returned to the Center's laboratory in Newport, OR, to be reared for use in behavioral experiments. Pollock were reared until age-2, and behavioral studies were conducted in controlled tanks to examine patterns in vertical migration (similar to methods outlined in Sogard and Olla 1994, 1996). Briefly, behavioral observations were made in two 15,000 l tanks with Plexiglas[1] walls. Stratified temperature conditions were created by slowly adding cold water to the bottom of the tank. Observations under isothermal (iso) and stratified (strat) conditions were made using a video monitoring system, and behavioral responses were scored according to level of activity. In this study we focused on the effects of food availability (fed and starved fish) on behavioral thermoregulation among age-2 pollock. Each experiment consisted of a set of two individuals (group) for each thermal treatment. A total of 25 groups were partitioned among treatments as follows: 6 iso-starved, 6 iso-fed, 7 strat-fed, 6 strat-starved. Data were analyzed using a nested ANOVA on vertical position (i.e., temperature) in the water column, with group used as the nesting factor. Similar studies using age-1 pollock and mixed schools of age-1 and age-2 pollock were planned, but poor survival of the age-1 cohort made it impossible to conduct these trials.

Energetics Simulations. A bioenergetics model (see Ciannelli 2002) was used to determine juvenile pollock growth response as a function of size and water temperature. In particular, we estimated the 50% thermal range (i.e. the temperature interval within which fish reach 50% of their maximum growth rate) as a function of juvenile pollock size.

Results

Gulf of Alaska – Field Surveys. Over 39,000 walleye pollock were collected from midwater trawls and nearly 2,000 pollock were collected in bottom trawls from the field survey conducted in August 2001. Over 4,000 individuals were collected from midwater trawls and nearly 400 individuals were collected from bottom trawls in the September 2001 survey. There were no statistical differences in vertical distribution of age-1 and age-2 walleye pollock ($p>0.05$), evidenced by similar catches of these individuals in bottom and mid-water trawls (Figure 2).

However, there was a tendency for adult walleye pollock (age-4+) to occur in greater numbers in bottom trawls, indicating that older walleye pollock are primarily demersal in the Gulf of Alaska.

Bering Sea – Acoustic Surveys. Echo integration trawl data were examined from surveys conducted in summer 1994, 1996, 1997, and 1999. At each trawl site, weighted average distance off bottom was computed for pollock in each of three age groups (age-1, age-2, and age-3+ pollock) and then stratified by known geographic-bathymetric features (east or west of 170 °W, and shallower or deeper than the 100 m isobath). The following observations apply to vertical stratification within the stratum west of 170 °W and deeper than the 100 m isobath, where juveniles and adults were most numerous; horizontal stratification (differences between areas and within and between years) is not treated here. In 1994, both age-1 and age-2 walleye pollock schooled higher in the water column than pollock age-3+. Age-1 vertical distribution was not found to be different from that of age-2s. In 1996, age-1 pollock tended to be found near the bottom, while age-2 individuals were again more often observed higher in the water column. In 1997, age-1 pollock were found in both dense, mid-water schools and in aggregations closer to the bottom, whereas age-2 pollock were found higher in the water column, as in 1994 and 1996. In 1999, all age groups were highly concentrated in one or two locations, and the age-1 and age-2 juveniles were not spatially separated. Thus, for some years, there is evidence for spatial separation between age-1 and age-2 pollock on the EBS shelf.

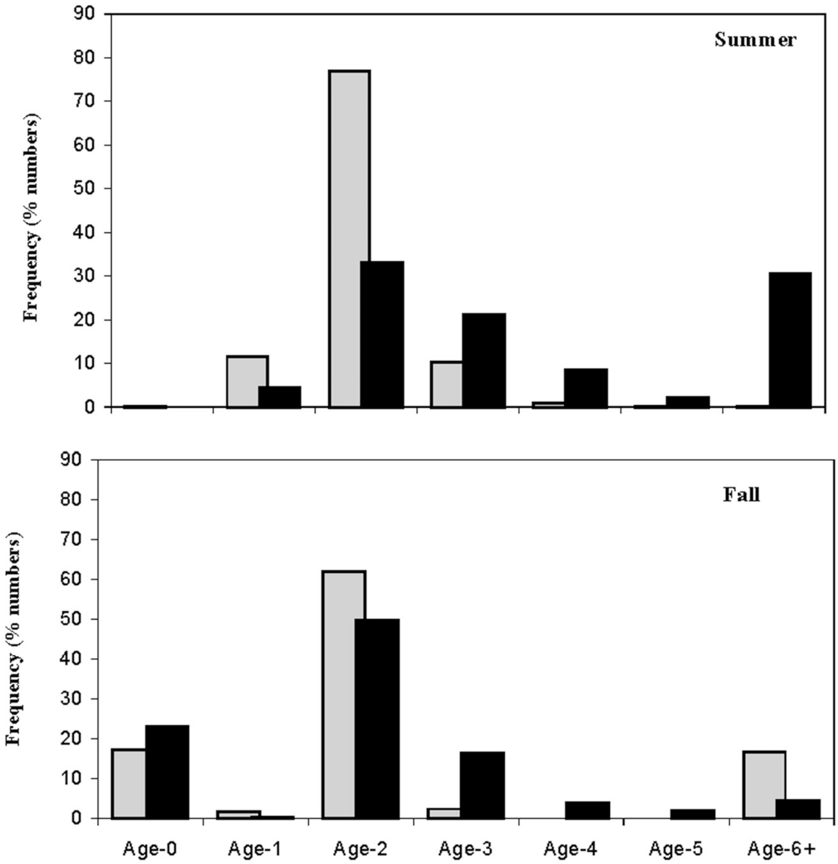

Figure 2. Age-frequency distribution of walleye pollock in the Gulf of Alaska in summer (top) and fall (bottom) 2001. Age-0 < 11 cm, age-1 = 12-18 cm, age-2 = 19-28 cm, age-3 = 29-36 cm, age-4 = 37-41 cm, age-5 = 42-47 cm, and age-6+ > 48 cm. Absence of age-0 individuals in summer collections was due to large mesh size used during towing. Black = bottom trawl, gray = midwater trawl.

Stomach Content Analyses. Over 300 walleye pollock were collected for diet analyses from cruises in the GOA in August and September 2001 (Figure 3), and to date, stomach content analyses have been performed on 61 of the individuals collected in August.

Data from these analyses suggest that the diets of age-1 and age-2 individuals were somewhat dissimilar, with age-1 pollock consuming proportionally more cumaceans than age-2 individuals (51% and 12%, respectively), though both age-classes consumed euphausiids in significant quantities (47% and 85%, respectively; $p < 0.001$). Fish made up a substantial portion (80%) of the diet of adult pollock. There was no evidence of inter-cohort cannibalism among any of the size classes, and all the fishes consumed by adults were identified as sticklebacks or other non-pollock fishes (Figure 4).

Observed differences in diet with age (size class) were not statistically significant because of the large variability in diet composition within size classes.

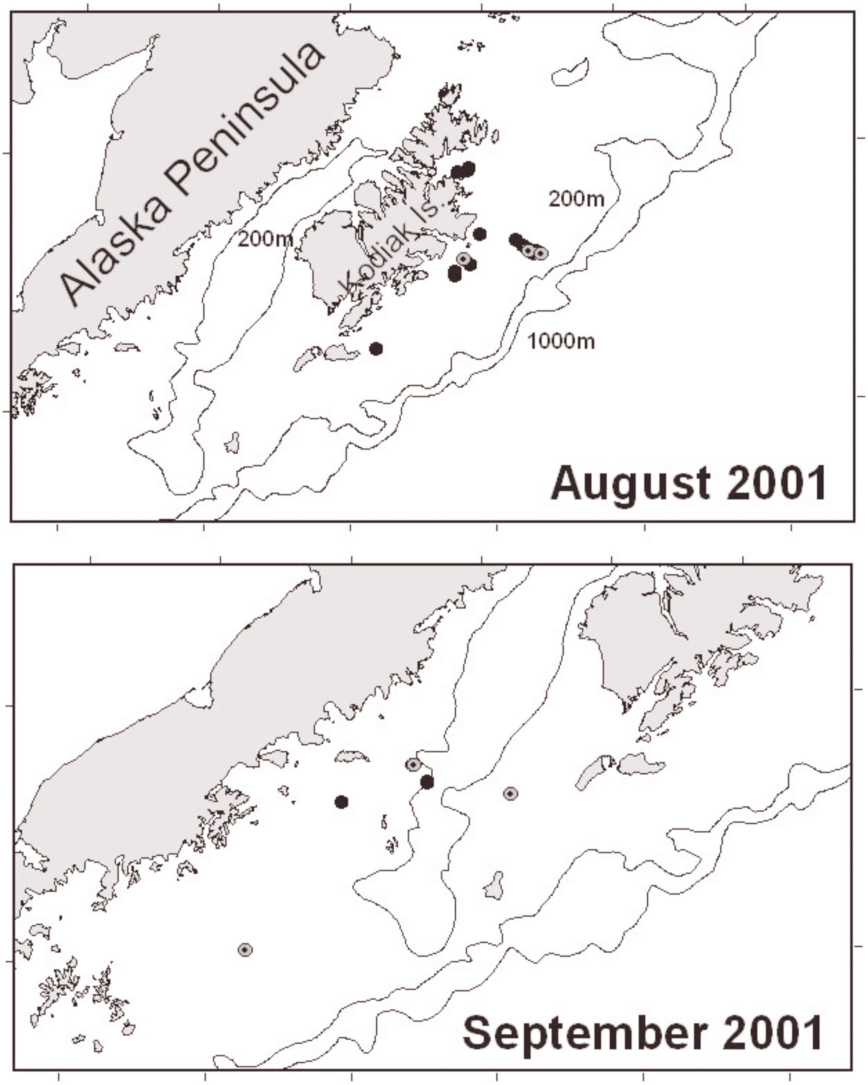

Figure 3. *Location of walleye pollock collections for stomach content analyses in summer (top) and fall (bottom). Filled circles = stations where midwater tows were conducted; circles with a dot = stations where bottom trawls were conducted.*

Walleye pollock diet data from fishes collected in the EBS indicated that the diet composition of juvenile pollock changed with size, especially with respect to cannibalism and copepod consumption. Importance of cannibalism increased from 5.5% in age-1 pollock to 46.9% in early age-2 (16-20 cm standard length) and then decreased to 28.6 % in later age-2 pollock (21-25 cm standard length). Cannibalism ranged between 1.1 % and 11.0% in later and larger individuals.

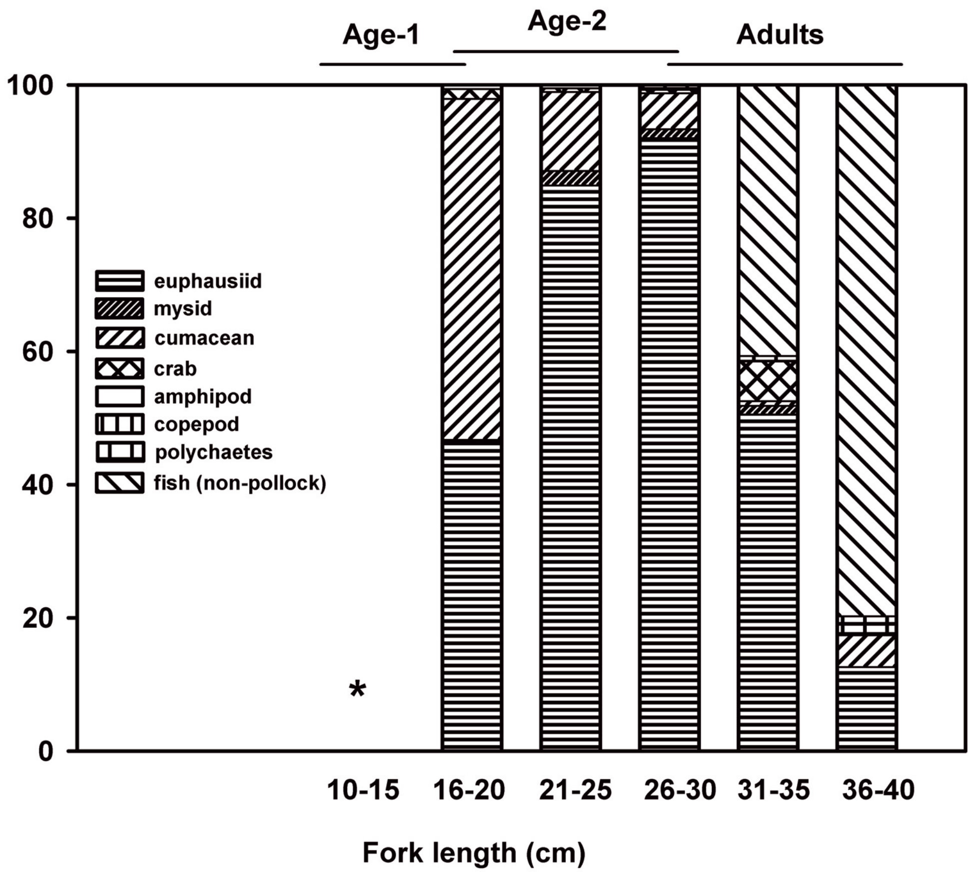

Figure 4. Percent composition by weight of the diet of walleye pollock collected in the Gulf of Alaska in summer 2001. Asterisks = no data available. Dominant prey categories are shown.

The proportion of copepods in the diet changed from 54.0% to 20.8% and 28.0% in age-1, early and late age-2 pollock, respectively. Copepods in the diet ranged between 47.0% and 50.1% in later age classes (Figure 5). All other major prey items included in the diet did not considerably change among age classes. Most of the fish consumed by larger pollock were age-0 pollock (< 100 mm SL).

Behavioral Experiments. We found no difference in behavioral thermoregulation between fed and starved age-2 pollock. In a vertical gradient tank, fed fish experienced an average temperature of 10.8°C (± 2.2 SD) while starved fish experienced 10.1°C (± 2.7 SD), and the two values were not statistically different ($F_{1,11}$, $p = 0.41$).

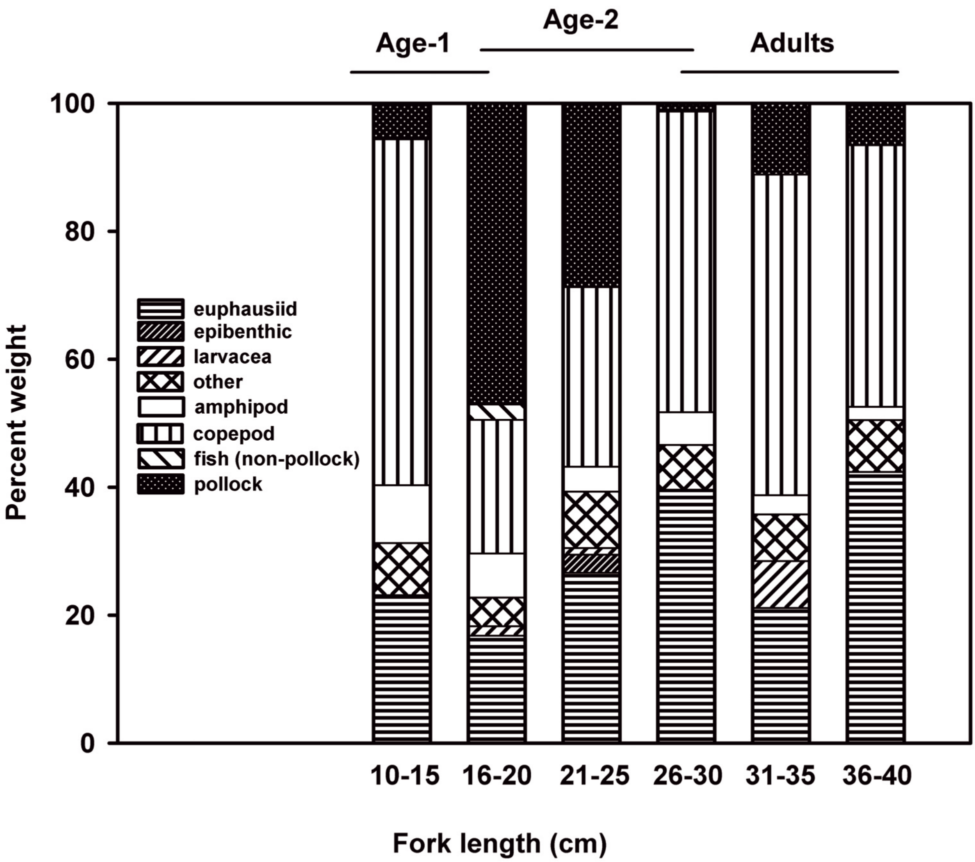

Figure 5. *Percent composition by weight of the diet of walleye pollock collected in the eastern Bering Sea in summer (1990-1997). Dominant prey categories are shown.*

Energetics Simulations. Estimates of thermal tolerance in juvenile pollock were considerably wider in younger and smaller fish (Figure 6). The bioenergetics simulation found that the 50% thermal range spanned over 7.6°C (from 3.3°C to 10.9°C) for a 0.5 g pollock, while it only spanned 2.7°C (from 2.4°C to 5.1°C) for a 500 g pollock.

Discussion

Based on our sampling, we suggest that the distributional ecology of immature walleye pollock may differ between the Eastern Bering Sea compared to the Gulf of Alaska, at least in some years. In the EBS, age-0 walleye pollock occurred throughout the water column (Tang et al. 1996), age-1 walleye pollock occurred near bottom (in 2 of 4 years examined), and age-2 and -3 individuals

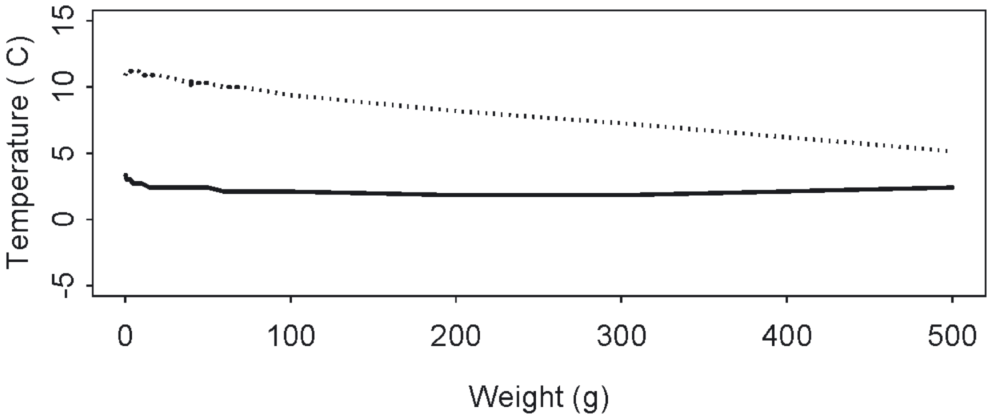

Figure 6. Thermal range of pollock as a function of weight (g). The thermal range includes temperature interval within which fish can reach 50% of its maximum daily growth rate.

schooled higher in the water column. Adults (age-4+) were demersal. In the GOA, age-0 individuals also occurred throughout the water column (Brodeur and Wilson 1996a), though cohorts of age-1 and age-2 individuals in the GOA appeared to co-occur throughout the water column. Adults in the GOA were primarily demersal.

We were able to provide several years of data for vertical distribution of immature walleye pollock in the EBS (1994, 1996, 1997, and 1999), though we were only able to make collections in the GOA in one year (2001). Our data show interannual differences in vertical distribution for the EBS, and it could be that there are interannual differences in vertical distribution of cohorts in the GOA as well. We cannot discount the possibility such occurrences also exist in the GOA, but our preliminary evidences of cohort-specific spatial differences between the two systems from this study warrant further consideration.

Results from our stomach content analyses indicate that diet differences could contribute to potential variations in the vertical distribution of age-1 and age-2 pollock between the EBS and GOA. A high degree of inter-year class cannibalism in the EBS, (Figure 5 in this study, Dwyer et al. 1987; Livingston 1991; Livingston 1993), particularly among age-1 and age-2 pollock on age-0s, may prompt differential vertical positioning in that system relative to the GOA. In the EBS, competition between the age-1 and age-2 cohorts for age-0 pollock prey could precipitate their spatial partitioning, alleviating competition between them. In contrast, the lack of piscivory (or availability of preferred prey) and a reduced degree of diet overlap between the two cohorts in the GOA permits vertical comingling. The finding of limited piscivory and cannibalism from our GOA diet analyses are similar to results from more extensive, multiyear diet analyses of walleye pollock in the GOA (Yang and Nelson 2000).

Further, our physiological analyses indicate that the temperature tolerance range of younger fish is greater than that of older fish, offering one explanation for our observations that adult fish occur almost exclusively on-bottom where temperatures are low and relatively consistent (0-2°C in the EBS, 4-6 °C in the GOA), while immature walleye pollock (age-0, age-1, age-2) schooled higher in the water column where temperatures are higher and more variable (4-7 °C in the EBS, 7-10 °C in the GOA). Our results indicate that adult pollock may not be able to endure the higher upper water column temperatures (or perhaps cannot move through the thermocline), effectively making them obligate demersals. However, since younger individuals can tolerate higher temperatures, they enjoy greater vertical flexibility, move through the thermocline (Brodeur and Wilson 1996b), and exploit a greater portion of the water column. The thermal range simulation is in part based on bioenergetics parameters derived from juvenile pollock captured in Washington, which are possibly genetically distinct from the North Pacific populations of walleye pollock (Ciannelli 2002). Thus, our results when applied to North Pacific populations are to be taken with caution, particularly because genetically distinct populations could have different thermal adaptations. However, while it is possible that at any given age, southern range populations of pollock can tolerate higher temperatures, the ontogenetic changes of thermal tolerance should remain unaltered across latitudinal gradients.

Of course, other factors are likely to affect vertical distribution as well, and while this study offers some explanations for potential differences, it does not attempt to characterize all the influences on vertical positioning. For example, there is evidence of diel variability which has been linked to ontogeny and feeding (Brodeur and Wilson 1996a, 1996b). Likewise, schooling, temperature and salinity gradients, and threat of predators all influence vertical distribution of walleye pollock (Sogard and Olla 1994). However, it should be noted that possible diel differences should have been mitigated to some extent since pollock from this study were collected day and night from both bottom and midwater trawls. Additionally, patterns of spatial separation of juvenile pollock in the EBS and our ability to detect differences between age groups was probably influenced by year-class strength. For example, in 1997, a year when age-1 and age-2 pollock were spatially separated, age-1 pollock were part of a very large year class (1996). In 1999, when no separation was detected, there were very few age-1 individuals. Spatial distribution is also likely to be influenced by environmental conditions and seasonality. Finally, we should also note that potential differences in catchability of age-1 and age-2 fish could have influenced estimates of their abundance in midwater and bottom trawls, as could differences in mesh size between the gears used.

Our laboratory studies of behavioral thermoregulation in age-2 pollock did not show differences in water column usage under starved and fed conditions. Fish used in this experiment were collected from Port Townsend, Washington, and may have been locally adapted to higher temperatures. As such, it was not altogether unexpected that they would use the majority of the water column under both conditions. Similar experiments with fish collected from the EBS and GOA are necessary to further examine putative differences between these systems.

Topographical differences between the EBS and the GOA may give rise to some of the differences in vertical distribution of immature walleye pollock in these systems. The GOA has a narrow continental shelf (65 – 175 km) which may limit the availability of suitable habitat for walleye pollock. If suitable horizontal space is limiting, immature pollock may be forced to co-occur vertically, piling the size classes on top of one another. In contrast, the EBS has a broad shelf (> 500 km), which may permit greater age class separation over horizontal space, resulting in less vertical stacking. Ultimately, these differences could have prompted diet specializations among fishes in the two areas over long time scales.

Overall in this study we have shown some differences in juvenile pollock vertical distribution between the EBS and the GOA. Such differences could be in part physiologically driven due to ontogenetic shifts in diet and metabolism, and in part ecologically driven, motivated by the partitioning of available resources (i.e., space or food), leading to a reduction of intra-specific competition. In both cases though, fish respond to environmental stimuli. Differences in spatial distribution is of particular interest in the study of energy transfer to upper trophic levels. Subadult pollock in both the EBS and the GOA are a primary prey item for a variety of demersal fishes (Livingston 1993), marine mammals (Sinclair et al. 1994) and seabirds (Hunt et al. 1996). Hence, the relative distribution of juvenile pollock throughout the water column is likely to have repercussions not only on their own survival but also on the feeding success of higher trophic level species. For example, northern fur seals breeding on the Pribilof Islands confine their feeding to mostly above the thermocline, particularly during years with a sharp temperature gradient (Robson 2001). It is speculated that fur seals follow the distributional response of prey fishes which are in turn affected by water column properties (Brodeur et al. 1999), thereby linking hydrography and fish prey distribution with energy transfer to upper trophic level species. It is likely that juvenile pollock distribution varies with changes in environmental conditions (i.e., annually). The interannual variability of juvenile pollock distribution and its relation to environmental variability in the GOA was unexplored in this study and, based on the pivotal role of subadult pollock in the local trophic webs, of considerable scientific relevance.

Acknowledgments

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA