Variation in groundfish predation on juvenile walleye pollock relative to hydrographic structure near the Pribilof Islands, Alaska

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Walleye pollock (Theragra chalcogramma) are an important forage fish in the eastern Bering Sea ecosystem. As part of an ongoing study of the processes affecting juvenile walleye pollock recruitment in the eastern Bering Sea, a concentrated effort has been focused on the hydrographic fronts near the Pribilof Islands, Alaska, as important nursery areas for these juveniles. Diel variation in the consumption of age-0 pollock by arrowtooth flounder (Atheresthes stomias) was examined from a series of collections at a station at the tidal front located north of St Paul Island, Alaska. Age-0 pollock were the primary prey of arrowtooth flounder throughout the day, but they were least digested in the late day, indicating a diurnal feeding pattern. A similar diurnal pattern was not seen in the vertical distribution of age-0 pollock, suggesting that the feeding pattern exhibited by arrowtooth flounder was based on their diel migratory behavior. Lengths of age-0 pollock consumed by arrowtooth flounder were similar to those sampled with midwater trawls. Walleye pollock cannibalism was examined along a transect that included samples collected at the front and offshore of the front. Age-0 fish were the primary prey (by weight) at all locations. Adjacent cohort cannibalism was prevalent (age-0 pollock were 79% of the diet by weight) at the frontal region. Estimates of age-0 pollock cannibalism rates were highest at the front for age-1 pollock and offshore for the adults. Prey selectivity analysis indicated that age-0 pollock were more highly selected offshore than at the front.

Introduction

Walleye pollock (Theragra chalcogramma) is the most abundant groundfish species in the eastern Bering Sea. It is also the target of a directed fishery with recent catches over 1 million tonnes, and is a common prey for marine mammals, seabirds, and groundfish (Livingston, 1993). Understanding the recruitment dynamics of such a key species is important in ecosystem management. Groundfish diet studies allow exploration of the groundfish predation component of walleye pollock natural mortality.

The four Pribilof Islands are located in the middle shelf domain of the central south-eastern Bering Sea (Fig. 1), which is characterized by a stratified two-layer water column (Coachman, 1986). However, the immediate waters surrounding the Pribilof Islands are shallow enough to allow complete tidal and wind mixing of the water column, creating a unique habitat for this region (Coyle and Cooney, 1993). The interface between the shallow, mixed water and the deeper, stratified water is marked by a hydrographic front.

Hydrographic structure is known to affect the distribution of marine fish and their prey (Taggart et al., 1989; Munk et al., 1995). Specifically, tidal fronts are known to concentrate planktonic organisms and therefore provide enhanced feeding conditions for fish and birds (Coyle and Cooney, 1993; Decker and Hunt, 1996). Age-0 walleye pollock have been found in higher abundance at frontal regions than offshore of the front.
suggested that they take advantage of the concentration of prey available there (Brodeur et al., 1997; Swartzman et al., 1999). Walleye pollock of all sizes prey upon zooplankton to some degree, but also cannibalize their own juveniles (Mito, 1974; Dwyer et al., 1987; Bailey, 1989; Livingston, 1991, 1993; Livingston and de Reynier, 1996; Livingston and Lang, 1996). Our goal was to assess the role of predation by two dominant groundfish predators, walleye pollock and arrowtooth flounder (Atheresthes stomias) on age-0 pollock in relation to the frontal structure around St Paul Island, the northernmost of the Pribilof Islands.

Methods and materials

Sampling methods

A total of 168 arrowtooth flounder stomachs were analysed from samples collected from eight bottom trawls during the period 13–15 September 1996. All hauls were made at approximately the same location within the tidal front located northeast of St Paul Island (Fig. 1). A total of 169 walleye pollock stomachs were also collected during the period 12–20 September 1995. These samples were collected from hauls made along a transect running perpendicular to the tidal front.

The sampling of plankton and juvenile pollock has been described in detail elsewhere (Brodeur et al., 1997). Briefly, depth-stratified plankton sampling was done using a 1 m² MOCNESS net with 500 µm mesh (Wiebe et al., 1976). Juvenile fish were sampled during oblique tows to within 10 m of the bottom using a 100 m² anchovy trawl containing 3 mm mesh in the codend. A subsample of 100 juvenile pollock from each tow was measured (fork length to the nearest mm; FL). Following the plankton tows and midwater-trawl hauls for age-0 pollock, short bottom-trawl hauls were made using a nylon Nor’easter trawl with 1.5 m × 2.1 m steel doors fished without roller gear. The mesh size varied from 13 cm in the forward part of the net to 8.9 cm in the codend. The net was also equipped with a 3.2 cm liner which precluded the capture of most age-0 pollock, thereby minimizing codend feeding by larger piscivorous fish. The mean effective path width of this trawl was estimated to be 13.4 m with a mean vertical opening of 9.2 m. The catch was processed aboard deck and numbers and weights of all taxa were recorded. Length measurements were made to the nearest centimeter on all potential predatory fish species, including age-1 pollock. Densities and biomass per square kilometer were then estimated for all these taxa using the area-swept method.

Diel vertical distributions of age-0 pollock and their predators were examined using hydroacoustics with validation of acoustic sign using depth-targeted tows and underwater video cameras on a remotely operated vehicle (Brodeur, 1998). A 38 kHz Simrad Ek500 split-beam echosounder provided information on backscatter and target strength of age-0 pollock in the presence of predators (Brodeur and Wilson, 1996).

MOCNESS samples were preserved in a 5% buffered formalin:seawater solution for later analysis. Samples were processed by the Polish Plankton Sorting Center (Szczecin, Poland) according to a standard protocol used for the Gulf of Alaska (Ince et al., 1997), except that the species list was altered to reflect changes in fauna between regions. Concentrations of each taxon (no. m⁻³) derived from individual nets in a tow were integrated over the maximum depth of the tow to estimate areal abundance (no. m⁻²).

Procedures described by Livingston (1991) were followed for stomach collection, processing, and analysis. Additionally, the state of digestion of each prey type was estimated and assigned a value between 2 and 6: 6 being fresh prey and 2 being a trace of the prey. All intact prey fishes were measured to the nearest millimeter FL.

Data analysis

Diel dietary variation of arrowtooth flounder was assessed by grouping samples into three time categories (0600–1400, early day; 1400–2100, late day; 2100–0600, night) after Bailey (1989). A Tukey multiple comparison test (Zar, 1984) was performed on the state of digestion of walleye pollock found in arrowtooth flounder stomachs and on the arcsine-transformed proportion of walleye pollock in the diet at each of the three time categories. Walleye pollock stomach samples were not collected during all three time categories. All age-1 fish were collected during early day, while adult fish were

Figure 1. Location of walleye pollock and arrowtooth flounder stomach sample collections north of St Paul Island. Triangles represent 1995 walleye pollock sample locations, circles 1996 arrowtooth flounder samples.
collected during night and early day tows. However, dietary variation was slight and diel variation was not considered a factor in the analyses.

Walleye pollock dietary data were pooled into five main food categories (walleye pollock, copepods, euphausiids, chaetognaths, and miscellaneous prey). A T-test was performed on the percent by weight and arcsine-transformed proportion by weight of each prey group, except miscellaneous, in the diet of age-1 and adult pollock at the frontal and offshore stations. Dietary preference comparing the numbers of prey consumed with those found in the environment was calculated using PREFER V5.1 (Johnson, 1980), a preference assessment program using the Waller and Duncan (1969) multiple comparison procedure. Prey preference is based on the difference in the rank of a given prey in the environment to its rank in the diet. One of the primary benefits of this method is that it allows flexibility in the prey included in the analysis with little effect on the overall estimate of the value of those prey that are included, therefore not requiring abundance data for all possible prey, but rather only those of interest. The analysis tests the null hypothesis that all prey are equally selected and, if rejected, it then tests the hypothesis that each prey pair is equally selected.

Estimates of age-0 pollock biomass cannibalized per day (kg/10^5 m^3) for the region were derived by multiplying the daily ration (fraction of body weight day^{-1}) by the proportion of age-0 prey in the diet (by weight) and the trawl-based predator biomass (kg/10^5 m^3) estimate for the region (Livingston, 1991).

Results

Of the 168 arrowtooth flounder stomachs collected, 113 (67%) contained food (40 early day, 26 late day, and 47 night). Walleye pollock represented between 60% and 77% of the diet by weight of arrowtooth flounder during the different times of day (Fig. 2), but paired differences were all non-significant (p=0.14), indicating no diel differences. However, walleye pollock found in stomachs were least digested in the late day (mean digestion stage=4; ≈ 50% digested) and most during the night (mean=3; ≈ 75% digested). ANOVA results indicated that the average digestion stage between the three time periods was significantly different (p<0.001). There was no significant difference between early day and night (p=0.2), but both differed significantly (p=0.004, p<0.001, respectively) from the late day time category.

Sizes of walleye pollock consumed by arrowtooth flounder were generally consistent with the size distribution of the age-0 fish caught in trawls. Two-sample Kolmogorov-Smirnov tests showed no significant difference between the sizes found in stomachs and those caught in the anchovy trawl approximately 1.25 h before the early day bottom trawl (p=0.6). A significant difference was seen for a late day haul (p<0.001). However, when the size composition of the pollock consumed was broken into two categories based on predator size (<20 cm, ≥20 cm), the large predators were consuming prey consistent with the size distribution seen in the environment (p=0.4), while the small predators were only consuming smaller prey (p<0.001).

Of the 169 walleye pollock stomachs collected, 150 (89%) contained food. The diet varied with location in relation to the front (Fig. 3). At the front, the diet of age-1 pollock was dominated by age-0 pollock. Euphausiids were important as well, whereas copepods and chaetognaths were completely absent. Both age-0 pollock and euphausiids were found in significantly (p=0.001) higher proportions of the diet at the front than offshore. Offshore of the front, age-0 pollock remained the most important prey by weight, but were closely followed by copepods as the second most important prey. The miscellaneous prey category, primarily unidentified crustaceans, was also important. Walleye pollock also dominated the diet (72% by weight) of adult

Figure 2. Percent by weight and state of digestion of walleye pollock found in arrowtooth flounder stomach samples by time of day. Error bars represent 1 s.d.

Figure 3. The diet of age-1 and adult walleye pollock by weight percentage in offshore and frontal stations.
pollock in the offshore region, while miscellaneous prey (primarily unidentified teleost remains) and chaetognaths accounted for the majority of the rest of the diet. Similarly, cannibalism was the primary feeding mode of adults in the frontal region. However, euphausiids and chaetognaths represented a significantly (p<0.001 and p=0.006, respectively) larger portion of the diet than offshore. There was no difference in the contribution of walleye pollock or copepods between the two areas (p=0.7 and p=0.5, respectively).

Based on trawl samples, the size range of available age-0 pollock in the frontal region was 30–120 mm FL, while the range cannibalized by age-1 fish was 40–62 mm FL (Fig. 4). The difference between the size distribution of prey found in stomachs and the environment was significant (Kolmogorov-Smirnov test, p=0.009). The average state of digestion of age-0 pollock cannibalized by age-1 fish was 4.1 (%50% digested).

Prey selectivity based on numbers consumed was significant (H₀: all prey selected equally) for all areas tested (Table 1). Age-1 pollock at the front selected euphausiids over all other prey, followed by chaetognaths, age-0 pollock and copepods. Offshore of the front, age-0 pollock were the most selected prey, followed by chaetognaths then euphausiids and copepods, which were selected equally. Adult pollock at the front selected chaetognaths over all other prey; euphausiids and age-0 pollock were selected equally over copepods. Offshore of the front, chaetognaths were again selected over all other prey, followed by age-0 pollock, euphausiids, and copepods.

The estimate of the rate of age-0 pollock biomass consumed by adults was higher in the offshore region than in the frontal region, whereas the estimate of the biomass consumed by age-1 fish was higher at the frontal region than offshore (Table 2). Total mortality due to cannibalism was substantially higher offshore than at the front.

Discussion

The importance of walleye pollock in the diet of arrowtooth flounder throughout all regions of the eastern Bering Sea is well documented (Shuntov, 1965; Mito, 1974; Yang and Livingston, 1986; Yang, 1991; Livingston et al., 1993). Our results are consistent with
previous reports that walleye pollock, particularly juveniles, are the primary prey. Juvenile pollock represented 60-80% of the diet by weight throughout the day. With the exception of the smallest individuals, arrowtooth flounder apparently consumed the full size range of age-0 pollock available to them based on the trawl catches at the same location. Small individuals (<20 cm FL) did not consume pollock larger than 55 mm FL despite the larger age-0 fish being available. Yang and Livingston (1986), Yang (1991), and Livingston et al. (1993) demonstrated that small arrowtooth flounder have an upper size limit of age-0 pollock that they are able to consume, while the larger fish consume large age-0 fish in addition to the small ones. Prey selectivity is likely based upon some physical limitation (i.e., gape size).

Walleye pollock found in the stomachs of arrowtooth flounder were in the freshest condition in late day (1400–2100) suggesting that most of the predation took place during this time period. These results are consistent with Bailey’s (1989) findings for walleye pollock cannibalism. Bailey associated the diurnal pattern of cannibalism with the migration pattern of juveniles following their prey toward the bottom where they become susceptible to demersal predators. His study focused on stations that were in the highly stratified offshore waters, while our diel stations were in weakly or non-stratified habitats. The frontal area was characterized by the lack of a pronounced thermocline and little vertical stratification (Brodeur et al., 1997), which may have influenced the extent of the vertical migration at this location. Age-0 pollock had the most food in their stomachs near sunset, exhibiting a diel periodicity in their feeding behaviour which was similar to the pattern of consumption of these fish by arrowtooth flounder (Brodeur et al., in press).

Age-0 pollock exhibited a diel migration pattern in the offshore region of this transect, although some individuals remained near the surface both day and night (Brodeur, 1998). Arrowtooth flounder are not generally detectable by hydroacoustics because they lack a swimbladder, making observation of their possible diel migratory behaviour difficult. It seems likely that the diurnal consumption pattern of walleye pollock exhibited by arrowtooth flounder is due to their diel feeding behaviour, rather than that of the age-0 pollock. Walleye pollock cannibalism by adults is also well documented (e.g., Bailey, 1989; Mito, 1974; Dwyer et al., 1987; Livingston, 1993; Livingston and Lang, 1996). The importance of cannibalism varies spatially and temporally, but is generally focused on the age-0 portion of the population (Dwyer et al., 1987). Age-0 pollock was the dominant dietary component of adult fish during summer, autumn, and winter in this region (Livingston et al., 1986; Dwyer et al., 1987). Our results, collected during September, are consistent with those of previous studies.

Cannibalism contributed significantly to the diet of age-1 pollock in both regions; however, it was much more prevalent at the frontal station than offshore. Livingston (1991, 1993) observed a relatively small contribution of age-0 fish to the diet of age-1 pollock, while Grover (1991) found no evidence of adjacent cohort cannibalism when examining the diet of age-1 fish collected concurrently with age-0 fish. One concern about our data is that the stomachs were collected from midwater hauls which were targeted at the heaviest age-0 pollock sign at a given station, suggesting that the prevalence of age-0 pollock in the diet may have resulted from net feeding. However, this seems unlikely owing to the relatively short tows and processing time (<1 h to catch, sample, and preserve), coupled with an average age-0 pollock state of digestion of 50%. Buckley and Livingston (1997) documented adjacent cohort cannibalism Pacific hake (Merluccius productus) an ecologically similar species. Smith (1995) proposed that such adjacent cohort cannibalism could be one of several mechanisms influencing year-class strength of Pacific hake, and this may similarly apply to walleye pollock in the eastern Bering Sea.

Prey selectivity by both adult and age-1 pollock was similar in both regions. Copepods dominated (>99.0%) prey composition numerically at all stations, but they were always the least favoured prey despite their relatively large proportion by weight in the age-1 fish diet in the offshore region. The importance (by rank) of pollock in the diet was higher in the offshore region for both groups of predators despite being much more prevalent by weight in the diet of age-1 fish at the front. The rankings used, however, are based on availability of prey by number rather than weight, and must be interpreted with caution. Without exception, the difference between the offshore and frontal prey selectivity was that age-0 pollock and euphausids reversed order in their rank: euphausids were ranked higher in the diet of both groups at the frontal station, while the reverse was true offshore. An alternative approach based on weight rather than number might be nutritionally more meaningful; however, prey availability data by weight were not available for this analysis.

Our selectivity analysis assumes that the plankton and trawl gear were able to capture the same taxonomic and size range of prey captured by walleye pollock. All sampling gear is prone to avoidance behaviour by larger organisms at the net’s mouth area and extrusion through the mesh of smaller organisms. Euphausids are particularly hard to sample (Hovekamp, 1989; Hill et al., 1996) and are assumed to be selected often by fish (Brodeur, 1998a). A further complication is that the foraging range and period of a large predator may be substantially greater than is normally sampled in a typical plankton tow or fish trawl. Finally, differential digestion rates of prey species, particularly soft-bodied prey like...
chaetognaths versus bony fishes, may further bias selectivity estimates. A much broader size range of age-0 pollock was available for age-1 cannibalism than was consumed, indicating size selectivity on the part of the predator. Livingston (1991) presented evidence of age-1 and age-2 pollock cannibalizing age-0 fish of a similar size range as reported here. The presence of an upper size limit is not surprising, as there are obvious physical restrictions to the size of prey that a predator can consume (Juanes, 1994). However, it is interesting that there was also a minimum size of age-0 pollock consumed, perhaps indicating that the smaller fish were unavailable to the predator. There are no known physical limitations on the consumption of small fish, since the walleye pollock are clearly able to locate and capture other small prey, such as copepods and euphausids. Therefore, their absence in the diet is likely due to spatial differences in distributions.

Livingston (1991, 1993) estimated that cannibalism in the area north of the Pribilof Islands during the primary feeding season (May–September) ranged from 0.042 t to 0.266 t during 1985–1989. Direct comparison with our estimates is difficult because of the differing spatial and temporal scales of the studies. Our estimates are based on a relatively small volume representing a daily rate of consumption, whereas Livingston’s estimates were based on area and extrapolated for an entire stratum (approximately 1/6th of the eastern Bering Sea shelf) in addition to representing an estimate of removal for a season. An extrapolation of our estimates would require multiplying the rate by the number of days in the season and by the volume of water in the region of interest.

The estimates of consumption rates are the product of daily ration, proportion by weight in the diet, and predator biomass. Differences in any of the three parameters between the two regions will affect the estimates. For our calculations, daily ration was assumed to be constant for each of the two size groups of walleye pollock predators, leaving only predator biomass and the dietary component to account for variation seen in the estimated rates of removal. The much higher rate of age-0 pollock removal by age-1 pollock at the front compared to the offshore region is due to an order of magnitude larger predator biomass at the front and nearly double the percentage by weight of walleye pollock in the diet. Adults cannibalizing juveniles at a much higher rate offshore than at the front is a result of higher adult biomass offshore than at the front.

The results suggest that larger age-0 pollock may be able to escape predation by some gape-limited predators (e.g., age-1 pollock). This is consistent with most laboratory and field studies of predation (Sogard, 1997) and emphasizes the importance of optimal feeding and growth conditions in enhancing survival in juvenile walleye pollock in the eastern Bering Sea.

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References


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