

Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska

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Synopsis

Juvenile walleye pollock, *Theragra chalcogramma*, is the dominant forage fish on the continental shelf of the Gulf of Alaska, yet little is known about the feeding habits of this important interval of pollock life history. The taxonomic composition and size of prey found in the stomachs of age-0 juveniles collected at three nearshore locations in the Gulf of Alaska in September 1990 were compared to the composition and size of zooplankton collected in concurrent plankton tows. The maximum length of prey consumed increased dramatically over the length range of pollock examined (58–110 mm) from approximately 7 mm to 30 mm, due mainly to the consumption of large euphausiids and chaetognaths by the bigger individuals. The maximum width of prey changed little over this size range although there was a general increase in prey width with increasing predator size. The minimum prey length and width did not change with increasing fish size. Juvenile pollock generally selected the larger prey sizes relative to what was available. Juvenile pollock showed a marked preference for adult euphausiids and decapod larvae and an avoidance of copepods and chaetognaths relative to the numbers collected in net tows. These results are discussed relative to the feeding ecology of these juvenile fishes.

Introduction

Much research has been conducted on the early life intervals of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska (Kendall et al. 1996). The rationale behind this research is that recruitment levels are probably set during the first year of life. Although the egg, embryo, and larva intervals are generally acknowledged to be critical periods in the life of most fishes, the juvenile period of pollock has received increased attention because of the potential for regulation to occur beyond the larva period in this population during some years (Bailey & Spring 1992, Bailey et al. 1996). During the juvenile period, predation is likely to be the major source of mortality, although the relative magnitude of pre-

dation may be influenced by interannual variations in food supply and growth rates. Clearly, in light of the extensive gauntlet of predation to which juvenile pollock are exposed to in the Gulf of Alaska (Brodeur & Wilson 1996a, Brodeur & Bailey 1996), it is extremely advantageous for juvenile pollock to efficiently exploit available food resources and grow as rapidly as possible to escape size-selective predators (Sogard 1997).

Although the food habits of juvenile pollock from this area (Merati & Brodeur 1996, Brodeur & Wilson 1996a) and other regions of the North Pacific Ocean (Kamba 1977, Lee 1985, Nakatani & Maeda 1987, Grover 1991) are known, there has been little effort to establish factors related to feeding selectivity. Lee (1985) analyzed ontogenetic changes

in the diet of age-0 pollock in the Bering Sea and related these to selectivity based on morphological criteria (i.e., changes in gill raker size and spacing). This is the first study to compare the size and taxonomic composition of prey of age-0 pollock with that available in their environment to examine whether these fish consume a particular subset of available prey.

Materials and methods

Fish collections

Juvenile pollock were collected 6-23 September 1990, as part of a survey for their abundance and distribution in the western Gulf of Alaska (Wilson et al. 1996). The collections used in this study were a subset of a larger study examining general food habits and dietary variability in age-0 pollock which found, based on diel variation in stomach fullness and prey condition, that pollock at approximately 6 months of age were feeding mainly at night in near surface waters (Merati & Brodeur 1996). To effectively compare the diets of these juveniles and available prey, I limited my analysis to three nighttime trawl stations (two hauls at each station). Other criteria used in selecting these three stations were that high densities of age-0 pollock occurred in each area as indicated by net tow catches and concurrent acoustic backscatter measurements (Brodeur & Wilson 1996b) and each had a plankton tow collected within 1 km and 1 h of the trawling.

Juvenile pollock were taken from midwater at three nearshore locations (depth range: 62-126 m) south of Kodiak Island, in Wide Bay and near Mitrofanina Island (Figure 1). The collecting gear was a 18.6 m high-opening shrimp trawl containing a 5 mm mesh liner (Wilson et al. 1996). Tows were made to within 10 m of the bottom at each station in a stepped-oblique fashion at an average ship speed of 5.9 km h^{-1} .

Juvenile pollock were quickly sorted from the catch and then counted and measured to the nearest millimeter (fork length). A random subsample of 20 fish from each haul was individually labelled and placed in a buffered 10% formalin-seawater mix-

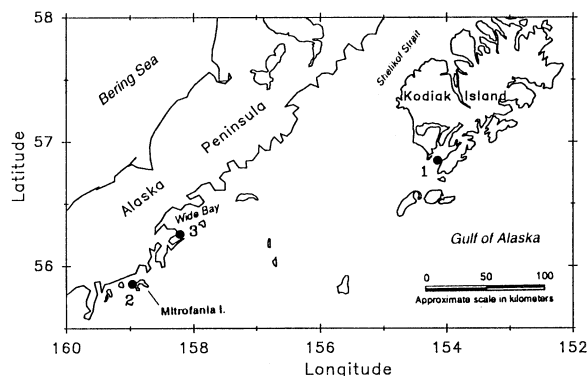


Figure 1. Three sampling locations where comparisons between juvenile pollock diets and zooplankton abundance were made in the western Gulf of Alaska.

ture. In the laboratory, the samples were transferred to 50% ethanol for later analysis.

Stomach analysis

In the laboratory, a random subsample of 40 fish from each station (20 per tow) was selected for diet analyses. Fish were again measured, weighed, and the stomach (from the esophagus to pylorus) was excised. The stomach contents were then blotted on absorbent paper to remove excess moisture and weighed to the nearest 0.1 mg.

The stomach contents were teased apart under a dissecting microscope and their relative condition was subjectively rated on a scale of 0 to 4 ranging from totally digested to fresh prey. Contents were identified to the lowest possible taxonomic level (genus or species). Each taxon was enumerated and individually weighed for every stomach examined. In addition, the total length and maximum width of each intact prey identified were measured using an optical scanning system (Optimas, Biosonics Inc.) and stored directly in a computer database.

Zooplankton collections and analysis

To determine which zooplankton prey were available for these juveniles, one tow with a 60 cm bongo plankton net (0.333 mm mesh) was made at each station. Oblique tows were made down to 10 m

above bottom at a ship speed of 5 km h⁻¹. All large macrozooplankton (e.g. medusae) and debris were removed from the catch at sea and the remaining sample was preserved in a 10% formalin-seawater mixture.

In the laboratory, the zooplankton samples were sorted for organisms greater than 2 mm in maximum dimension as a previous analysis had indicat-

ed that this is the approximate lower size limit of food particles eaten by juvenile pollock of the size range (49-113 mm) examined (Merati & Brodeur 1996). The sample was first sorted in its entirety for ichthyoplankton. Each sample was then split with a Folsom Plankton Splitter until subsamples containing approximately 100-200 organisms of the most abundant zooplankton taxa were obtained. All or-

Table 1. Percent composition by abundance and biomass of prey found in the stomachs of age-0 walleye pollock at the three stations (-- indicates that taxa not found). The percentages for each station represent a total of 40 non-empty juvenile pollock stomachs.

Taxon	Station 1		Station 2		Station 3	
	Number (%)	Weight (%)	Number (%)	Weight (%)	Number (%)	Weight (%)
Ostracoda						
<i>Conchoecia</i> spp.	1.5	0.2	--	--	--	--
Pteropoda						
<i>Clione limacina</i>	--	--	0.2	0.1	--	--
Copepoda						
<i>Neocalanus cristatus</i>	--	--	--	--	1.7	0.7
<i>Calanus marshallae</i>	--	--	17.7	1.4	8.6	7.0
<i>Calanus pacificus</i>	0.8	0.1	3.1	0.1	1.7	0.3
<i>Eucalanus bungii</i>	--	--	0.9	0.1	--	--
<i>Metridia pacifica/lucens</i>	--	--	6.2	0.6	12.1	4.2
<i>Metridia</i> spp.	--	--	6.0	0.6	--	--
Euphausiacea						
<i>Thysanoessa inermis</i>	18.3	27.6	12.4	30.7	5.2	10.2
<i>Thysanoessa spinifera</i>	7.6	16.7	1.8	3.1	--	--
<i>Thysanoessa longipes</i>	--	--	8.1	22.1	--	--
<i>Thysanoessa raschii</i>	0.8	1.0	0.2	0.7	5.2	16.9
<i>Euphausia pacifica</i>	0.8	1.5	--	--	--	--
Unidentified furcillae	46.8	46.2	40.8	38.2	11.4	8.3
Amphipoda						
<i>Themisto pacifica</i>	1.3	0.1	--	--	6.9	1.1
<i>Primno macropa</i>	0.4	0.1	--	--	--	--
Gammaridea unidentified	0.2	0.1	--	--	--	--
Mysidacea						
<i>Meterythrops robusta</i>	0.8	0.3	--	--	3.4	18.2
<i>Acanthomysis nephrothalma</i>	--	--	--	--	1.7	6.7
Decapoda						
<i>Cancer</i> sp. megalopae	8.4	4.7	1.1	0.7	21.4	7.2
<i>Chionoecetes</i> sp. zoeae	1.5	0.4	--	--	3.4	0.3
Natantia zoeae	2.3	0.3	--	--	--	--
Hippolytidae zoeae	3.1	0.1	--	--	--	--
Paguridae megalopae	--	--	0.2	0.1	1.7	1.7
Larvacea						
<i>Oikopleura dioica</i>	3.1	0.5	--	--	5.2	0.6
Chaetognatha						
<i>Sagitta elegans</i>	--	--	--	--	6.9	1.9
Osteichthyes						
<i>Ammodytes hexapterus</i>	--	--	0.2	0.3	--	--
<i>Mallotus villosus</i>	2.3	0.2	0.7	0.7	1.7	9.1
Unidentified fish larvae	--	--	0.4	0.5	1.7	5.7

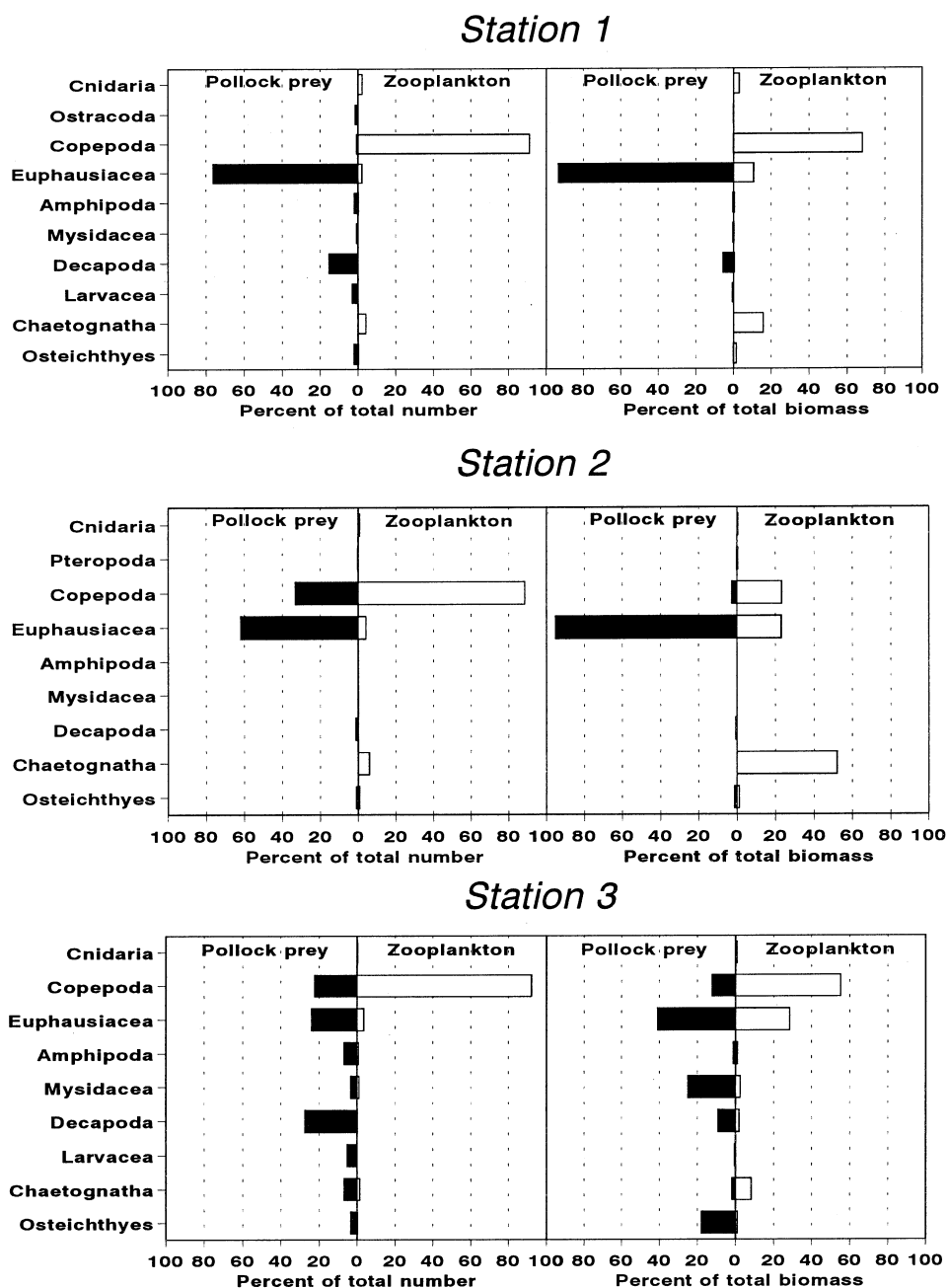


Figure 2. Comparison of percent composition by number and weight of the diet and zooplankton collected at each station.

ganisms were identified to species whenever possible and, in the case of copepods and euphausiids, life history interval was also determined. The maximum dimensions (length and width) were measured for all individuals or for a subsample of abundant taxa using methods described earlier for the stomach contents. These samples were then placed

in 50% ethanol and wet weights of each taxon were determined to the nearest 0.1 mg. Since a similar preservation treatment was applied to both the stomach contents and zooplankton samples, no corrections were applied either to account for shrinkage or weight loss due to preservation.

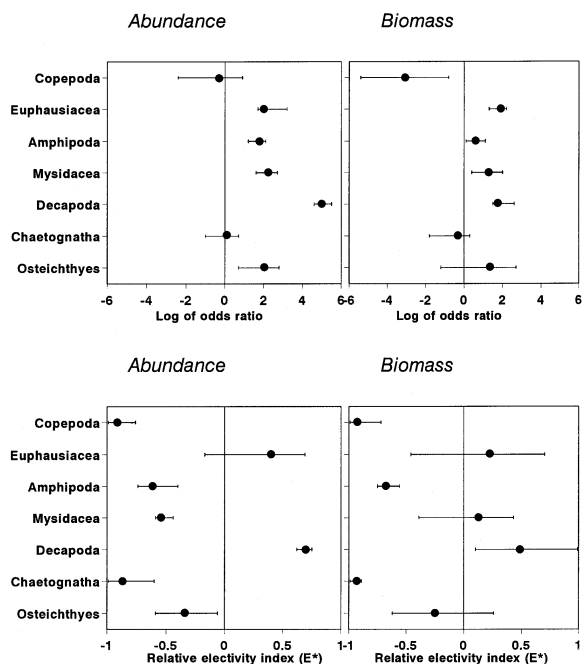


Figure 3. Electivity using the 'log of the odds ratio' (top) and 'relative electivity index' (bottom) for major prey categories. Shown are the overall mean values (filled circle) and ranges for each prey taxa that had at least 3 available comparisons.

Data analysis

Prey selection was determined for both prey type and size. Since electivity indices are strongly influenced by rare species (Lechowicz 1982), all prey that occurred in less than 0.1% of the dietary or environmental samples were excluded from my analyses. Since many prey were digested to the point that species identification was impossible, selectivity comparisons were made mostly for higher taxonomic levels. For size selection, prey lengths or widths were grouped into five equivalent size classes for comparison with the same classes caught in the plankton tows.

Prey selection was determined using two indices with substantially different properties. First, an index of preference based on the 'log of the odds ratio' (LOR) was computed which is symmetric around zero and varies from $+\infty$ to $-\infty$ (Gabriel 1978):

$$\text{LOR} = \ln (d_i (100 - d_j)) / (e_i (100 - e_j)), \quad (1)$$

where d_i and e_i are the percentages of taxon i in the diet and environment, respectively.

Second, the 'relative electivity index' (E^*) of Vanderploeg & Scavia (1979) was used, which is based on the selectivity coefficient of Chesson (1978) and the number of available prey. Although this index is nonlinear and asymmetrical, it is stable through changes in relative abundance of food types and was preferred by Lechowicz (1982) as the most suitable electivity index of the several indices that he examined. This index is computed as:

$$E^* = (W_i - (1/n)) / (W_i + (1/n)), \quad (2)$$

where

$$W_i = (d_i / e_i) / \sum_{j=1}^n (d_j / e_j), \quad (3)$$

and n is the number of prey items. If this index is positive, the food item is designated as preferred. If the value of E^* is negative, the item is not preferred or avoided. A value of zero implies neutral selection.

Regression analysis was used to determine the relationship between maximum length or width of prey and predator length. Since the variance of these metrics increased with increasing predator size, the regressions were fit to a logarithmic transformation of prey sizes as suggested by Pearre (1986). In addition to all prey combined, separate regressions were fitted to euphausiids, copepods, and decapods to determine specifically how the sizes of these prey taxa were related to predator length.

Results

Comparison of taxonomic composition

The stomach contents from all three stations were found to be in fresh condition (mean condition index of 3.87, 3.85 and 2.75 out of a possible 4.00 at Stations 1, 2, and 3, respectively), indicating that most fish had recently fed. Although 10 major taxonomic categories were observed in stomach samples, the diet tended to be dominated by adult euphausiids in both numerical or biomass composition (Table 1). Euphausiids were the dominant component of the diet at Stations 1 and 2, but their

taxonomic composition varied among the three stations with *Thysanoessa inermis* found most frequently and consistently in the diet. Unidentified euphausiid furcilia were commonly found at all three stations. Copepods, which were predominantly late-stage (C5 and C6) *Calanus marshallae*

and *Metridia* spp., and decapod larvae were also numerically important in the diet at two stations (Table 1). The plankton collections showed a preponderance of copepods (C4 – C6) at all stations (Table 2). However, by wet weight, chaetognaths (*Sagitta elegans*) and euphausiids were also very important

Table 2. Densities and biomass (per 10 cubic meters) of meso- and macrozooplankton collected in bongo tows at each station (-- indicates that taxa not found at that station).

Taxon	Station 1		Station 2		Station 3	
	Density (no.)	Biomass (g)	Density (no.)	Biomass (g)	Density (no.)	Biomass (g)
Cnidaria						
<i>Aglantha digitale</i>	131.9	0.56	30.4	0.03	6.3	0.04
Pteropoda						
<i>Clione limacina</i>	--	--	4.3	0.02	3.2	0.07
Copepoda						
<i>Neocalanus cristatus</i>	47.1	0.26	--	--	3.2	0.03
<i>Neocalanus plumchrus/flemingeri</i>	502.4	0.67	17.4	0.07	--	--
<i>Calanus marshallae</i>	1218.2	4.37	903.4	0.61	2241.1	2.29
<i>Calanus pacificus</i>	488.4	1.06	--	--	--	--
<i>Eucalanus bungii</i>	25.1	0.35	34.7	0.08	22.2	0.04
<i>Metridia pacifica/lucens</i>	1737.9	0.88	2351.7	0.91	2109.8	0.57
<i>Metridia</i> spp.	832.7	4.50	191.1	0.07	--	--
<i>Euchaeta elongata</i>	560.4	0.62	8.7	0.07	--	--
Euphausiacea						
<i>Thysanoessa inermis</i>	94.2	0.85	82.5	0.63	44.4	0.34
<i>Thysanoessa spinifera</i>	18.8	0.77	--	--	6.3	0.29
<i>Thysanoessa longipes</i>	--	--	78.8	1.16	--	--
<i>Thysanoessa raschii</i>	--	--	--	--	66.6	0.81
<i>Euphausia pacifica</i>	12.6	0.39	--	--	--	--
Unidentified furciliae	--	--	--	--	50.7	0.07
Amphipoda						
<i>Themisto pacifica</i>	9.4	0.07	--	--	--	--
<i>Primno macropa</i>	6.3	0.01	--	--	--	--
<i>Monoculodes</i> spp.	--	--	--	--	6.4	0.01
Gammaridea unidentified	--	--	--	--	31.7	0.04
Mysidacea						
<i>Meterythrope robusta</i>	3.1	0.03	--	--	3.2	0.04
<i>Acanthomysis nephrophthalma</i>	--	--	--	--	44.8	0.09
Decapoda						
<i>Crangon alaskensis</i>	--	--	--	--	3.2	0.04
<i>Crangon communis</i>	--	--	--	--	6.3	0.06
<i>Spirontocaris</i> spp.	3.1	0.07	--	--	--	--
Chaetognatha						
<i>Sagitta elegans</i>	244.8	2.94	230.2	4.05	66.6	0.44
Osteichthyes						
<i>Mallotus villosus</i>	3.5	0.09	23.9	0.07	6.5	0.04
<i>Radulinus asprellus</i>	0.4	0.05	--	--	--	--
<i>Parophrys vetulus</i>	0.8	0.14	--	--	--	--
<i>Pleuronectes quadrituberculatus</i>	--	--	--	--	0.3	0.01
<i>Hippoglossoides elassodon</i>	--	--	0.5	0.02	--	--
Sum	5941.1	18.67	3957.6	7.79	4722.8	5.32

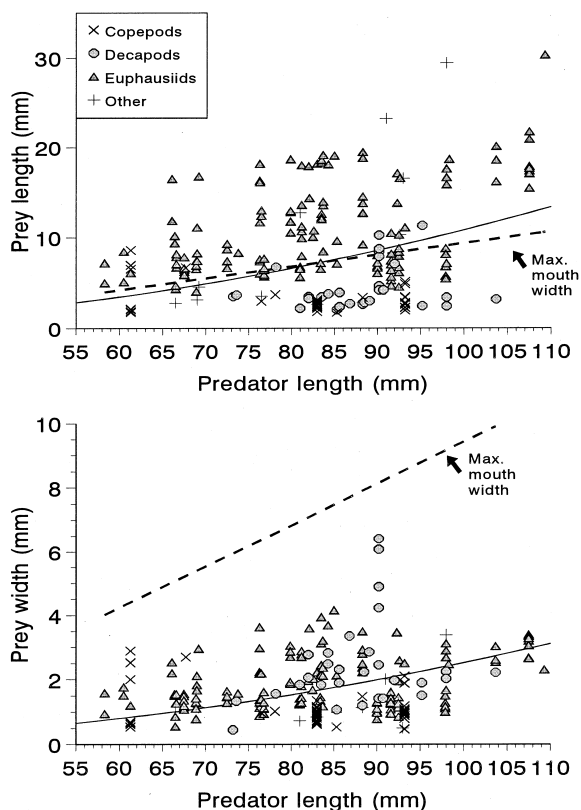


Figure 4. Relationship of prey length (top) and prey width (bottom) to predator length for copepods, decapods, euphausiids, and other prey taxa. The solid line represents the best-fit logarithmic relationship between the two variables, and the dashed line represents the maximum gape size predicted for various predator lengths (Sogard & Olla 1994).

(Figure 2). Cnidarians were found exclusively in the plankton, whereas larvaceans (*Oikopleura dioca*) occurred only in the diet, but in relatively low percentages.

Among the major taxa, copepods exhibited the highest negative selection, especially in terms of biomass, and chaetognaths exhibited slightly negative or neutral selection compared to their abundance or biomass availability based on the log of the odds ratio (Figure 3). All other taxa showed positive selection, with decapod larvae, euphausiids, and fish larvae exhibiting the highest positive electivities. Preferences calculated using E^* provided more variable results compared with the LOR index in that a wider range of electivities was observed for most taxa. Only decapod larvae and euphausiids had positive electivities in terms of abundance,

in contrast to the LOR index by which almost all taxa were positive. Similar results were seen for the biomass comparisons, but in this situation, mysids and fishes also show some positive electivities.

Comparison of size composition

The prey consumed by age-0 pollock ranged from 2 to 31 mm in length and 0.6 to 6.4 mm in width (Figure 4). Euphausiids and chaetognaths were the longest prey consumed overall whereas decapod larvae (mainly *Cancer megalopae*) were the widest prey consumed. Mean and maximum prey length increased with increasing predator size. However, the smallest prey lengths consumed, which were mostly copepods and decapod larvae, changed little over the size range of pollock examined. The regression relating the natural log of prey length to predator length was highly significant ($F_{1,215} = 12.08$, $p = 0.0006$), but much of the significance in this relationship was due to consumption of euphausiids ($F_{1,142} = 18.51$, $p < 0.0001$). Neither copepod nor decapod lengths showed a significant relationship with predator length. Approximately one-half of the prey eaten were greater in length than the estimated maximum mouth width of pollock of that size (Figure 4, calculated from mouth width = $0.129 \times$ total length - 3.50 (Sogard & Olla 1994)). Similarly, the regression of the natural log of prey width to predator length was also significant ($F_{1,215} = 18.05$, $p < 0.0001$) over the size range examined, but euphausiids did not contribute as much to the overall prey width increase ($F_{1,142} = 6.78$, $p = 0.01$) as they did to the length increase. Most prey widths were substantially narrower than the maximum gape size, and the majority were less than half the maximum gape size.

The size distributions of prey consumed were variable among the three stations, but the length distributions found in the plankton were similar (Figure 5). Because of apparent multimodality in the length distributions, the prey and zooplankton distributions were compared using both parametric t-tests on log-transformed data and nonparametric Kolmogorov-Smirnov tests. Both methods yielded similar results in that the prey at Stations 1 and 2

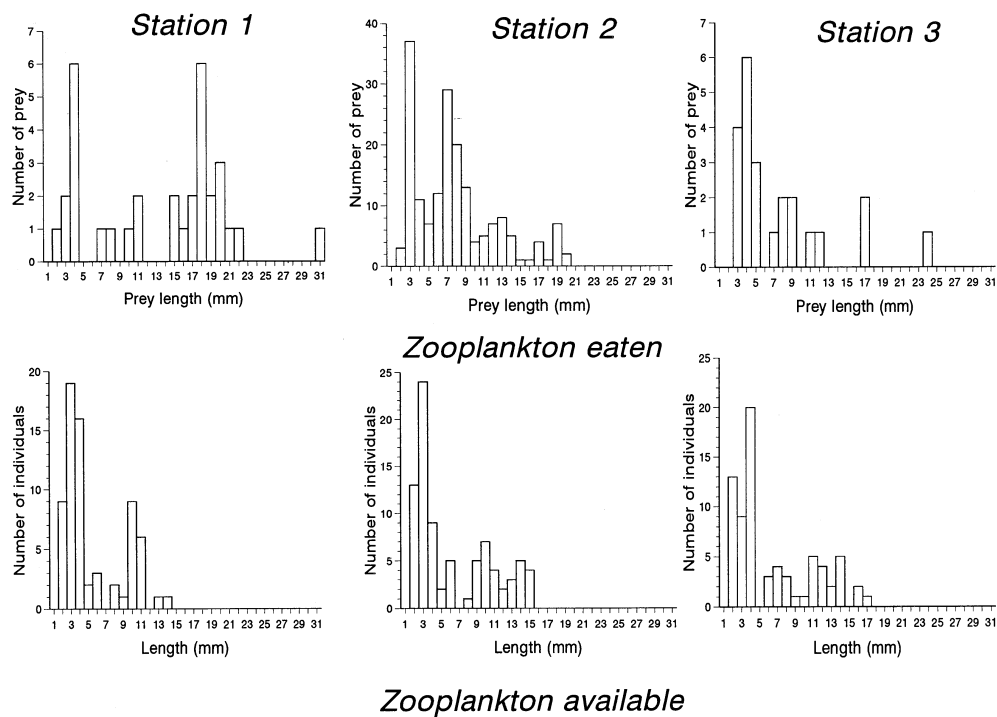


Figure 5. Comparison of prey lengths found in the stomachs of age-0 pollock (top) to those collected in plankton nets (bottom) at each station.

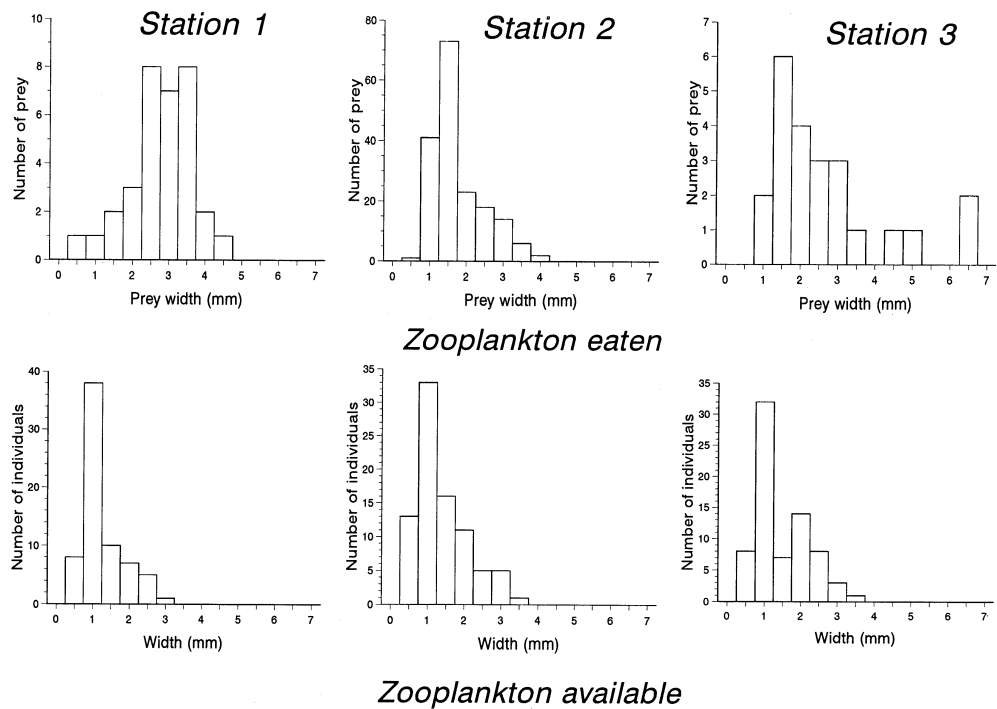


Figure 6. Comparison of prey widths found in the stomachs of age-0 pollock (top) to those collected in plankton nets (bottom) at each station.

were significantly greater in length than those caught in the plankton net, but there was no significant difference ($p > 0.05$) in the distributions for Station 3. For prey width, all three comparisons showed a significantly larger prey spectrum consumed than that caught in the plankton hauls (Figure 6).

Electivities for the different length and width classes show that age-0 pollock preferentially select the larger prey sizes available (Table 3). The LOR shows a strong preference for the two largest size classes and an avoidance of the smallest class, especially in terms of prey width. A more gradual transition from avoidance of small prey to preference for large prey is seen with E^* .

Discussion

Possible sources of error

There are a number of factors other than predator selectivity that may cause the taxonomic and size composition of prey in the diet of any predator to differ substantially from that sampled in the environment (Luo et al. 1996). First and probably foremost, both predators and prey are not homogeneously distributed in both the horizontal and vertical dimensions. Since a plankton net integrates over much smaller time or space scales than a predator, it is likely to sample a much more restricted population than a typical fish may encounter foraging over several hours (O'Brien & Vinyard 1974, Giske & Salvanes 1995). Both the trawls and plankton tows sampled roughly the same part of the water column (surface to within 10 m of the bottom), but acoustic data (Brodeur & Wilson 1996b) and depth-discrete plankton sampling (Napp et al. 1996) suggest that both age-0 pollock and their major planktonic prey are in surface waters at night. If the pollock were feeding mainly at night (Merati & Brodeur 1996) and were feeding shortly before capture, as suggested by the relative freshness of the food in many of the stomachs, then the distribution bias may be minimal.

Another factor to consider is that all prey may not be equally vulnerable to capture by the plank-

ton gear that we used (Giske & Salvanes 1995). Euphausiids, in particular, are strong swimmers with a well-developed escape response and may not be as adequately sampled in the bongo nets as copepods or other smaller plankton (Napp et al. 1996). If this is the case, an apparent positive electivity in the diet may actually be a negative selectivity on the part of the sampling gear. Since the plankton tows were all at night when light-aided avoidance is minimal and when euphausiids and other vertical migrants are well off the bottom, this bias is likely to be less than during daytime collections. Although it is difficult to get unbiased abundance estimates of euphausiids, it is likely that magnitude of the changes in LOR and E^* would be affected but the sign would not.

It is probable that digestion time is size-dependent, therefore, smaller prey may be evacuated from the gut or digested beyond identification faster than larger prey (Pearre 1986). This would also lead to an apparent selection for larger prey over smaller prey. In the present study, many small copepods and larvae of euphausiids in the diets were not identifiable to species and selectivity comparisons at this taxonomic level have less certainty. It was possible to classify all prey to major taxonomic categories and selectivity estimates made at this level are probably more reliable, although faster evacuation of smaller prey remains a problem.

Finally, significant sources of error in diets of trawl-caught predators are net-feeding and regurgitation of stomach contents due to pressure changes when they are brought to the surface. Neither of these are likely to be important in this study. Net feeding is unlikely since the mesh size was large relative to the size of most prey and not even the largest prey (euphausiids, chaetognaths, and decapods) eaten by age-0 pollock were retained in the codend. Moreover, we found no evidence of regurgitation in the stomachs examined here or elsewhere (Merati & Brodeur 1996) so it is probably not a major source of error if it occurs at all.

Diets and prey selection

A more comprehensive study of juvenile pollock feeding, of which these samples are a subset,

showed that the diet of juvenile pollock can be quite spatially and temporally variable (Merati & Brodeur 1996). This study found a gradual ontogenetic shift from feeding mainly on small prey such as copepods by smaller pollock (< 70 mm) to mainly euphausiids for larger age-0 fish (> 90 mm). Fish of intermediate size consumed mainly larvaceans, but these were consumed mainly in the regions to the west of the present study area (Merati & Brodeur 1996). In the present study, larvaceans were not an important component of the diet nor did they make up an appreciable part of the zooplankton composition.

Euphausiids, the major constituent of the prey biomass consumed by pollock at all stations I examined, were consumed more consistently than the other prey types and appear to be a preferred prey when available. Copepods were readily available at all stations but exhibited mostly negative electivities, which is similar to the results reported for juvenile Atlantic cod, *Gadus morhua* (Sameoto et al. 1994). Many factors contribute to the detection and capture of prey by planktivorous fishes besides relative abundance (Lazzaro 1987, Kaiser & Hughes

1993). Among these are the shape, contrast, swimming behavior, and micro-scale distribution (patchiness or aggregation patterns) of prey and the sensory modalities and capture mechanisms of the predator.

Although the exact prey detection and capture methods used by pollock are poorly known, it is likely that they detect their prey using vision. Pollock larvae are able to feed under very low light conditions but cease feeding in total darkness (Paul 1983). Euphausiids have darkly pigmented eyes that may provide sufficient visual contrast to be detected by juvenile pollock compared with lightly pigmented copepods or transparent chaetognaths. It has also been shown in the laboratory that pollock feed more successfully in groups than alone (Baird et al. 1991), which may be an adaptation for feeding upon ephemeral and patchy food sources such as euphausiids. Both field (Brodeur & Wilson 1996b) and laboratory (Sogard & Olla 1996) data suggest that larger age-0 pollock are found closer to the surface and form less cohesive groups at night, when they are apparently feeding on prey that also migrate on a diel basis such as euphausiids (Merati & Brodeur 1996).

An advantage to specializing on euphausiids is that they occur over a broad range of sizes compared with many of the other prey taxa (copepods, decapod larvae, larvaceans) consumed by pollock. Thus, juvenile pollock can take progressively larger prey as they grow, thereby maximizing their energy intake without having to pursue and capture an equivalent biomass of smaller prey, assuming that the handling times and digestion rates of the prey are equivalent. A similar response may be seen in juvenile piscivorous fishes, such as Pacific salmon *Oncorhynchus* spp. (Brodeur 1991) and bluefish *Pomatomus saltatrix* (Juanes et al. 1993), which both utilize an expanding size range of fish prey as they grow. Since age-0 pollock are morphologically capable of feeding on fish, including members of their own cohort (Sogard & Olla 1994, R. Brodeur personal observation), at a relatively small size, it is uncertain why they do not adopt a more piscivorous feeding mode during their first year. It may be that fish are more difficult for juvenile pollock to capture than copepods or small euphausiids. It is also

Table 3. Frequencies of prey sizes and LOR and E* calculations of electivity by 5 mm length classes and 1 mm width classes where d_i and e_i are the percentage composition of that size class in the diet and the environment, respectively.

Prey length				
Size class (mm)	d_i %	e_i %	LOR	E*
1-5	34.19	57.27	- 0.08	- 0.60
6-10	36.75	20.00	0.37	- 0.13
11-15	13.68	19.09	- 0.27	- 0.54
16-20	13.25	3.18	1.32	0.27
>20	2.14	0.45	1.53	0.32
Prey width				
Size class (mm)	d_i %	e_i %	LOR	E*
0-1.0	2.27	58.15	- 2.39	- 0.98
1.1-2.0	58.64	28.63	0.17	- 0.30
2.1-3.0	28.18	11.89	0.66	- 0.23
3.1-4.0	9.09	0.88	2.25	0.46
>4.1	1.82	0.44	1.40	0.04

possible that the densities of suitably-sized fishes are too low or of limited temporal availability to sustain such a large population of juvenile pollock. Since most fish species are spring spawners in this region and subsequently settle out to a demersal existence by late summer, ichthyoplankton densities generally decline to low levels during the fall (Kendall & Dunn 1985, Brodeur et al. 1995, Doyle et al. 1995). In contrast, euphausiids are found in high abundance at this time of the year (Inzce et al. 1997).

In addition to the faster swimming speeds and increased gape size that occur through the ontogenetic development of this species, it is likely that both visual acuity and reaction distance to prey also increase markedly (Breck & Gitter 1983, Wahl et al. 1993, Walton et al. 1994). It is interesting to note that despite the ability to capture prey of increasing length throughout their ontogeny, juvenile pollock continue to feed on relatively small prey at all sizes examined here and this may be the result of a shortage of larger prey items. Similar results were seen by Kamba (1977) for walleye pollock from a bay in Japan and by Juanes (1994) for piscivorous fishes in general. It appears in general that the maximum width and not maximum length of prey limits the overall prey spectrum of planktonic predators (Pearre 1986, Hambright 1991, Ghan & Sprules 1993). Whether consuming larger prey is advantageous to the predator from the standpoint of energetics is dependent on the balance between increased energy derived from larger prey and the additional pursuit and handling time required to obtain the prey. Although the range of prey sizes available to juvenile pollock increases as they grow, the assumption that the available food resources also increases cannot be substantiated since the available biomass of food as a proportion of predator biomass does not increase (Munk 1992). Although the characteristics of prey size and type selection can be better examined under controlled laboratory conditions, field studies such as this one provide useful background information on the actual prey spectrum consumed relative to what is available.

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