

Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*

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ABSTRACT: Pelagic forage fishes are an important component in the transfer of trophic energy in marine ecosystems. Capelin *Mallotus villosus* and age-0 walleye pollock *Theragra chalcogramma* are pelagic forage fishes whose alternate fluctuations in abundance have been associated with system-wide biotic reorganization of the Gulf of Alaska (GOA) ecosystem. To better understand differences between these fishes, we compared their feeding ecology using samples of similar-sized (39 to 126 mm) individuals collected together in midwater trawl hauls during September 2000 to 2001 in the western GOA. Zooplankton samples were used to characterize prey availability. The comparative analysis focused on diet, feeding chronology, daily ration, and prey selectivity. The diet of both species mostly consisted of small copepods, large copepods, adult and juvenile euphausiids, thecosome pteropods, and larvaceans; consequently, the overall diet overlap was high. The diet overlap of fish from some samples, however, was low. Capelin fed mostly during crepuscular periods while pollock mostly fed at night. The daily ration estimate for capelin was low (1.8% body weight [BW]) relative to pollock (5.2% BW). Chesson's index of selectivity indicated preferential selection of euphausiids (adult and juvenile) by capelin and age-0 pollock. At euphausiid-poor locations, capelin stomachs were mostly empty while pollock stomachs contained alternate prey. Selectivity of amphipods, large copepods, larvaceans, and reptantians was higher for age-0 pollock than for capelin. Consumption of euphausiids increased with their abundance in the plankton, and consumption:biomass ratios indicate that localized depletion could occur. We hypothesize that capelin increase foraging mobility while age-0 pollock switch to alternate prey as a competitive response to limited euphausiid availability.

KEY WORDS: Capelin · Age-0 walleye pollock · Diet overlap · Prey selectivity

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INTRODUCTION

Predator-prey interactions can reveal mechanisms that are important in structuring animal communities. In marine ecosystems, small fishes are an important intermediate trophic link due to their abundance and availability as prey (Cury et al. 2000, Hunt et al. 2002). Although taxonomically diverse, these fishes are collectively referred to as 'forage fishes' (Springer & Speckman 1997). In the pelagic realm, most forage fishes are planktivorous and vary in energy density (Iverson et al. 2002, Eder & Lewis 2005). Consequently,

the collective nutritional value of pelagic forage fishes (hereafter referred to as forage fishes) changes with species composition. Anderson & Piatt (1999) demonstrated that in the Gulf of Alaska (GOA) climate-related change in forage fish community composition during the 1980's was related to large-scale biotic restructuring. Notable in this restructuring was a decline in capelin abundance and a subsequent increase in walleye pollock abundance. Spatial differences in forage fish community composition have since been demonstrated (Abookire & Piatt 2005). Due to heterogeneity in the prey field (Folt & Burns 1999),

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feeding ecology is relevant to fish spatial distribution. Accordingly, in this study, we compare the feeding ecology of 2 pelagic forage-fish species for evidence that might subsequently be related to differences in spatial distribution.

Capelin *Mallotus villosus*, Osmeridae and juvenile walleye pollock *Theragra chalcogramma*, Gadidae, often dominate forage fish communities in the North Pacific and Bering Sea. Both are noted as key ecological links in the transfer of energy to larger fishes, birds, and marine mammals (Hatch & Sanger 1992, Yang & Nelson 2000, Zeppelin & Sinclair 2002). Payne et al. (1999) found that capelin were 33% greater in energy density (kcal g^{-1}) than juvenile walleye pollock, although this varies with capelin reproductive state (Anthony et al. 2000). Too little is known about the feeding ecology of these fishes to judge whether the difference in energy density can be explained by diet.

Capelin are small, short-lived (max. age 5 yr), streamlined schooling fishes common in coastal pelagic habitats (Gjøsæter 1998, Brown 2002, Mecklenburg et al. 2002). They spawn during the spring and summer mostly as age-2 and age-3 individuals (ca. ≥ 10 cm fork length [FL]) (Pahlke 1985). In contrast, walleye pollock are relatively large, long-lived (max. age 22 yr) gadids that congregate semi-pelagically in deep parts of the continental shelf and slope (Mecklenburg et al. 2002, Dorn et al. 2004). They spawn in early spring mostly as age-4 and older individuals (ca. ≥ 40 cm FL, Dorn et al. 2004). Many pollock spend their first year in coastal pelagic nurseries (Brodeur & Wilson 1996). By autumn, in the GOA, they are comparable in size to the capelin (ca. 10 cm) with which they commonly co-occur. Later, as yearlings, walleye pollock are relatively large, occur in deep water, and their interaction with capelin is characterized more as a potential predator than a potential competitor (Yang et al. 2005). Thus, the temporal and geographic overlap between capelin and walleye pollock during autumn in the GOA represents a near ideal field setting in which to compare their feeding ecology because similar-sized individuals can be collected at the same location (i.e. syntopically), which minimizes fish size and prey-field effects.

In general, capelin and walleye pollock exploit similar prey resources. Calanoid copepods and euphausiids are the major prey (Vesin et al. 1981, Naumenko 1984, Brodeur & Wilson 1996, Sturdevant 1999, O'Driscoll et al. 2001, Orlova et al. 2002), but larvaceans, amphipods, and other prey are important in relatively euphausiid-poor areas (Gjøsæter 1998, Wilson et al. 2005). Evidently, there is some potential for these fishes to compete for prey. Furthermore, evidence is accumulating that their grazing can substantially depress standing stocks of prey (Vesin et al. 1981,

Gjøsæter 1998, Duffy-Anderson et al. 2002, Ciannelli et al. 2004). Competition might be expected to intensify during autumn due to further reduction in prey availability resulting from a seasonal decline in zooplankton (Coyle & Pinchuk 2003). Thus, the field study we undertook was designed to rigorously compare the feeding ecology of 2 central and potentially competing pelagic forage fishes in the GOA by minimizing effects of fish size and prey-field in order to resolve possible species-specific and competition effects.

MATERIALS AND METHODS

Field collections. The study area was situated immediately downstream of Shelikof Strait (Fig. 1), which is where the largest aggregation of GOA pollock spawn in early spring (Dorn et al. 2004). Historically, age-0 pollock and capelin are abundant in this area (Wilson et al. 1996, Wilson 2000). Samples were collected during 2 research cruises of the NOAA Ship 'Miller Freeman' during September 2000 and 2001. Samples used in this study were selected from a larger collection based on the co-occurrence of capelin and age-0 pol-

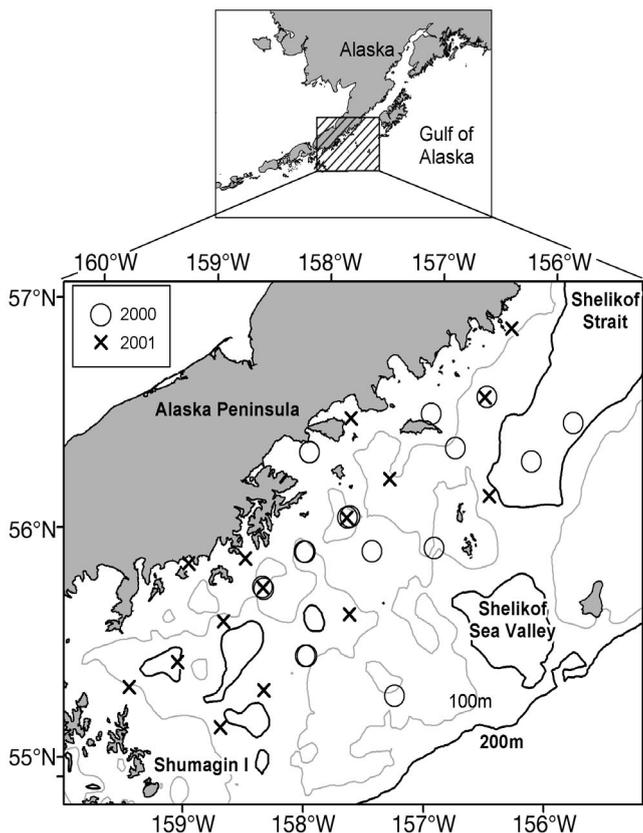


Fig. 1. Station locations where 698 capelin and age-0 pollock were collected during September 2000 to 2001 in the western Gulf of Alaska

lock in midwater trawl catches, which included day (09:00 h to 20:00 h Alaska Daylight Time [ADT]), night (before 07:00 h or after 22:00 h ADT), and twilight collections. Sunrise and sunset occurred at ca. 08:00 h and 21:00 h ADT.

Fish were collected in 37 trawl hauls (see Table 1). Each sample was collected using a midwater trawl fished with 1.5 × 2.1 m steel V-doors (566 kg each) and equipped with a 3 mm codend liner. The trawl was fished obliquely through the water column at a ship speed of 2.5 to 3.0 knots and a wire retrieval rate of 10 m min⁻¹. Fish were frozen (-80°C then transferred to -20°C) within an hour of landing. Relative to preservation in 10% formalin, freezing did not affect prey count (paired-*t*, *n* = 5, *p* = 0.656) or prey weight (paired-*t*, *n* = 5, *p* = 0.518). All capelin were post-larval (>60 mm standard [SL]) individuals, and all walleye pollock were age-0 juveniles (<113 mm SL), which were distinctly smaller than older individuals (>119 mm SL) (Brodeur & Wilson 1996).

Plankton samples were collected at 34 of the fish sampling locations to obtain information on the background prey field and enable calculation of prey selectivity (Table 1). Each plankton sample was collected with a 1 m² Tucker trawl (0.333 mm mesh nets) fished obliquely from 200 m to the surface. Towing speed was adjusted to maintain a 45° wire angle at a wire retrieval rate of 20 m min⁻¹. A SBE 19 SeaCat CTD profiler (Sea-Bird), attached in-line between the wire terminus and trawl, was used for real-time monitoring and recording of net depth, water temperature, and salinity. The first net was used to sample that portion of the path below the thermocline or 40 m depth. The second net was used to sample the shallower portion of the path. All nets were mechanically tripped to open and close. The plankton sample was preserved in a sodium borate-buffered solution of 5% formalin. Numerical composition of plankton samples was determined in Szczecin, Poland, by the Plankton Sorting and Identification Center following Alaska Fisheries Science Center protocol. This protocol mandates a much finer resolution of copepod and euphausiid species and life stages than is practically available from the stomach content data. Therefore, estimates of copepod abundance in the plankton were combined into 2 categories: Copepoda <2 mm prosome length (PL), and Copepoda ≥2 mm PL, which conformed to the prey-size categories (see 'Laboratory examinations' subsection, below) used to group the diet data. Similarly, euphausiid taxa were combined into 2 categories: Euphausiid adult and juvenile (a + j), and euphausiid furcilia and calyptopis (f+c), which are larval forms.

Laboratory examinations. Up to 10 individuals of each species were selected by size from the preserved samples so that the different sizes in each sample were

reasonably well represented. Overall, 698 fish were selected from 37 samples. Fish were thawed in seawater. Standard length (SL) and whole wet body weight of each thawed fish was used to estimate species-specific length-weight relationships. Each fish was measured to the nearest 1 mm SL, blotted dry, and weighed to the nearest 1 mg. Lengths and weights were converted to fresh-fish equivalents (Buchheister & Wilson 2005) assuming that the effect of freezing on capelin SL was equivalent to its effect on FL. Least-squares linear regression models were fitted to the ln-transformed fresh-fish data.

Diet was determined by analyzing fish stomach contents. Stomachs were excised between the esophagus and pylorus and stored individually in a sodium borate-buffered 10% formalin solution. None of the stomachs were flaccid so regurgitation was not believed to be a problem.

Stomach contents were dissected from the preserved samples, blotted dry and weighed to the nearest 0.01 mg. This weight was used to calculate stomach content weight as percent body weight (% BW = stomach content weight / (preserved whole wet body weight - stomach content weight) × 100). The contents were then teased apart and sorted into broad taxonomic categories following Brodeur et al. (2000). Each taxonomic category was comprised of subcategories (prey-quality categories) to indicate digestion and fragment size: 1 = <50% intact and well-digested, 2 = >50% intact but well-digested, 3 = largely intact but digested, 4 = intact and fresh. Most prey showed signs of digestion (i.e. prey-quality categories 1 to 3) so net feeding was probably negligible. Taxonomic composition was quantified by prey count, prey weight, and frequency of occurrence. Weight was measured to the nearest 0.01 mg.

Diet analysis. To ensure that conclusions regarding comparative feeding ecology were independent of the coarse taxonomic categorization of stomach contents, finer taxonomic composition and individual weight of prey was examined using subsets of the diet data. Subsamples of mostly intact (prey-quality categories 3 and 4) copepods (<2 mm and ≥2 mm PL) and euphausiids (adults and juveniles) were identified to the lowest possible taxonomic level (Szabo & Gardner 1982, Kathman et al. 1986) and compared between predator species. Individual weight was calculated for prey groups represented by prey items of quality category 3 and 4. Individual prey weight was first calculated for each fish (prey weight divided by prey number) and then averaged by sample and predator. Pairwise *t*-tests were used to detect differences in mean individual prey weight between predators. Prey groups represented in fewer than 5 samples were excluded from the comparisons.

Diet overlap between capelin and age-0 walleye pollock was quantified using Horn's index of resource overlap (Horn 1966). This index was chosen because it (1) performs well in comparison to other overlap indices (Cailliet & Barry 1979), (2) has low bias due to variation in sample size and resource categories (Smith & Zaret 1982), and (3) was previously used to study age-0 pollock diet in the northeast Pacific (Sturdevant et al. 2001). Horn's index, R_0 , was calculated as

$$R_0 = \frac{\sum_{i=1}^m (p_{1i} + p_{2i}) \ln(p_{1i} + p_{2i}) - \sum_{i=1}^m p_{1i} \ln(p_{1i}) - \sum_{i=1}^m p_{2i} \ln(p_{2i})}{2 \ln(2)} \quad (1)$$

where p_{1i} and p_{2i} are the percentages of the i^{th} group of m prey taxa in the stomach contents of predator 1 and 2, respectively. The value of R_0 ranges from -1 (no overlap) to 1 (perfect overlap). Following Sturdevant et al. (2001), diets were considered similar for $R_0 > 0.6$. Overlap was first calculated using prey weight and then using prey count. In either case, the Miscellaneous (rare items of uncertain identification) and Unidentified (unidentifiable digested material) prey categories were excluded. Diet overlap between capelin and age-0 pollock was calculated by year, and then for each of the 37 samples.

Nonlinear regression and Spearman's rank correlation were used to examine diel collection time and mean fish size effects on among-sample variability in diet overlap. A nonlinear least-squares procedure was used to evaluate the model,

$$R_0 = a + b_1 \{\sin[2\pi/24(t - b_2)]\} \quad (2)$$

for evidence of a significant association between diet overlap (R_0) and collection time (t , decimal h) using SAS for Windows (release 8.02). The model was fitted using the Newton method of iteration and an assumed, fixed, periodicity ($2\pi/24$), based on apparent pattern, to reduce the number of parameters to be estimated: a (vertical shift), b_1 (amplitude), and b_2 (time shift). Spearman's rank correlation was used to determine the significance of the relationship between diet overlap and mean length of each predator species, and the difference in mean predator length. Finally, correlation analysis was used to elucidate what dietary components were most responsible for the variation in diet overlap among samples.

The implications of different predator feeding chronologies were explored using daily trajectories of stomach content weight to estimate feeding parameters (periodicity and rates of ingestion, egestion, and ration) (Sainsbury 1986). Stomach fullness, as indicated by median % BW, was input to MAXIMS models

as implemented using SAS following Richter et al. (1999) to provide parameter and parameter variance estimates. The model assumes constant ingestion during the feeding period, and an exponential rate of evacuation:

$$dS/dt = J - ES \quad (3)$$

where S is stomach content weight (% BW), J is the rate of ingestion (% BW h^{-1}), and E is the instantaneous rate of evacuation (h^{-1}). The model can be applied to feeding chronologies that include 1 or 2 feeding periods per 24 h. Brodeur et al. (2000) applied the same model to age-0 walleye pollock in the Bering Sea, but our parameter estimates for capelin in the Pacific are new. Following Brodeur et al. (2000), the % BW data were grouped into 3 h time bins as a somewhat arbitrary compromise between maximizing both the number of samples in each time bin and the number of time bins. Sample sizes were not sufficient to construct separate time series for each year; therefore, the resulting feeding chronologies integrate potential interannual effects.

Prey selectivity. Prey selectivity was quantified using Chesson's index of selectivity, α_i (Chesson 1978). This index is useful for among-sample comparisons because it incorporates the relative abundance of each prey type, but is unaffected by total prey abundance (Lechowicz 1982). Chesson's index was calculated as

$$\alpha_i = \frac{d_i/e_i}{\sum_{i=1}^m (d_i/e_i)} \quad (4)$$

where d_i and e_i are the percent abundance of prey taxa group i in fish stomachs and in plankton samples, respectively, and m is the number of prey types (e.g. taxonomic groups). The value of α_i ranges from 0 to 1 with a critical value of $1/m$, values $< 1/m$ indicate negative selectivity (i.e. avoidance) and values $> 1/m$ indicate positive selection (i.e. preference). Plankton catches were expressed as individuals m^{-2} , which was calculated using the volume filtered and the depth range fished with each net, followed by the summing of the standardized catches from both nets. Volume filtered was measured using a calibrated flow meter (General Oceanics) suspended in the center of each net mouth. Prey selectivities for capelin and age-0 walleye pollock were calculated for all samples pooled by year, and for each of the 34 samples. Prey groups not represented in the plankton samples were omitted. Statistical comparisons were made using Wilcoxon paired- t tests for each prey group. Bonferroni corrections were applied to maintain a $p = 0.05$ significance level.

RESULTS

There was considerable overlap in the size of fish examined in this study but on average the capelin were 10 mm longer than the age-0 walleye pollock (Table 1). The length (L) - weight (W) relationships reflect the relatively streamlined morphology of capelin [$W = (2.138 \times 10^{-7})L^{3.769}$, $R^2 = 0.97$, $n = 330$] as compared to age-0 walleye pollock [$W = (3.686 \times 10^{-6})L^{3.195}$, $R^2 = 0.97$, $n = 368$]. The average water temperature (50 m depth) at the sampled locations was 8.3°C and 9.8°C in 2000 and 2001, respectively.

Diet analysis

Horn's index of dietary overlap was high in 2000 ($R_0 \geq 0.95$) and in 2001 ($R_0 \geq 0.89$) indicating very similar

composition in the diets of capelin and age-0 walleye pollock. The 5 most frequently encountered, identifiable prey groups were similar for both predator species: copepods <2 mm PL, copepods ≥ 2 mm PL, euphausiid adults and juveniles, thecosome pteropods, and larvaceans (Table 2). Despite the high overlap index, many prey groups were more prevalent among age-0 walleye pollock than among capelin. Cumaceans, mysids, and larval crabs (Reptantia, mostly megalopae) occurred exclusively among age-0 walleye pollock, and the proportional abundance of larvaceans was especially high in pollock stomachs collected during 2001. Of the fishes consumed (Osteichthys), some were identified as larval capelin and the remains of most others appeared smelt-like.

No differences were apparent between pollock and capelin with regard to copepod and euphausiid species consumed. The most common copepods were

Table 1. Midwater and Tucker trawl samples of (N_f) fish and (N_p) plankton, respectively, used to compare the feeding ecology of age-0 walleye pollock *Mallotus villosus* and capelin *Theragra chalcogramma* in the western Gulf of Alaska during September 2000 and 2001. No. of fish comprising midwater trawl samples, averages of maximum trawl depth, temperature (°C) and salinity (psu) at 50 m water depth, and standard length (SL) are included

Year	N_f	Midwater trawl hauls (fish samples)									Tucker trawl hauls N_p
		Max. depth per haul (m)	50 m depth °C	psu	Age-0 pollock			Capelin			
					No. fish	SL (mm) Mean	SL (mm) Range	No. fish	SL (mm) Mean	SL (mm) Range	
2000	19	20–237	8.3	31.8	194	72	39–100	155	83	63–118	16
2001	18	66–183	9.8	31.5	174	74	52–100	175	85	66–126	18

Table 2. *Mallotus villosus* and *Theragra chalcogramma*. Taxonomic composition of stomach contents of age-0 walleye pollock and capelin by percent frequency of occurrence (FO), percent of total prey number (No.), and percent of total prey weight (Wt). 'All groups combined': number of non-empty stomachs and total number and total weight (g) of all prey items in the respective 'FO', 'No.', and 'Wt' columns (see Table 1 for sample sizes and number of fish). PL: prosome length; (a + j): adult + juvenile; (f + c): furcilia + calyptopis; na: not applicable

Taxonomic group	September 2000						September 2001					
	Age-0 pollock			Capelin			Age-0 pollock			Capelin		
	FO	No.	Wt	FO	No.	Wt	FO	No.	Wt	FO	No.	Wt
Amphipoda	7	0.31	0.64	1	0.02	0.03	18	0.71	0.99	3	0.19	0.09
Chaetognatha	7	0.44	2.04	4	0.22	0.25	11	0.35	0.80	2	0.08	0.02
Cirripedia	3	0.11	0.00	0	0.00	0.00	1	0.02	0.00	1	0.05	0.00
Copepoda, <2 mm PL	63	78.31	6.93	44	71.74	4.83	51	25.52	1.52	20	48.50	2.26
Copepoda, ≥ 2 mm PL	26	4.97	3.22	17	2.13	1.55	45	9.27	3.99	14	10.82	2.60
Cumacea	1	0.02	0.01	0	0.00	0.00	1	0.01	0.00	0	0.00	0.00
Euphausiid (a + j)	42	4.38	61.80	35	4.92	66.32	69	6.95	78.08	49	15.61	89.90
Euphausiid (f + c)	7	0.64	3.02	6	7.99	10.94	10	0.34	0.14	2	0.29	0.03
Osteichthys	3	0.13	13.85	3	0.36	10.13	2	0.06	5.96	0	0.00	0.00
Larvacea	14	1.88	0.24	7	1.36	0.08	47	44.01	2.59	9	12.62	0.37
Mysidacea	0	0.00	0.00	0	0.00	0.00	1	0.01	0.03	0	0.00	0.00
Reptantia	15	0.78	2.19	0	0.00	0.00	5	0.20	0.67	0	0.00	0.00
Thecosomata	16	7.48	0.48	21	10.37	0.56	25	12.23	2.20	18	11.33	1.15
Miscellaneous	4	0.17	0.06	6	0.75	0.00	1	0.01	0.11	0	0.00	0.00
Unidentified/digested	44	na	5.52	51	na	5.31	58	na	2.91	47	na	3.56
All groups combined	186	6377	7.92	138	4129	3.76	174	8342	7.85	138	3779	6.57

Calanus marshallae and *Metridia* spp., and the most common euphausiid species was *Thysanoessa inermis* (Table 3). The other prey groups consumed were too digested to enable identification within a practical amount of examination time.

Mean individual weight of prey items did not differ between predator species (Table 4). Data were sufficient to test 4 prey groups. Mean weight ranged from 0.083 mg ind.⁻¹ for thecosome pteropods to 29.789 mg ind.⁻¹ for adult and juvenile euphausiids. Given the similarity in specific composition of the major prey items and the mean weights of prey items, it is unlikely that our subsequent use of coarser prey taxonomy greatly affected our conclusions regarding diet comparability.

Table 3. *Mallotus villosus* and *Theragra chalcogramma*. Specific taxonomic composition of adult and juvenile euphausiids, and copepods of all sizes (<2 mm and ≥2 mm prosome length) that were found in the stomachs of capelin and age-0 walleye pollock collected in the western Gulf of Alaska, September 2000 to 2001. (a + j): adult + juvenile

Prey	Proportion % (by number)	
	Age-0 walleye pollock	Capelin
Euphausiids (a + j)		
<i>Euphausia pacifica</i>	0.9	0.3
<i>Thysanoessa inermis</i>	31.3	24.1
<i>Thysanoessa raschii</i>	0.6	1.6
<i>Thysanoessa spinifera</i>	17.7	9.3
<i>Thysanoessa</i> spp.	49.6	64.6
No. ind. identified	368	330
Copepods, all sizes		
<i>Acartia longiremis</i>	0.6	0.0
<i>Calanus marshallae</i>	38.9	33.5
<i>Calanus</i> spp.	0.6	2.2
<i>Centropages abdominalis</i>	15.3	14.7
<i>Epilabidocera longipedata</i>	2.5	0.0
<i>Eucalanus</i> spp.	3.2	8.5
<i>Metridia okhotensis</i>	0.0	1.8
<i>Metridia</i> spp.	32.5	32.1
<i>Pseudocalanus</i> spp.	6.4	7.1
No. ind. identified	157	224

Table 4. *Mallotus villosus* and *Theragra chalcogramma*. Paired-*t* test results of difference in mean individual weight of intact prey in the stomachs of capelin and age-0 walleye pollock collected in *n* pairs of trawl samples. PL: prosome length; (a + j): adult + juvenile

Prey	No. pairs	Mean ind. prey wt (mg)		Mean difference	<i>t</i>	<i>p</i>
		Capelin	Pollock			
Copepods, <2 mm PL	12	0.129	0.152	0.023	1.008	0.335
Copepods, ≥2 mm PL	9	0.551	1.289	0.738	1.455	0.184
Euphausiids (a + j)	13	21.312	29.789	8.477	0.912	0.380
Thecosomata	6	0.138	0.083	-0.055	-0.639	0.551

Capelin and age-0 walleye pollock generally exhibited similar size-related diet composition patterns (Fig. 2). The numerical importance of small copepods decreased with fish length while the gravimetric importance of euphausiids increased. The abundance of larvaceans increased with predator size among the age-0 walleye pollock despite indications from larvacean remains recovered from the stomachs that these were relatively small prey items. Closer examination of the data indicates that this unexpected trend largely reflects spatial coincidence during 2001 of high larvacean abundance and large-size age-0 pollock in the northeastern part of the study area.

Diel variability in diet composition at 3 h intervals was also generally similar between predators (Fig. 3). In terms of count, euphausiids were relatively abundant in fish collected after midnight and before noon; this was especially evident among capelin. The percentage of stomach content weight due to small prey items (larvaceans, small copepods, and thecosome pteropods) was highest in samples collected near sunset. These general patterns in diet composition were useful in guiding our more rigorous comparison of capelin and age-0 walleye pollock feeding, which utilized fish samples paired by trawl haul to minimize interannual and geographic variation in the prey field.

The analysis of sample-to-sample variation in Horn's index indicated that diet overlap varied from 0 to 0.99. Only 8 samples had low weight-based overlap. This was associated with low weights of euphausiids (adult and juvenile) in stomach contents ($p < 0.001$), but it was not associated with collection time ($F = 0.03$, $p = 0.975$) or predator length (Spearman correlation, $p > 0.05$). Consequently, weight-based overlap was dropped from further analysis. Diet overlap based on numerical composition was associated with collection time ($F = 5.40$, $p = 0.009$). It increased throughout the day, peaked just after sunset, and decreased at night with all low (<0.6) values occurring between midnight and 17:00 h ADT (Fig. 4). Within this time frame, overlap was not correlated with predator length ($p > 0.25$).

It was, however, associated with low abundance of small-size prey items (copepods, larvaceans, and thecosome pteropods) in capelin stomachs (Spearman's $\rho \geq 0.41$, $p < 0.043$) and a high frequency of empty capelin stomachs (Spearman's $\rho = -0.55$, $p = 0.006$). Thus, diel variation in overlap was associated with capelin stomach fullness suggesting differences in feeding chronology.

Diel trajectories of stomach fullness suggest that capelin feeding intensified during twilight in contrast to a more

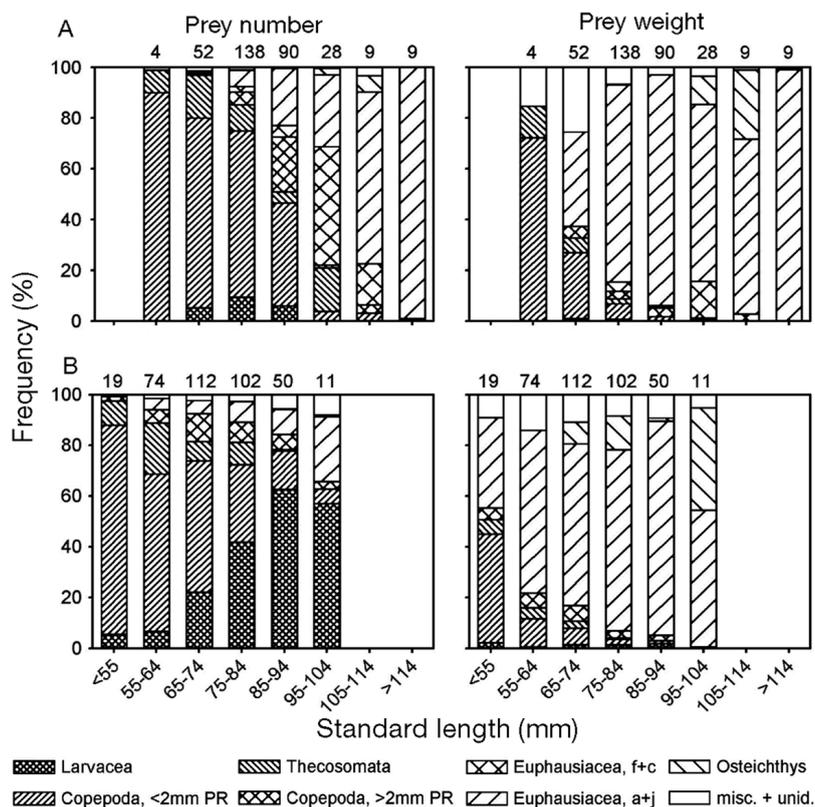


Fig. 2. *Mallotus villosus* and *Theragra chalcogramma*. Diet composition by predator length for (A) capelin and (B) age-0 walleye pollock collected during September 2000 and 2001 in the western Gulf of Alaska. Numbers above vertical bars: number of fish stomachs examined

nighttime-based pattern of feeding by age-0 pollock, although variation in stomach fullness was considerable (Fig. 5). Overall, median stomach fullness for capelin was 0.21 % BW ($n = 330$) and median absolute weight of stomach contents was 6.27 mg. Capelin stomach fullness peaked during the 3 h period after sunrise (09:00 to 12:00 h, 0.46 % BW) and again after sunset (21:00 to 24:00 h, 0.43 % BW). The effect of collection time was highly significant (Kruskal-Wallis test statistic = 20.87, $p = 0.004$); however, after applying a Bonferroni correction for multiple comparisons, the only significant pairwise difference was between the time periods 15:00 to 18:00 h and 21:00 to 24:00 h (Mann-Whitney $U = 720$, $p < 0.001$). For age-0 pollock, overall median stomach fullness was 0.69 % BW ($n = 368$) and median absolute weight of stomach contents was 19.80 mg. Median values increased after sunset and remained at about 1.0 % BW throughout the night. Fullness decreased during the day to a low of 0.21 % BW just prior to sunset. Similar to capelin, collection time was highly associated with stomach fullness (Kruskal-Wallis test statistic = 20.67, $p = 0.004$); however, no pairwise comparisons were significant after applying a Bonferroni correction. Based on these pat-

terns, the MAXIMS model was fit to the capelin stomach fullness data assuming 2 feeding periods, and to the pollock stomach fullness data assuming one feeding period in a 24 h period.

Feeding parameter estimates fit to diel trajectories of median % BW were bounded by large SEs (Table 5). For capelin, the 95 % CI of the ingestion (± 0.614) and evacuation (± 1.465) parameters and the estimate of daily ration (± 8.020) included zero. Furthermore, the model did not account for a significant amount of the variation in median stomach fullness ($F = 8.57$, $p = 0.108$). Thus, the capelin feeding parameters must be considered a first approximation. The model fit to the age-0 walleye pollock data was significant ($F = 41.99$, $p = 0.002$) but again the CI for ingestion (± 0.336) and evacuation (± 0.404) parameters and the estimate of daily ration (± 6.525) included zero.

Prey selectivity

Overall, 6 of the 16 prey groups were preferentially selected by capelin and age-0 walleye pollock (Table 6). Adult and juvenile euphausiids were preferentially selected by both predator species consistently during each year. Associated selectivities (α_i) for this prey group ranged from 0.208 to 0.619, well above the critical value ($1/m = 0.063$, see 'Materials and methods'). Mean ($\pm 95\%$ CI) abundance of adult and juvenile euphausiids in the plankton was estimated to be 135 ± 92 ind. m^{-2} during 2000 and 647 ± 655 ind. m^{-2} in 2001. Other prey groups (larvaceans, Osteichthys, large copepods, euphausiid calyptopis and furcillae, and thecosome pteropods) were also subject to positive selectivity, but the trends were not as strong or consistent as for large euphausiids. The remaining taxonomic groups were proportionally underrepresented in stomachs relative to the plankton samples, except for Cumacea, which are epibenthic and not identified in the plankton samples.

Preferential selection for adult and juvenile euphausiids was further supported by evidence of capelin and pollock switching from other prey to euphausiids as the abundance of euphausiid increased in the water column. Using the 18 samples collected at night, to account for a possible diurnal decrease in euphausiid net catch efficiency, we observed an increase in the mean number of euphausiids in capelin (ANCOVA, $F = 25.89$,

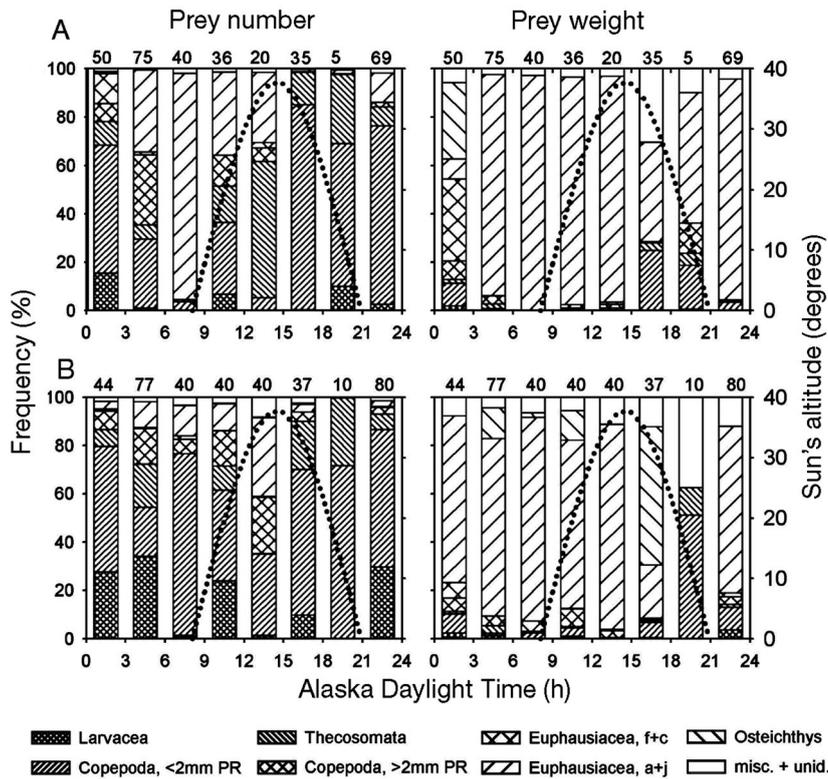


Fig. 3. *Mallotus villosus* and *Theragra chalcogramma*. Diet composition by 3 h time bins (Alaska Daylight Time) for (A) capelin and (B) age-0 walleye pollock collected during September 2000 and 2001 in the western Gulf of Alaska. Numbers above vertical bars: number of fish stomachs examined. Dotted line: hourly predictions of sun altitude at 158° 24' W, 56° 18' N during 11 September (<http://aa.usno.navy.mil/>)

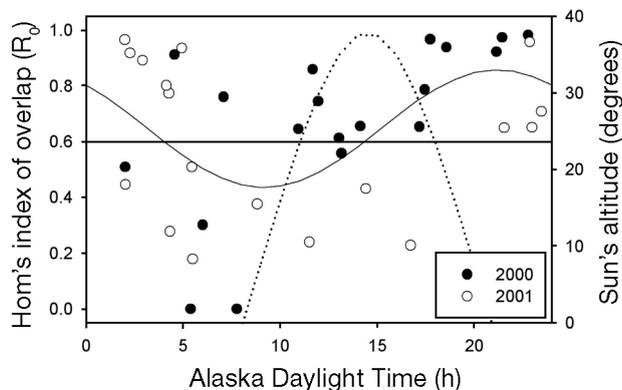


Fig. 4. *Mallotus villosus* and *Theragra chalcogramma*. Horn's index of overlap in diet between capelin and age-0 walleye pollock versus Alaska Daylight Time (ADT). Diet composition was based on prey counts. Horizontal line ($R_0 = 0.6$) delineates low and high overlap values. Curved line: curvilinear relationship between diet overlap and ADT ($R_0 = 0.646 - 0.211[\sin[0.262 \times (t + 3.177)]]$); $n = 37$). Dotted line: hourly predictions of sun altitude (see Fig. 3 for coordinates and data source)

$p < 0.001$) and pollock (ANCOVA, $F = 31.48$, $p < 0.001$) stomachs as the abundance of euphausiids in the plankton increased among sample sites (Fig. 6). A corresponding decline in the mean number of other prey items consumed (capelin, $F = 4.53$, $p = 0.039$; pollock, $F = 13.92$, $p < 0.001$) suggests that predators switched to euphausiids in euphausiid-rich areas. This pattern could not be explained by predator size, which was included as a categorical (10 mm size bins) effect in the ANCOVA, or by a scarcity of alternate prey in euphausiid-rich areas (i.e. the abundance of euphausiid and non-euphausiid planktoners were not inversely related: $F = 0.33$, $p = 0.573$, $n = 18$). The importance of euphausiids as the principal prey acquired by these predators is further underscored by the increase in predator stomach fullness with euphausiid plankton abundance (Fig. 6), which indicates that euphausiids comprise the bulk of the diets of these fishes. In fact, euphausiids may be especially important to capelin as evidenced by few mean gut content weights $>0.5\%$ BW at sites where euphausiid abundance was <256 euphausiids m^{-2} . In contrast, the pollock at these sites readily consumed alternate prey.

Prey selectivities differed between capelin and age-0 walleye pollock for 4 prey groups. Pairwise differences in prey selectivity were significantly different from 0 for Amphipoda (Wilcoxon, $n = 27$, $p < 0.001$), Copepoda ≥ 2 mm PL ($n = 34$, $p = 0.004$), Larvacea ($n = 24$, $p = 0.001$), and Reptantia ($n = 28$, $p < 0.001$). Selectivity for each of these groups was relatively high for age-0 walleye pollock.

DISCUSSION

Many comparative diet studies have repeatedly demonstrated high potential for competition among forage fishes (Huse & Toresen 1996, Willette et al. 1997, Sturdevant et al. 2001). Our study indicates that despite much similarity in feeding ecology, differences exist in the way capelin and age-0 walleye pollock utilize zooplankton. These differences might be interpreted as evidence of competition, but competition is difficult to prove when it is unclear that the resource(s) in common are limiting (Robinson & Wilson 1994).

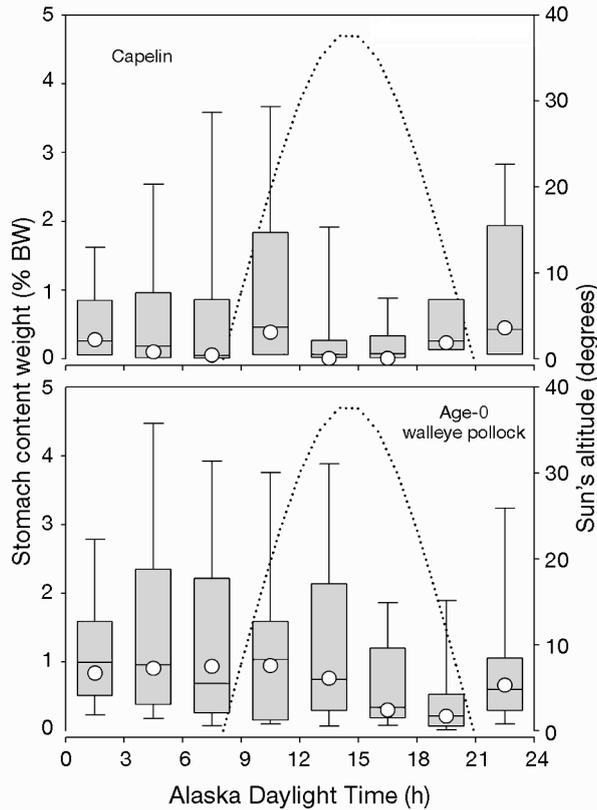


Fig. 5. *Mallotus villosus* and *Theragra chalcogramma*. Box plots of stomach content weight (10th, 25th, 50th, 75th, and 90th percentiles), as a percentage of somatic body weight (% BW), for 3 h intervals of Alaska Daylight Time (ADT). Dotted line: hourly predictions of sun altitude (see Fig. 3 for coordinates and data source). (O) predicted % body weight (BW) from the MAXIMS model. See Fig. 3 for number of fish in each time period

Table 5. *Mallotus villosus* and *Theragra chalcogramma*. Feeding parameters estimated by fitting MAXIMS models to median stomach fullness (% BW) of capelin and age-0 walleye pollock for 3 h intervals ($n = 8$). Feeding period start and end times are Alaska Daylight Time

Species	Parameter	Estimate	SE
Capelin	Ingestion (% BW h ⁻¹)	0.1966	0.1428
	Evacuation (h ⁻¹)	0.3524	0.3405
	1st feeding period (start)	7.4048	0.5842
	1st feeding period (end)	10.5000	2.4042
	2nd feeding period (start)	17.9857	1.2403
	2nd feeding period (end)	23.8750	2.0704
	Daily ration (% BW)	1.7664	1.8639
Age-0 walleye pollock	Ingestion (% BW h ⁻¹)	0.2957	0.1210
	Evacuation (h ⁻¹)	0.3128	0.1455
	Feeding period (start)	19.1714	0.5917
	Feeding period (end)	12.8003	0.9782
	Daily ration (% BW)	5.2129	2.3504

Grover (1990) examined the stomach contents of larval and small age-0 walleye pollock, collected in the GOA during summer, and found high prevalence of small-size copepod genera: *Pseudocalanus*, *Centropages*, and *Acartia*. Similarly, Coyle & Paul (1992) found these genera in the stomachs of small capelin collected during late spring in southeastern Alaska. Our results indicate that age-0 walleye pollock and capelin continue to feed on small copepods during autumn. However, it was also obvious that larger prey, primarily euphausiids, become increasingly important as predator size and gape width increases, which is consistent with previous studies (Naumenko 1984,

Table 6. *Mallotus villosus* and *Theragra chalcogramma*. Chesson's index of prey selectivity, α_i , for capelin and age-0 walleye pollock. Preferential selection: $\alpha_i > 0.063$. Cumacea omitted from Taxonomic group because it was not included in the plankton sample processing protocol. PL: prosome length; (a + j): adult + juvenile; (f + c): furcilia + calyptopis

Taxonomic group	September 2000			September 2001		
	α_i		Plankton No./m ²	α_i		Plankton No./m ²
Pollock	Capelin	Pollock		Capelin		
Amphipoda	0.020	0.001	260	0.009	0.003	1473
Chaetognatha	0.017	0.003	420	0.012	0.004	554
Cirripedia	0.027	0.000	74	0.000	0.001	1491
Cladocera	0.000	0.000	52	0.000	0.000	60282
Radiata (Cnidaria, Ctenophora)	0.000	0.000	279	0.000	0.000	361
Copepoda, <2 mm PL	0.016	0.008	80058	0.008	0.020	62881
Copepoda, ≥2 mm PL	0.045	0.010	1969	0.042	0.064	4315
Euphausiid (a + j)	0.427	0.216	135	0.208	0.619	647
Euphausiid (f + c)	0.046	0.348	228	0.003	0.004	1885
Osteichthys	0.182	0.333	11	0.041	0.000	28
Larvacea	0.127	0.028	254	0.579	0.220	1469
Mysidacea	0.000	0.000	7	0.037	0.000	6
Natantia	0.000	0.000	41	0.000	0.000	94
Ostracoda	0.000	0.000	3	0.000	0.000	19
Reptantia	0.033	0.000	403	0.008	0.000	496
Thecosomata	0.061	0.053	1590	0.053	0.065	4462

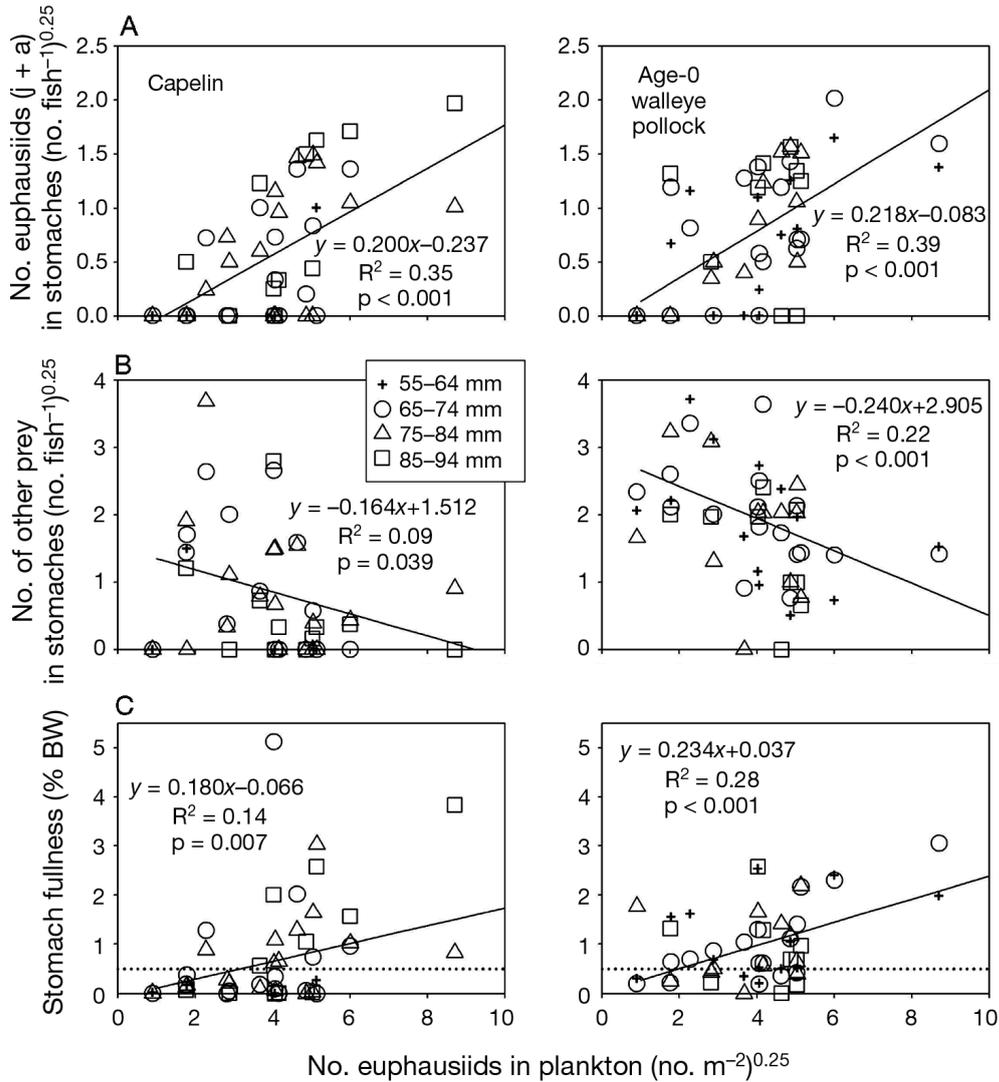


Fig. 6. *Mallotus villosus* and *Theragra chalcogramma*. (A) Mean number of juvenile and adult euphausiids, (B) number of alternate prey in capelin and age-0 walleye pollock stomachs, and (C) median stomach fullness vs the abundance of euphausiids collected from the plankton. Symbols: predator standard-length. Solid lines: least-squares regression from ANCOVA. Dotted horizontal line: reference stomach fullness of 0.5% BW (see 'Prey selectivity' in 'Results'). Abundances are 4th-root transformed (e.g. axis value of 4 back-transforms to 256)

Schabetsberger et al. 2000). In fact, size-related dietary transitions have been demonstrated for capelin (O'Driscoll et al. 2001) and age-0 pollock (Brodeur 1998). Transition in diet with body size means that the capelin, which were larger on average, should have consumed proportionally few small prey items relative to pollock. However, the prey groups associated with differences in selectivity were not the smallest prey items. In fact, the prey groups differentially consumed suggest that age-0 walleye pollock more readily utilize a broader suite of zooplankton. We recognize that selectivity estimates are vulnerable to difficulties associated with identification of prey in stomach contents and quantitative sampling of potential prey populations (Brodeur 1998), but these are less problematic

when a standard method is used to gauge relative differences between predators. Such methodological problems would therefore not likely alter the conclusion that age-0 walleye pollock more fully utilize the range of available prey resources. Indeed, in our study area, the geographic distribution of age-0 walleye pollock encompassed that of capelin indicating a more extensive occupation of the coastal environment (M. Wilson unpubl. data); however, it is not yet evident that capelin were more geographically constrained by prey availability than were age-0 pollock.

Daily ration estimates for capelin (1.8% BW) and age-0 walleye pollock (5.2% BW) in the GOA during September 2000 to 2001 were within the range of most other field-based estimates. Capelin daily ration was

previously estimated to be 1.3 to 2.2% BW (Barents Sea, Ajiad & Pushchaeva 1992), 1.8% BW (Bering Sea, Naumenko 1987), and 2.5 to 5% BW (Gulf of St. Lawrence, Vesin et al. 1981). Ajiad & Puschaeva (1992) report a gastric evacuation rate of 0.1037% BW h^{-1} , which is lower than our estimate possibly due to colder Arctic water and somewhat larger fish (6 to 18 cm). For age-0 walleye pollock, our estimate of gastric evacuation rate was similar to the estimates (0.25 to 0.28% BW h^{-1}) of Merati & Brodeur (1996). Daily ration for age-0 walleye pollock was previously estimated to be 1.0 to 2.5% BW (eastern Bering Sea, Brodeur et al. 2000) and 7.4 to 8.5% BW (western GOA, Merati & Brodeur 1996); this latter estimate may be relatively high due to the inclusion of samples collected near Kodiak Island where euphausiids were an especially prominent dietary component. Ciannelli et al. (2004) estimated a very high daily ration (16 to 21% BW) relative to both our estimate and to the ad libitum (10% BW) ration of laboratory-held fish (Sogard & Olla 1996). This discrepancy might be due to the relatively small size of fish examined by Ciannelli et al. (2004), and to errors associated with model-based estimates (Bajer et al. 2004).

Feeding parameter estimates depend heavily on observed diel patterns in stomach fullness. This can be problematic because stomach fullness data are characterized as highly variable (Richter et al. 1999). Our observation of crepuscular feeding by capelin, however, agrees with that observed by Vesin et al. (1981) studying capelin in the northwest Atlantic. Vesin et al. (1981) associated crepuscular feeding with transitional periods in the diel vertical migration of prey and predator, possibly in response to predator-prey perception dynamics (Johnsen 2005). For small fishes foraging in exposed areas, crepuscular feeding optimizes the trade-off between food intake and predation risk (Clark & Levy 1988). Vesin et al. (1981) noted that during winter, capelin shift to diurnal feeding possibly in response to photoperiod compression. In contrast, age-0 pollock ≥ 50 mm tend to feed nocturnally (Brodeur et al. 2000), and have been shown to be effective foragers in low-light conditions (Ryer & Olla 1999). The decrease in stomach fullness during the day, when capelin (Mowbray 2002) and age-0 walleye pollock (Brodeur and Wilson 1996) are at depth, suggests that prey availability or some other factor, e.g. predation risk (Lang et al. 2000, Mowbray 2002), inhibits feeding.

Our observation of low daily ration for capelin as compared to age-0 walleye pollock was not explained by any indication of poor body condition. The capelin length-weight relationship was similar to those of capelin in the Barents Sea during autumn (Gjøsæter 1998) and, after conversion to FL (Buchheister & Wilson 2005), similar to capelin in Prince William Sound

(Brown 2002). However, autumn appears to be a time of reduced feeding by capelin as noted by Vesin et al. (1981). Furthermore, the low daily ration of capelin might also reflect their nearly mature size (10 to 13 cm FL, Pahlke 1985) and reduced somatic growth (0.3 mm d^{-1} , Brown 2002, Gjøsæter 1998). In contrast, age-0 walleye pollock grow at approximately 0.9 mm d^{-1} (Bailey et al. 1996a) undergoing a 4-fold increase in length before spawning as age-4 individuals. Thus, differences in stomach fullness likely reflect different ontogenetic states and consequent nutritional demands and physiological priorities with regard to energy storage versus utilization for growth. Alternatively, because capelin and age-0 walleye pollock share major prey groups, the observed differences in diet and feeding intensity could reflect the adverse effects of competition; however, again, it is not clear that prey resources were limiting.

Gjøsæter et al. (2002) and Yamamura et al. (2002) studied capelin and walleye pollock respectively and suggested that these fishes can significantly impact the standing stocks of large zooplankton, possibly to the point of becoming prey limited. The positive association we observed between euphausiids in predator stomachs and in the plankton indicates that the variation in euphausiid availability was sufficient to affect predator diet. This response was somewhat species-specific in that age-0 walleye pollock were inclined to consume other prey while capelin reduced consumption at euphausiid-poor locations. The apparent avoidance by capelin to utilize alternate prey may indicate a relatively specialized diet and could relate to their relatively high body energy density. The body lipid content of *Thysanoessa inermis* increases in autumn (Falk-Petersen et al. 2000) such that they become one of the more energy-rich prey groups available to these predators (M. Wilson unpubl. data). On average, daily consumption of euphausiids by the capelin and age-0 walleye pollock populations in the study area was only 2.4% (± 1.6 SE, $n = 18$) of the standing stock, which agrees with Ciannelli et al. (1998) that in the western GOA there is little evidence of widespread limitation of prey. These estimates, however, may not be generally applicable due to fluctuations in predator (Bailey et al. 1996b, Dorn et al. 2004) and prey (Sugimoto & Tadoro 1997) populations, and because they do not account for consumption by other zooplanktivores, or spatial patchiness in predator and prey populations (De Robertis 2002). With regard to localized depletion, based on our daily ration and diet proportion estimates for capelin and age-0 walleye pollock, it seems likely that the standing stock of euphausiid abundance was depleted in at least some locations within our study area. Using only samples collected at night, the maximum site-specific daily consumption by fish was 30%

of the euphausiid standing stock suggesting that local depletion of euphausiids could occur. Thus, it seems likely that localized depletion of euphausiids could be a governing force in the adaptation of foraging strategy by capelin and age-0 walleye pollock.

If localized depletion of euphausiids commonly occurs in the presence of capelin and age-0 walleye pollock, then these fishes can be expected to compete. Capelin may be relatively specialised at foraging on euphausiid patches based on their tendency to reduce feeding when these prey were in low abundance. We therefore suggest that capelin may be superior to age-0 walleye pollock at locating and cropping euphausiid patches. In contrast, age-0 walleye pollock readily consume alternate prey types indicating that they may be superior to capelin at grazing on a variety of ambient zooplankton. As such, capelin may have feeding advantages over pollock during periods when euphausiids are present but underexploited. Conversely, pollock feeding may be favoured during periods when euphausiids are limiting or absent since pollock demonstrate a tendency toward greater diet diversity and foraging flexibility. These traits could contribute to the success of one species over the other in differing regimes.

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