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Seasonal changes in the diet composition and prey selection of walleye pollock (*Theragra chalcogramma*) in the northern Gulf of Alaska

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Abstract

Walleye pollock, *Theragra chalcogramma*, are one of the dominant fishes in the Gulf of Alaska (GOA) ecosystem, yet relatively little information is available on the diet and prey selectivity of pollock in the northern GOA. Stomachs of midwater trawled adult pollock were collected in April, August and November 2003 in the northern GOA. Euphausiids were the dominant prey in April, averaging 59% by number and 70% by weight. Euphausiids persisted as the dominant prey in August, averaging 84% by number and 95% by weight. Decapods were the dominant prey item in November. This was primarily due to the shrimp *Pandalus borealis*, which averaged 68% by number and 53% by weight. Stomach contents were also compared with available prey fields using chi-square-based resource selection statistics. This analysis revealed significant differences between the environmental and dietary distributions of prey types. Additional analysis found significant selection for euphausiids over all other categories of available zooplankton in both spring and summer. Amongst euphausiids, there was significant selection for *Thysanoessa inermis* in spring and *T. spinifera* in summer.

Keywords: Walleye pollock; *Theragra chalcogramma*; Diet; Prey selection; Feeding ecology

1. Introduction

In the Gulf of Alaska (GOA) walleye pollock, *Theragra chalcogramma* (hereafter referred to as pollock), make up the second largest groundfish biomass (Yang and Nelson, 2000). They are important prey for apex predators such as Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), common murres (*Uria aalge*) and tufted puffins (*Fratercula cirrhata*); pollock are also important prey for the dominant groundfish in the GOA, arrowtooth flounder (*Atheresthes stomias*), and commercially important species such as Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*) and other pollock (Smith, 1981; Springer, 1992).

As a predator with a biomass averaging 1 million tonnes in the GOA, pollock may remove a considerable amount of prey from the ecosystem (Bailey et al., 2005). Much research has been done on the diet of pollock, both on juvenile (see review in Brodeur and Wilson, 1996) and adult stages (e.g., Dwyer et al., 1987; Shuntov et al., 2000; Yamamura et al., 2002). Not surprisingly, there is geographical variation in the diet of adults. For example, adults cannibalize juveniles in the Bering Sea (Dwyer et al., 1987), whereas in the Gulf of Alaska (GOA) euphausiids contribute the most to the diet of adults (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000). There is also seasonal variation in the diet of adult pollock. In the southeastern Bering Sea, the largest component of the diet in spring and summer is euphausiids, while in fall and winter it is juvenile pollock (Dwyer et al., 1987). However, no seasonal information exists on the diet of adult pollock in the GOA. Additionally, the aforementioned studies all sampled pollock with bottom gear, and relatively little information is available on the diet of pelagic adults. Two studies that did sample with midwater gear found very different diets: in the western GOA the diet of adults consisted primarily of (non-pollock) fishes (Duffy-Anderson et al.,

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2003), whereas off northern Japan the diet of adults consisted primarily of amphipods and euphausiids (Kooka et al., 1998). No information is available on the diet of pelagic adults in the northern GOA.

Prey selection is defined as a difference between the environmental and dietary distributions of prey types (Eggers, 1977). Although several studies have examined prey selection by juvenile pollock (Brodeur, 1998; Purcell and Sturdevant, 2001; Sturdevant et al., 2001; Wilson et al., 2006), only one study has examined prey selection by adults. Off northern Japan adult pollock exhibit positive selection primarily for amphipods (Kooka et al., 1998). Nothing is known about prey selectivity by adult pollock in the northeastern Pacific Ocean.

As fisheries science moves toward an ecosystem-based approach it is clear that diet information collected in one area cannot be extrapolated to other regions. Nor can the results of dietary data collected in summer be considered representative of diet in other seasons (Hanson and Chouinard, 2002). In this paper we provide seasonal information on the diet of pelagic adult pollock in the northern GOA, which complements previous work on the summer diet of demersal adults in the region. We also provide evidence that the observed diet was due to prey selectivity, rather than random feeding, which complements previous work on juvenile pollock in the GOA.

2. Materials and methods

2.1. Study area

The study site (Fig. 1) was centered around Chiswell Island (59°36′N, 149°34′W), a Steller sea lion rookery in the northern GOA, where two of us (CFA, KOC) did an acoustic assessment of potential fish prey available to foraging sea lions as part of another study. Midwater trawls provided biological samples that allowed us to investigate seasonal changes in the diet of pollock in the present paper. The study area was adjacent to Global Ocean Ecosystems Dynamics (GLOBEC) stations 1 through 4. GOA shelf waters are characterized by two major currents: the Alaska stream, which flows westward at or near the shelf break, about 200 km offshore; and the Alaska Coastal Current, a buoyancy-driven current flowing westward within 40 km of the coast (Weingartner et al., 2002). Given the flow characteristics of the latter current, we assumed that data on zooplankton abundances taken from GLOBEC stations 1 through 4 could be used as a rough estimate of available prey fields in our study area.

2.2. Field sampling

Pollock were collected at night, between evening and morning civil twilights, in April, August and November 2003. The April cruise was conducted aboard the 20 m R/V Pandalus, while the August and November cruises were conducted aboard the 23 m F/V Nightwatch. Midwater trawls were done with a Gourock, Inc., research scale net with vertical and horizontal openings of 12 and 22 m, respectively, in April and August. In contrast, November midwater trawls were done with an LFS, Inc., commercial fishing scale net with vertical and horizontal openings of 26 and 51 m, respectively. However, both nets were outfitted with the same 1.9 cm mesh cod end liner. Opportunistic midwater trawls were aimed at layers of high acoustic backscatter observed in a Hydroacoustic Technology, Inc., 38 kHz transducer, a standard frequency for the detection of pollock (e.g., Traynor, 1996). Up to 200 specimens of each species per tow were retained for shipboard measurements of fork length (FL). Stomachs were removed from at least five pollock per haul. Fish that showed signs of regurgitation (food in the mouth or throat) were not used. Each stomach was placed in an individual cloth sample bag with a tag containing the FL and haul number of the sample and preserved in 10% formalin.

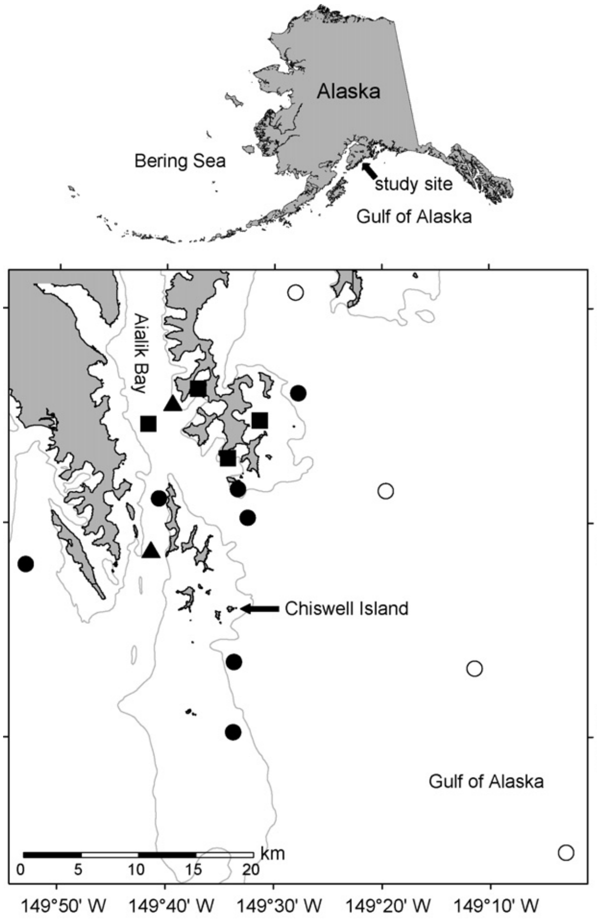

Fig. 1. General map of Alaska (above), with a close up of the study area (below), centered around Chiswell Island. Trawl stations where pollock stomachs were sampled are shown for April (●), August (■) and November (▲). Empty circles (○) show GLOBEC stations where zooplankton were sampled. Bathymetry contour is 100 m.

Zooplankton were collected at night at GLOBEC stations 1 through 4 in April and August 2003. A 1 m^2 multiple opening/closing and environmental sampling system (MOCNESS), equipped with an externally mounted flowmeter and 500 μm mesh black nets, was towed at 4.5 km/h behind the 41 m R/V Alpha Helix. Five oblique samples were collected in 20 m increments from 100 m depth to the surface. Samples were preserved in 10% formalin (Coyle and Pinchuk, 2005).

2.3. Laboratory procedures

Stomach contents were identified to the lowest taxonomic category possible, enumerated and weighed. All unidentifiable material was categorized as digested material and omitted from data analysis.

Stomach fullness was assessed with the total fullness index:

$$\mathrm{TFI} = \frac{1}{n}\sum_{j=1}^{n}\frac{\text{stomach contents}_j}{\mathrm{FL}_j} \times 10^4 \tag{1}$$

where n is the total number of j stomachs examined per cruise, stomach contents is in g, and FL is in cm (Nielsen and Andersen, 2001). TFI values ≤ 0.05 are considered indicative of minimal feeding (Mello and Rose, 2005).

MOCNESS samples from the same tow are autocorrelated and cannot be considered independent when running statistical analyses. Thus an integrated estimate of abundance for each station was computed as follows. The total number of each taxon was divided by the total volume sampled and expressed as number/m^3. These data were then integrated through the 20 m depth interval for each net to estimate number/m^2. All five of these values were then summed to give the number/m^2 during the entire 100 m MOCNESS tow. The number/m^3 for each station was determined by dividing the number/m^2 by the total depth interval (100 m) sampled by the tow. A recent multiyear monitoring study in the coastal GOA showed that the cross-shelf distribution of water properties and zooplankton could be characterized by dividing the shelf into four separate zones, with GLOBEC stations 1 through 4 comprising a nearshore zone (Coyle and Pinchuk, 2005). Thus, results for all four stations were averaged, and the coefficient of variation was calculated as the standard deviation divided by the mean.

2.4. Trophic diversity curves

Trophic diversity curves (Pielou, 1966; Hurtubia, 1973) were used to determine whether a sufficient number of stomachs were examined to describe the diet of pollock for each cruise. Trophic diversity was calculated with the Brillouin index:

$$H_k = \frac{1}{u_{+k}}\log_{10}\frac{u_{+k}!}{\prod_{i=1}^{I}u_{ik}!} \tag{2}$$

where u_{+k} is the total number of prey in k pooled stomachs, u_{ik} the number of prey category i in k pooled stomachs, and I is the total number of prey categories. For each cruise, 100 random orders of stomachs were calculated, and the mean H_k was plotted against the cumulative number of stomachs. Curves were considered asymptotic if at least two values prior to the total trophic diversity (H_z) were within the range $H_z \pm 0.05H_z$ (Koen Alonso et al., 2002).

2.5. Diet composition

Standard diet indices were calculated according to Bowen (1996). Frequency of occurrence (*%FO*) is the percentage of stomachs containing prey category i. High *%FO* values indicate whether fish in the sample can be characterized as a single feeding unit.

Composition by number (*%N*) is the number of prey category i expressed as a percentage of the total number of prey in the jth stomach. Composition by weight (*%W*) is the weight of prey category i expressed as a percentage of the total weight of prey in the jth stomach. Results for *%N* and *%W* were summarized for each cruise by calculating the mean and 95% confidence intervals. Percentage data are not normally distributed and were arcsine-transformed to calculate proper confidence intervals. Note that when such confidence intervals are back-transformed to the original units they are centered around the median rather than the mean (Zar, 1999).

2.6. Resource selection statistics

We used the resource selection statistics of Manly et al. (2002) to test for differences between the dietary and environmental distributions of prey types. These statistics are based on chi-square tests, which require count data. Thus, all resource selection statistics were only done on prey numbers, and not on prey weight. In the Design II protocol of Manly et al. (2002) the resource units used by the jth fish are known, allowing statistical inference based on the use of individuals as replicates. There are three null hypotheses that can be tested:

H1. Individual fish used prey categories in the same proportions, regardless of whether selection occurred. The test statistic is

$$\chi^2_{L1} = 2\sum_{j=1}^{n}\sum_{i=1}^{I}u_{ij}\log_e\left(\frac{u_{ij}}{E(u_{ij})}\right) \tag{3}$$

where u_{ij} is the number of prey category i consumed by fish j, and $E(u_{ij})$ is the expected number of prey category i consumed by the jth fish. For this equation $E(u_{ij}) = u_{i+}u_{+j}/u_{++}$, where u_{i+} is the total number of prey category i in all stomachs, u_{+j} is the total number of prey consumed by fish j, and u_{++} is the total number of all prey found in all stomachs. The test statistic is compared to the chi-square distribution with $(I-1)(n-1)$ d.f.

H2. Prey selection occurred in proportion to availability. The test statistic is:

$$\chi^2_{L2} = 2\sum_{j=1}^{n}\sum_{i=1}^{I}u_{ij}\log_e\left(\frac{u_{ij}}{E(u_{ij})}\right) \tag{4}$$

In this case $E(u_{ij}) = \pi_i u_{+j}$, where π_i is the proportion of prey category i in the environment. There are $n(I-1)$ d.f.

H3. On average, fish used prey in proportion to availability, regardless of whether they were selecting categories in the same proportions. This null is tested with:

$$\chi^2_{L2} - \chi^2_{L1} \tag{5}$$

with $I-1$ d.f.

For all resource selection statistics α levels were set to 0.05.

2.7. Selection ratios

When resource selection statistics revealed that pollock were feeding selectively, we used selection ratios to test the null hypothesis of random feeding on discrete prey categories. Continuing with the Design II protocol of Manly et al. (2002), the estimator of the average selection ratio for the population is given by

$$\hat{w}_i = \frac{u_{i+}/u_{++}}{\pi_i} \tag{6}$$

The variance of (6) is calculated by

$$\operatorname{var}(\hat{w}_i) = \frac{\sum_{j=1}^{n}(u_{ij}/\pi_i - \hat{w}_i u_{+j})^2}{n-1}\frac{n}{(u_{++})^2} \tag{7}$$

The standard error follows as:

$$\operatorname{se}(\hat{w}_i) = \sqrt{\operatorname{var}(\hat{w}_i)} \tag{8}$$

Simultaneous Bonferroni confidence intervals for (7) can be constructed with overall confidence level of $100(1-\alpha)\%$, so that the probability of all the intervals containing the true value is approximately $1-\alpha$. These intervals are given by

$$\hat{w}_i \pm z_{\alpha/2I}\,\operatorname{se}(\hat{w}_i) \tag{9}$$

Unlike standard confidence intervals that are centered around 0, these confidence intervals are centered around 1 (Manly et al., 2002, p. 70). In other words, when these intervals include the value 1 there is no selection for or against the prey category. Intervals greater than 1 indicate significant selection for the prey category, while intervals less than 1 indicate significant selection against the prey category.

The difference $(\hat{w}_h - \hat{w}_i)$ between two selection ratios can be estimated by

$$\operatorname{var}(\hat{w}_h-\hat{w}_i)=\frac{n/(n-1)}{(u_{++})^2}\sum_{j=1}^{n}\left(\frac{u_{hj}}{\pi_i}-\frac{u_{ij}}{\pi_i}-\hat{w}_h u_{+j}+\hat{w}_i u_{+j}\right)^2 \tag{10}$$

Finally, Bonferroni intervals for (10) can be constructed by

$$(\hat{w}_h - \hat{w}_i) \pm z_{\alpha/2I'}\,\operatorname{se}(\hat{w}_h - \hat{w}_i) \tag{11}$$

where $I' = I(I-1)/2$ is the number of differences that can be calculated between different selection ratios. In this case, intervals that include zero indicate no significant difference between selection ratios.

3. Results

3.1. Field sampling

Sampled pollock ranged in size from 29.5 to 60.5 cm in April; 28.1 to 54.4 cm in August; and 37.1 to 61.0 cm in November (Table 1). In the GOA these size classes can be considered adults (Hughes and Hirschhorn, 1979; Duffy-Anderson et al., 2003).

All April stomachs were sampled from pollock caught in the upper 87 m of the water column (Table 1). Four of 40 April stomachs examined were empty and were excluded from all subsequent statistical analyses. Mean fullness was 0.40, eight times higher than minimal feeding.

One August haul occurred at depths greater than 100 m (Table 1). Although these data were used in the diet composition analysis, they were excluded from resource selection statistics, as zooplankton samples were only taken in the upper 100 m of the water column. Thus, data from this haul are presented separately in Table 1. Two of nine stomachs from this deeper haul were empty. In the 3 tows <100 m, 7 of 43 stomachs were empty. All empty stomachs were excluded from the diet composition analysis. Mean fullness for the deeper haul was 0.37, while mean fullness for the tows <100 m was 0.57. Both values were well above minimal feeding.

All November stomachs were sampled from pollock caught >100 m (Table 1). All 21 stomachs examined contained prey. Mean fullness was 1.02, the highest value observed in all three cruises.

Table 2 shows that copepods were the most abundant taxon in our study area in April (122.12/m^3) and August (58.04/m^3). Amongst euphausiids, *T. spinifera* had the highest abundance in April (0.95/m^3), while *T. inermis* was more abundant in August (0.86/m^3).

3.2. Trophic diversity curves

The trophic diversity curves reached an asymptote around $n = 22$ stomachs in April, $n = 18$ stomachs in August, and $n = 16$ stomachs in November (Fig. 2). Thus, samples sizes were considered large enough to evaluate the diet.

Table 1
Trawl catch data for adult walleye pollock, *T. chalcogramma*

	Trawls	Minimum HR (m)	Maximum FR (m)	Minimum FL (cm)	Maximum FL (cm)	Stomachs	%Empty	TFI
April	7	18.3	86.6	29.5	60.5	40	10.0	0.40
August	1	100.6	124.4	37.3	54.5	9	22.2	0.37
	3	18.2	49.4	28.1	39.5	43	16.3	0.57
November	2	100.6	236.0	37.1	61.0	21	0.0	1.02

Trawls: number of tows from which pollock stomach samples were taken. Minimum HR: minimum headrope depth during trawls. Maximum FR: maximum footrope depth during trawls. Minimum FL: fork length of smallest sampled pollock. Maximum FL: fork length of largest sampled pollock. Stomachs: number of stomachs examined. %Empty: percentage of examined stomachs that were empty. TFI: total fullness index. Data for the deeper August haul are presented separately. Note that Minimum HR and Maximum HR were recorded when the net was at the desired fishing depth and does not include deployment/retrieval.

Table 2
Abundance (number/m^3) of zooplankton categories at GLOBEC stations 1 through 4

	April		August	
	$\bar{x}$	CV	$\bar{x}$	CV
Order				
Amphipoda	0.05	1.29	0.56	0.71
Copepoda	122.12	0.45	58.04	0.50
Decapoda	0.49	1.63	0.14	1.11
Euphausiacea	1.57	0.89	1.93	0.61
Larvacea	2.95	1.06	0.15	1.51
Pteropoda	1.12	0.62	3.48	0.83
Euphausiacea				
E. pacifica	0.02	1.22	0.44	0.40
T. inermis	0.42	1.17	0.86	1.49
T. longipes	0.02	0.62	<0.01	1.43
T. raschii	0.17	1.74	<0.01	1.41
T. spinifera	0.95	1.30	0.62	0.31

Prey are grouped by taxonomic order above, while data for Euphausiacea are detailed below. CV: coefficient of variation.

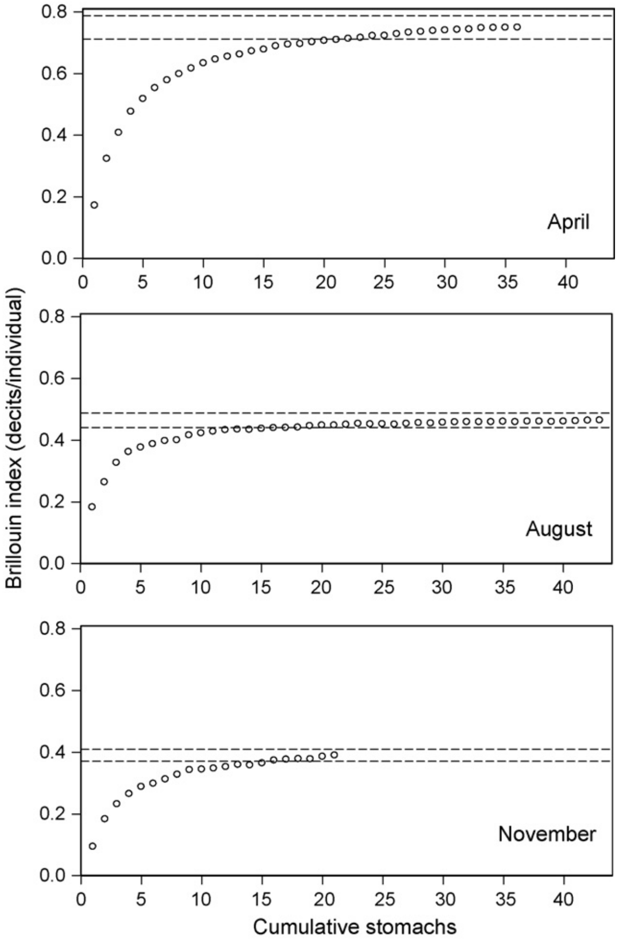

Fig. 2. Cumulative trophic diversity (H_z) in the diet of walleye pollock, *T. chalcogramma*. Dashed lines indicate the range of asymptotic diversity $H_z \pm 0.05H_z$.

3.3. Diet composition

Euphausiids were found in 83% of April stomachs (Table 3). Decapods and larvaceans ranked second in terms of occurrence at 39%. Euphausiids were also the primary component of the diet in terms of numbers and weight, averaging 59% and 70%, respectively. All but one of the euphausiids identified to species in April stomachs were *Thysanoessa inermis* and *T. spinifera*, with the latter contributing more to the diet at 33% by number and 32% by weight.

Euphausiids were found in 98% of August stomachs (Table 3). Copepods ranked second in terms of occurrence at 35%. Euphausiids were also the primary component of the diet in terms of numbers and weight, averaging 84% and 95%, respectively. Once again *T. spinifera* was the dominant euphausiid, averaging 58% by number and 51% by weight. *Euphausia pacifica* entered the diet in August, ranking second amongst euphausiids at 19% by number and 13% by weight.

Decapods were found in all November stomachs (Table 3). Amphipods ranked second in terms of occurrence at 33%. Decapods were also the primary component of the diet in terms of numbers and weight, averaging 77% and 96%, respectively. This was largely due to the shrimp *Pandalus borealis*, which averaged 68% and 53% by number and weight, respectively.

The high frequency of occurrence values for the primary prey items in each month indicate that the sampled pollock could be treated as a single feeding unit within each month (Bowen, 1996).

The 95% confidence intervals for %*N* and %*W* can be found in Appendix A.

3.4. Resource selection statistics

All three null hypotheses were rejected for the April data with respect to taxonomic order (Table 4), suggesting that individual fish were not using prey categories in the same proportions, and that prey selection was not in proportion to availability. For the August data, H1 was not rejected, indicating that individual fish were selecting prey categories in the same proportions. However, both H2 and H3 were rejected, suggesting that, on average, fish were not using prey in proportion to availability, regardless of whether individual fish were selecting prey categories in the same proportions.

Amongst euphausiids, H1 was not rejected for either the April or August data (Table 4), indicating that individual fish were selecting prey in the same proportions in the respective months. However, both H2 and H3 were rejected for both sets of data, suggesting that, on average, fish were not using prey in proportion to availability in the respective months, regardless of whether individual fish were selecting prey categories in the same proportions.

3.5. Selection ratios

In April there was statistically significant selection for euphausiids and decapods, random feeding on amphipods, larvaceans and pteropods, and significant selection against cope-

Table 3
Diet of adult walleye pollock, *T. chalcogramma*

Prey category	April (*n* = 36)			August (*n* = 43)			November (*n* = 21)		
	%FO	*%N*	*%W*	*%FO*	*%N*	*%W*	*%FO*	*%N*	*%W*
Amphipoda									
Byblis spp.	–	–	–	2.33	0.07	0.04	–	–	–
Parathemisto libellula	–	–	–	4.65	1.13	1.11	4.76	0.75	0.03
Parathemisto pacifica	5.56	1.67	0.82	16.28	2.58	0.46	9.52	7.02	0.03
Parathemisto spp.	–	–	–	2.33	0.69	0.04	–	–	–
Primno macropa	–	–	–	2.33	0.06	0.03	–	–	–
Cyphocaris challengeri	–	–	–	–	–	–	9.52	2.63	0.01
Unidentified Amphipoda	–	–	–	–	–	–	9.52	+	0.01
Total Amphipoda	5.56	1.67	0.82	25.58	4.53	1.68	33.33	10.40	0.08
Cephalopoda									
Berryteuthis magister	–	–	–	–	–	–	4.76	1.75	3.37
Copepoda									
Calanus marshallae	27.78	4.91	3.42	27.91	7.97	2.61	4.76	1.75	<0.01
Candacia columbiae	–	–	–	–	–	–	4.76	1.32	<0.01
Eucalanus bungii	2.78	0.02	0.01	2.33	0.14	<0.01	–	–	–
Metridia okhotensis	2.78	0.03	<0.01	–	–	–	–	–	–
Metridia pacifica	–	–	–	4.65	0.66	0.01	–	–	–
Neocalanus cristatus	2.78	0.01	0.02	2.33	0.21	0.06	–	–	–
Neocalanus plumchrus/flemingeri	25.00	12.39	1.94	4.65	1.96	0.12	4.76	1.32	<0.01
Pareuchaeta elongata	–	–	–	–	–	–	4.76	0.88	0.01
Unidentified Copepoda	8.33	+	2.58	–	–	–	–	–	–
Total Copepoda	36.11	17.35	7.96	34.88	10.94	2.80	19.05	5.27	0.01
Decapoda									
Cancridae megalopae	–	–	–	4.65	0.68	0.21	–	–	–
Chionoecetes megalopae	8.33	0.78	0.14	–	–	–	–	–	–
Crangon communis	–	–	–	–	–	–	4.76	3.51	0.29
Pasiphaea pacifica	2.78	1.52	2.77	–	–	–	9.52	6.14	1.67
Pandalus spp.	–	–	–	–	–	–	14.29	+	8.05
Pandalus borealis	2.78	0.07	2.16	–	–	–	80.95	67.67	52.93
Pandalidae zoeae	30.56	5.12	1.40	–	–	–	–	–	–
Pinnotheridae megalopae	–	–	–	2.32	0.06	0.01	–	–	–
Unidentified Caridea	–	–	–	–	–	–	90.48	+	32.65
Total Decapoda	38.89	7.49	6.47	4.65	0.74	0.22	100.00	77.32	95.59
Euphausiacea									
Euphausia pacifica	–	–	–	53.49	19.32	13.04	–	–	–
Thysanoessa inermis	55.56	25.86	20.98	27.91	6.01	4.89	4.76	2.63	0.14
Thysanoessa longipes	–	–	–	2.33	0.63	0.81	–	–	–
Thysanoessa raschii	2.78	0.05	0.01	–	–	–	–	–	–
Thysanoessa spinifera	69.44	32.71	31.93	83.72	57.83	50.47	–	–	–
Unidentified Euphausiacea	72.22	+	17.48	67.44	+	26.10	9.52	+	0.72
Total Euphausiacea	83.33	58.62	70.40	97.67	83.79	95.31	14.29	2.63	0.86
Larvacea									
Oikopleura spp.	38.89	13.93	13.36	–	–	–	–	–	–
Pteropoda									
Clione limacina	–	–	–	–	–	–	4.76	1.32	0.01
Limacina helicina	5.56	0.94	0.13	–	–	–	–	–	–
Unidentified Pteropoda	2.78	+	0.86	–	–	–	–	–	–
Total Pteropoda	8.33	0.94	0.99	–	–	–	4.76	1.32	0.01
Stomiiformes									
Unidentified stomiiform fish	–	–	–	–	–	–	4.76	1.32	0.05

n: number of stomachs examined. *%FO*: percent frequency of occurrence. *%N*: mean percent composition by number. *%W*: mean percent composition by weight (g). +: category contained fragments that could not be enumerated.

pods (Table 5). Furthermore, the selection ratio for euphausiids was significantly greater than the selection ratio for all other categories, except larvaceans (Table 6). The latter was due to the large amount of variation associated with these two selection ratios, resulting in overlap between the two intervals (Table 5). In August there was statistically significant selection for euphausiids, random feeding on amphipods and decapods, and significant selection against copepods (Table 5). Larvaceans and pteropods

Table 4
Resource selection statistics for hypotheses regarding prey selection by adult walleye pollock, *T. chalcogramma*

Hypothesis	April			August		
	χ^2 statistic	d.f.	*P*-value	χ^2 statistic	d.f.	*P*-value
Order						
H1	2584.10	175	$<1.0 \times 10^{-15}$	149.62	175	0.92
H2	16718.84	180	$<1.0 \times 10^{-15}$	2885.68	180	$<1.0 \times 10^{-15}$
H3	14314.74	5	$<1.0 \times 10^{-15}$	2736.06	5	$<1.0 \times 10^{-15}$
Euphausiacea						
H1	123.68	105	0.10	124.62	105	0.09
H2	461.53	108	$<1.0 \times 10^{-15}$	620.01	108	$<1.0 \times 10^{-15}$
H3	337.85	3	$<1.0 \times 10^{-15}$	495.39	3	$<1.0 \times 10^{-15}$

H1: Individual fish used prey categories in the same proportions, regardless of whether selection occurred. H2: Prey selection occurred in proportion to availability. H3: On average, fish used prey in proportion to availability, regardless of whether they were selecting categories in the same proportions.

Table 5
Selection ratios $\hat{w}_i$, standard errors and simultaneous 95% confidence intervals for adult walleye pollock, *T. chalcogramma*

Prey category	April				August			
	$\hat{w}_i$	se($\hat{w}_i$)	Confidence limits		$\hat{w}_i$	se($\hat{w}_i$)	Confidence limits	
			Lower	Upper			Lower	Upper
Order								
Amphipoda	5.45	4.29	0.00[a]	16.75	3.77	1.79	0.00[a]	8.50
Copepoda	0.35	0.11	0.05	0.65	0.06	0.02	<0.01	0.13
Decapoda	6.40	1.89	1.58	11.21	1.98	1.32	0.00[a]	5.47
Euphausiacea	33.23	8.16	11.74	54.72	30.28	1.02	27.58	32.97
Larvacea	8.29	3.88	0.00[a]	18.50	0.00	0.00	–	–
Pteropoda	4.71	3.68	0.00[a]	14.40	0.00	0.00	–	–
Euphausiacea								
E. pacifica	0.00	0.00	–	–	0.77	0.14	0.43	1.11
T. inermis	2.12	0.16	1.73	2.51	0.06	0.03	0.00[a]	0.12
T. spinifera	0.85	0.09	0.64	1.07	2.47	0.11	2.19	2.75
Other[b]	0.01	0.01	0.00[a]	0.05	0.80	0.85	0.00[a]	2.93

Limits were calculated using the Bonferroni inequality with a confidence level of 99.16% for $I = 6$ prey categories (order) and 98.75% for $I = 4$ prey categories (Euphausiacea). Note that confidence intervals for $\hat{w}_i$ are centered around 1, not 0 (Manly et al., 2002): intervals that include 1 indicate no selection for or against the prey category; intervals greater than 1 indicate significant selection for the prey category; and intervals less than 1 indicate significant selection against the prey category.

[a] Impossible negative confidence limits were replaced with 0.

[b] Includes *T. longipes* and *T. raschii*.

Table 6
Significant differences (+) between estimated selection ratios $\hat{w}_i$ for adult walleye pollock, *T. chalcogramma*

	April					August		
	Amphipoda	Copepoda	Decapoda	Euphausiacea	Larvacea	Amphipoda	Copepoda	Decapoda
Order								
Copepoda	–					–		
Decapoda	–	+				–	–	
Euphausiacea	+	+	+			+	+	+
Larvacea	–	–	–	–				
Pteropoda	–	–	–	+	–			

	April			August		
	E. pacifica	*T. inermis*	*T. spinifera*	*E. pacifica*	*T. inermis*	*T. spinifera*
Euphausiacea						
T. inermis	+			+		
T. spinifera	+	+		+	+	
Other	–	+	+	–	–	–

Note that Larvacea and Pteropoda did not appear in the August diet.

did not appear in the diet at this time. The selection ratio for euphausiids was significantly greater than the selection ratio for all other categories (Table 6).

Amongst euphausiids, the selection ratios for April show that there was statistically significant selection for *T. inermis*, random feeding on *T. spinifera* and significant selection against *T. raschii* (Table 5). *E. pacifica* did not appear in the diet at this time. The selection ratio for *T. inermis* was significantly greater than the selection ratio for all other categories (Table 6). In August there was significant selection for *T. spinifera*, random feeding on *E. pacifica* and other *Thysanoessa* spp., and significant selection against *T. inermis* (Table 5). The selection ratio for *T. spinifera* was significantly greater than the ratio for *E. pacifica* and *T. inermis*, but not from other *Thysanoessa* spp. (Table 6). The latter resulted from a single occurrence of *T. longipes* in one stomach. The Bonferroni intervals for differences between selection ratios (Eq. (11)) are particularly sensitive to this situation (Manly et al., 2002).

4. Discussion

4.1. Field sampling

Various authors have discussed the effect of fishing gear on abundance estimates of gadids (e.g., Godø et al., 1998). Although logistical constraints required us to switch to a commercial scale net for the November cruise, we used the same cod end liner throughout the study to minimize variation in capture efficiency. It should also be noted that the November hauls were not deeper because of the switch to a commercial scale net, but simply because that was where layers of high acoustic backscatter were observed in the 38 kHz.

In the analysis of stomachs contents some prey categories may be underestimated due to rapid digestion times, while others may be overestimated due to slow digestion times (Bowen, 1996). Our stomach fullness values were well above the minimal feeding value, and were within the range of TFI values reported for other gadids (Nielsen and Andersen, 2001; Mello and Rose, 2005). Thus, we considered digestive effects to be minimized.

The seasonal increase in stomach fullness that we observed may at first appear inconsistent with generally accepted models of a decrease in feeding between fall and winter (e.g., Paul et al., 1998). However, we note that off southern Japan, stomach fullness of 30–40 cm pollock increases between August and November, and then decreases sharply after November (Yamamura et al., 2002). Thus, it is likely that our November sampling occurred just prior to the expected winter decrease in feeding.

4.2. Trophic diversity curves

Trophic diversity in April was almost double what it was in August and November. Other dietary studies of marine fishes have reported relatively consistent trophic diversity throughout the seasons, except in winter (Braccini et al., 2005; Figueiredo et al., 2005). The reduced trophic diversity we observed in August was coincident with a seasonal decrease in the abundance of copepods, decapods and larvaceans, suggesting that this was simply due to reduced availability of these prey categories. Alternatively, there was an increase in euphausiid abundance between April and August, suggesting that some critical density threshold was reached allowing pollock to abandon other prey types in favor of euphausiids. Significant selection ratios for euphausiids in both April and August support this latter explanation.

4.3. Diet composition

The primary component of the diet of adult pollock in our study area in April was euphausiids, both in terms of percent numbers and percent wet weight. Euphausiids are also the largest component of the spring diet of 25–35 cm pollock in southeast Alaska (Clausen, 1983) and all size classes of adults in the southeastern Bering Sea (Dwyer et al., 1987). However, in the northeastern Bering Sea euphausiids are only the primary prey item for pollock <40 cm, while larger individuals feed on larvaceans and decapods (Dwyer et al., 1987). Off northern Japan there is interannual variation in the spring diet, with amphipods being the dominant prey item in some years and euphausiids in others (Kooka et al., 1998). Euphausiids are the dominant food item for 30–40 cm pollock off southern Japan, while individuals >40 cm prey on juvenile pollock (Yamamura et al., 2002). Spring feeding on euphausiids appears to be a consistent trend for pollock <40 cm. In contrast, pollock >40 cm show geographic variation in the diet. Our study suggests that the northern GOA is one of the areas where all sizes of adult pollock feed primarily on euphausiids in spring.

Euphausiids persisted as the primary prey item of adult pollock in our study area in August. This is consistent with data collected in the northern GOA during the NMFS triennial groundfish surveys in the 1990s (Yang, 1993; Yang and Nelson, 2000). Euphausiids are also the primary component of the diet in the GOA east of our study area (Smith et al., 1978). However, in the western GOA, fishes other than pollock make up 80% of the diet of adult pollock (Duffy-Anderson et al., 2003). In the southeastern Bering Sea euphausiids make up the largest component of the diet of pollock >40 cm. This is similar to the northeastern Bering Sea, except that individuals >50 cm cannibalize juveniles in summer (Dwyer et al., 1987). Similarly, in the western Bering Sea euphausiids are the primary food item for pollock <50 cm, while larger adults prey on juvenile pollock and other fishes (Shuntov et al., 2000). Off northern Japan amphipods are the most frequent prey item (Kooka et al., 1998). Finally, off southern Japan mesopelagic fishes are the dominant prey item for pollock >30 cm in summer (Yamamura et al., 2002). There is a trend towards piscivory in the summer diet of adult pollock in the western GOA. Previous reports have noted that this does not appear to be the case in the northern GOA (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000). Our findings provide further evidence that euphausiids are the dominant prey item for adult pollock in summer in the northern GOA.

Amongst euphausiids, *T. spinifera* was the primary species consumed in April and August, both in terms of percent number and weight. This is in contrast with southeast Alaska and the western Bering Sea, where *T. raschii* is the primary euphausiid consumed in spring and summer, respectively (Clausen, 1983; Shuntov et al., 2000). In August, *E. pacifica* ranked second in terms of both percent number and percent wet weight in our study area. Off southern Japan, *E. pacifica* is the dominant euphausiid consumed by all age classes of pollock (Yamamura et al., 2002). These differences may be explained by the distribution and biology of the respective euphausiids. *T. spinifera* is neritic, being most abundant near shore (Brinton et al., 2000), and so would be readily available on the northern GOA shelf. In contrast, *T. raschii* occurs along the inside passages of southeast Alaska (Brinton et al., 2000), and in the Bering Sea it is particularly abundant in shallower waters (<100 m) inshore (Coyle and Pinchuk, 2002). Therefore it is not surprising that *T. raschii* would be the dominant euphausiid in southeast Alaska and in the shallow western Bering Sea. *E. pacifica* is an oceanic species found primarily in the major currents of the North Pacific, including the Oyashio (Brinton et al., 2000). Thus it might be expected that this species would be the primary euphausiid in the diet off southern Japan. In the northern GOA *E. pacifica* is most abundant on the outer shelf, but often occur in substantial densities nearshore in late summer, apparently being advected by seasonal onshore transport of sub-halocline water over the shelf (Coyle and Pinchuk, 2005; Weingartner et al., 2005).

Decapods, primarily the shrimp *P. borealis*, were the primary component of the diet of adult pollock in our study area in November, suggesting that a dietary shift occurred sometime between late August and early November. This was coincident with a shift in habitat: all pollock hauls were deeper than 100 m in November, whereas in April and August all but seven stomachs used in the diet composition analysis were from pollock caught in the upper 100 m of the water column. Shrimp are also the primary component of the diet of pollock in southeast Alaska in autumn (Clausen, 1983). However, in the eastern Bering Sea, juvenile pollock are the primary prey item for adults in autumn (Dwyer et al., 1987). In the western Bering Sea euphausiids are the primary component of the diet of adult pollock, except for individuals >50 cm, which consume primarily fish (Shuntov et al., 2000). Off northern Japan amphipods are the dominant prey item in the fall (Kooka et al., 1998). Off southern Japan mesopelagic fishes are the primary prey item for pollock >30 cm in fall (Yamamura et al., 2002). The preponderance of piscivory in other geographic areas suggests that shrimp consumption in fall may be a local trend in southeast Alaska and the northern GOA. Indeed, the only region in the GOA where levels of pandalid shrimp consumption remained high throughout the 1990s was our study area (Yang and Nelson, 2000).

Only one instance of piscivory was observed in our study. Previous reports have already noted that fish are not nearly as important in the diet of adult pollock in the northern GOA as compared with the Bering Sea (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000).

4.4. Resource selection statistics

The extreme chi-square values of our resource selection analysis left little doubt that pelagic, adult pollock in our study area were exhibiting prey selection. The chi-square tests provided in Manly et al. (2002) have also recently been used to detect significant differences between environmental and dietary distributions of prey types in marine butterflyfishes (Berumen et al., 2005).

4.5. Selection ratios

Adult pollock in our study area showed significant selection for euphausiids and decapods in April, and only euphausiids in August. The confidence intervals developed by Manly et al. (2002) have also been used to detect significant selection in a variety of other marine fishes (Lukoschek and McCormick, 2001; Berumen et al., 2005; Martinetto et al., 2005). Our findings are somewhat consistent with a study off northern Japan, where adult pollock showed positive selection for amphipods in 1 year, and euphausiids in another (Kooka et al., 1998). Amongst euphausiids, pollock in our study area showed significant selection for *T. inermis* in April and *T. spinifera* in August. Off northern Japan adult pollock showed positive selection for *T. longipes* in the year when there was overall selection for euphausiids (Kooka et al., 1998).

Studies of prey selection by juvenile pollock in the western GOA suggest an ontogenetic shift in selectivity towards euphausiids as predator size and gape width increases (Brodeur, 1998; Wilson et al., 2006). Our findings suggest that selection for euphausiids may persist throughout adult stages in the northern GOA.

Resource selection statistics are designed to detect and measure the degree to which a resource is selected for or against (Manly et al., 2002). If these techniques reveal disproportionate use or avoidance of a resource category then this provides a basis for further study of the mechanisms underlying such selectivity. A variety of factors contribute to prey selection in fishes including encounter rate, prey density, handling time, profitability, mechanical/morphological constraints, competition, predation risk, sensory modalities, hunger and learning (Hughes, 1997).

Laboratory studies have shown that juvenile pollock are capable of both visual and non-visual foraging (Ryer et al., 2002), and that a number of factors affect this behavior, including temperature (Sogard and Olla, 1996), light (Ryer and Olla, 1999), turbidity (De Robertis et al., 2003), predation risk (Ryer and Olla, 1998), social cues (Baird et al., 1991) and prey density (Ryer et al., 2002). Our resource selection analysis allows us to make inferences on the latter two factors with respect to prey selectivity by adult pollock.

When food is spatially clumped juvenile pollock forage in social groups, as this allows individuals to observe each other and rapidly aggregate at locations where food patches have been discovered (Ryer and Olla, 1992). In contrast, when food is spatially dispersed juvenile pollock forage independently, ignoring the behavior of conspecifics (Ryer and Olla, 1995). Our resource selection analysis suggests that this applies to adult pollock as well. While euphausiids often occur in horizontal patches, copepods do not, unless they are passively aggregated by eddies or frontal circulation (Coyle and Pinchuk, 2005). We found significant selection for euphausiids among the local pollock population as a whole, which corresponds to large scale group foraging. On the other hand, while copepods were selected against by the local population as a whole, the high counts of this taxon in relatively few stomachs corresponds to independent foraging by individual pollock, perhaps in the upper 20 m of the water column, where copepod abundance is highest (Coyle and Pinchuk, 2005).

Prey density affects non-visual foraging by juvenile pollock (Ryer et al., 2002). This may explain the apparent discrepancy between the mean abundances of *T. inermis* and *T. spinifera* and the selection ratios for these species. *T. inermis* form dense spawning aggregations in the spring, while *T. spinifera* spawn throughout the production season (Pinchuk, unpublished data). Thus, even though the mean abundance of *T. spinifera* was higher in April, *T. inermis* was more likely to have been encountered in dense spawning aggregations, rendering them more susceptible to large-scale predation by pollock once they were detected. Conversely, *T. spinifera* would have occurred in spawning aggregations in August, making them more susceptible to large-scale predation once they were detected, even though the mean abundance of *T. inermis* was higher at this time.

In spite of relatively small samples sizes that were limited to a single year, our findings add to the literature that geographic and seasonal variation in the diet of marine fishes must be incorporated into ecosystem-based fisheries management strategies (Hanson and Chouinard, 2002). In addition to previous work on prey selectivity by juvenile pollock (Brodeur, 1998; Purcell and Sturdevant, 2001; Sturdevant et al., 2001; Wilson et al., 2006), our resource selection analysis adds to a growing body of evidence that prey selectivity is common in marine fishes (Juanes et al., 2001; Lukoschek and McCormick, 2001; Schabetsberger et al., 2003; Berumen et al., 2005; Martinetto et al., 2005), and that such complex feeding behaviors need to be incorporated into ecosystem-based management models as well (Pinnegar et al., 2003).

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Appendix A

95% confidence limits for the diet of adult walleye pollock, *T. chalcogramma*

Prey category	April ($n = 36$)				August ($n = 43$)				November ($n = 21$)			
	%*N*		%*W*		%*N*		%*W*		%*N*		%*W*	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Amphipoda												
Byblis spp.	–	–	–	–	<0.01	0.02	<0.01	<0.01	–	–	–	–
Parathemisto libellula	–	–	–	–	0.01	0.36	0.01	0.33	0.05	0.40	<0.01	0.01
Parathemisto pacifica	0.04	0.65	<0.01	0.28	0.01	1.28	<0.01	0.16	0.46	8.62	<0.01	0.01
Parathemisto spp.	–	–	–	–	0.02	0.18	<0.01	<0.01	–	–	–	–
Primno macropa	–	–	–	–	<0.01	0.01	<0.01	<0.01	–	–	–	–
Cyphocaris challengeri	–	–	–	–	–	–	–	–	0.07	1.81	<0.01	<0.01
Unidentified Amphipoda	–	–	–	–	–	–	–	–	+	+	<0.01	<0.01
Total Amphipoda	0.03	0.65	<0.01	0.28	0.16	2.81	<0.01	0.75	<0.01	13.92	<0.01	11.51
Cephalopoda												
Berryteuthis magister	–	–	–	–	–	–	–	–	0.13	1.01	0.27	2.14
Copepoda												
Calanus marshallae	0.02	4.73	0.01	2.81	0.48	5.64	0.01	1.51	0.13	1.01	<0.01	<0.01
Candacia columbiae	–	–	–	–	–	–	–	–	0.09	0.73	<0.01	<0.01
Eucalanus bungii	<0.01	<0.01	<0.01	<0.01	<0.01	0.03	<0.01	<0.01	–	–	–	–
Metridia okhotensis	<0.01	<0.01	<0.01	<0.01	–	–	–	–	–	–	–	–
Metridia pacifica	–	–	–	–	0.01	0.19	<0.01	<0.01	–	–	–	–
Neocalanus cristatus	<0.01	<0.01	<0.01	<0.01	<0.01	0.05	<0.01	0.01	–	–	–	–
N. plumchrus/flemingeri	0.31	10.72	<0.01	1.04	0.02	0.67	<0.01	0.01	0.09	0.73	<0.01	<0.01
Pareuchaeta elongata	–	–	–	–	–	–	–	–	0.06	0.47	<0.01	<0.01
Unidentified Copepoda	+	+	<0.01	1.11	–	–	–	–	–	–	–	–
Total Copepoda	1.26	19.69	0.08	7.87	0.90	9.84	<0.01	2.00	<0.01	4.59	<0.01	3.78
Decapoda												
Cancridae megalopae	–	–	–	–	0.01	0.20	<0.01	0.05	–	–	–	–
Chionoecetes megalopae	<0.01	0.30	<0.01	0.05	–	–	–	–	–	–	–	–
Crangon communis	–	–	–	–	–	–	–	–	0.31	2.41	0.02	0.13
Pasiphaea pacifica	0.06	0.52	0.19	1.63	–	–	–	–	0.53	7.75	0.05	0.98
Pandalus spp.	–	–	–	–	–	–	–	–	+	+	0.18	8.79
Pandalus borealis	<0.01	0.02	0.10	0.83	–	–	–	–	49.98	91.35	29.37	68.02

Appendix A (*Continued*)

Prey category	April ($n = 36$)				August ($n = 43$)				November ($n = 21$)			
	%*N*		%*W*		%*N*		%*W*		%*N*		%*W*	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Pandalidae zoeae	0.12	3.60	0.01	0.76	–	–	–	–	–	–	–	–
Pinnotheridae megalopae	–	–	–	–	<0.01	0.01	<0.01	<0.01	–	–	–	–
Unidentified Caridea	–	–	–	–	–	–	–	–	+	+	16.46	46.34
Total Decapoda	0.23	7.37	0.05	5.59	<0.01	0.25	<0.01	0.05	67.39	97.26	95.86	100.00
Euphausiacea												
Euphausia pacifica	–	–	–	–	5.14	22.21	2.33	13.95	–	–	–	–
Thysanoessa inermis	7.06	30.33	5.57	21.45	0.34	4.13	0.10	2.95	0.21	1.63	<0.01	0.07
Thysanoessa longipes	–	–	–	–	0.02	0.16	0.02	0.20	–	–	–	–
Thysanoessa raschii	<0.01	0.01	<0.01	<0.01	–	–	–	–	–	–	–	–
Thysanoessa spinifera	12.90	43.62	12.51	38.23	46.22	73.78	34.96	64.05	–	–	–	–
Unidentified Euphausiacea	+	+	5.94	20.73	+	+	9.17	31.40	+	+	0.03	0.38
Total Euphausiacea	40.22	80.33	57.95	91.20	83.04	96.41	96.15	99.89	0.21	1.63	0.01	0.53
Larvacea												
Oikopleura spp.	0.15	12.71	0.65	14.13	–	–	–	–	–	–	–	–
Pteropoda												
Clione limacina	–	–	–	–	–	–	–	–	0.09	0.73	<0.01	<0.01
Limacina helicina	0.01	0.35	<0.01	0.04	–	–	–	–	–	–	–	–
Unidentified Pteropoda	–	–	0.03	0.25	–	–	–	–	–	–	–	–
Total Pteropoda	0.01	0.35	0.01	0.34	–	–	–	–	0.09	0.73	<0.01	<0.01
Stomiiformes												
Unidentified stomiiform fish	–	–	–	–	–	–	–	–	0.09	0.73	<0.01	0.02

n: number of stomachs examined. %*N*: mean percent composition by number. %*W*: mean percent composition by weight (g). +: category contained fragments that could not be enumerated. Note that back-transformed confidence limits are biased for the median may not be symmetrical around the means presented in Table 3.

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