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Food habits of Pacific cod and walleye pollock in the northern Gulf of Alaska

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ABSTRACT: Seasonal variations in the diets of Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma* were examined from fish collected during 5 sampling periods from August 1998 to June 1999 in the Kodiak Island area in the Gulf of Alaska. Both species were shown to be generalist predators, eating a wide variety of fish and invertebrates. Pollock, which are limited to pelagic prey, can be considered more specialized than cod. Cod consumed 78 prey items, and pollock consumed 45 prey items, with 28 items shared by both species. Individual pollock, however, typically concentrated on a single prey item, while individual cod stomachs contained a wider variety of prey. The principal prey of Pacific cod was Tanner crab *Chionoecetes bairdi*, comprising >28% of the cod diet by weight. The most common prey item for walleye pollock was the euphausiid *Thysanoessa.* Over the 5 sampling periods, the prey evenness and niche width occupied by the 2 species were similar, but seasonal differences were evident.

KEY WORDS: Pacific cod · Ealleye pollock · Tanner crab · Northern shrimp · predator/prey · Gulf of Alaska

INTRODUCTION

Food habits have long been an important topic in fisheries science (e.g. Faber 1829), helping to define the niche that a fish occupies (Hutchinson 1957, Sargeant 2007) and also playing a key role in the development of basic ecological theory (MacArthur & Levins 1967, MacArthur 1972, Chesson 2000). Numerous indices based on food habits have been developed which attempt to quantify and analyze the different dimensions of a species' niche such as niche overlap, niche width, and the evenness of resource use (Smith & Wilson 1996, Krebs 1999).

The present study examines the seasonal food habits of 2 co-occurring gadids, Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma*. Their diets, which have been relatively well studied across their shared range in the North Pacific (Jewett 1978, Bailey & Dunn 1979, Dwyer et al. 1987, Yamamura et al. 2002, Yang 2004, Yang et al. 2006, Adams et al. 2007, Poltev & Stominok 2008), have shown that both Pacific cod and walleye pollock (hereafter cod and pollock) are upper trophic level, generalist predators that consume a number of the same prey items (Jewett 1978, Adams et al. 2007, Aydin et al. 2007).

Standard diet indices including niche width, diet overlap, diet richness, and diet evenness were used to compare the food habits of these 2 commercially important predators. Niche width is a measure of how broad a spectrum of prey items are utilized by a predator. Diet overlap quantifies the overlap in prey items. Diet richness is simply a count of the number of different prey items consumed, while diet evenness attempts to quantify how equally prey items are targeted (Krebs 1999). This study compares cod and pollock food habits both seasonally and with ontogeny, with the goal of inferring differences in the role of these predators in the ecosystem, including their potential effects on prey populations and their relative susceptibility to ecosystem changes.

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MATERIALS AND METHODS

Data collection

The Alaska Department of Fish and Game (ADF&G) conducted 5 trawl surveys at 31 stations in Marmot Bay on the northeast corner of Kodiak Island (Fig. 1): 24–29 August 1998, 26–31 October 1998, 7–17 January 1999; 30 March–5 April 1999, and 19–23 June 1999. These sampling periods covered the full seasonal range of temperatures and reproductive cycles of predators and prey in the area. The vessel made 1 tow per station during each sampling period. Cod and pollock were captured by the ADF&G RV 'Resolution' towing a 400-Eastern otter trawl net targeting soft substrates. The net was constructed with 102 mm stretch mesh in the mouth, 89 mm stretch mesh in the body, and a 32 mm stretch mesh liner in the codend (Pengilly et al. 1999). This net catches cod and pollock approximately 5 cm in length and larger, although the catchability at size is unknown. Stomachs were collected at sea and preserved in 10% formalin and later transferred to 70% ethyl alcohol.

A total of 699 cod stomachs and 882 pollock stomachs were collected during the 5 sampling periods (Table 1). For cod 40 to 85 cm fork length (FL) and pollock 30 to 70 cm FL, significant differences were found in the size distributions between sampling periods, but the differences were <3 cm and not considered biologically important. Use of those size ranges excluded 27 cod stomachs and 54 pollock stomachs from the calculation of the diet evenness, diet richness, and niche width indices. Diet overlap was calculated for 3 size classes of fish: 20–50 cm, 51–60 cm, and 61–80 cm. Due to the small numbers of cod in the smallest category, calculation of diet overlap by sample period was not possible and only an overall value could be calculated. Seven cod stomachs and 20 pollock stomachs were excluded from the diet overlap calculations.

Fish that showed signs of either ingesting prey during the capture process or with signs of prey regurgitation were not collected. Stomach content analysis was conducted at the National Marine Fisheries Service, Alaska Fisheries Science Center's Resource Ecology and Fisheries Management Division (REFM) laboratory in Seattle, Washington (Yang 1993). Contents were identified to the lowest taxonomic level possible, and commercially important species were enumerated and measured. Predator length and sex were recorded. Wet weights of prey items were recorded to the nearest 0.1 g after the contents were blotted with paper towels.

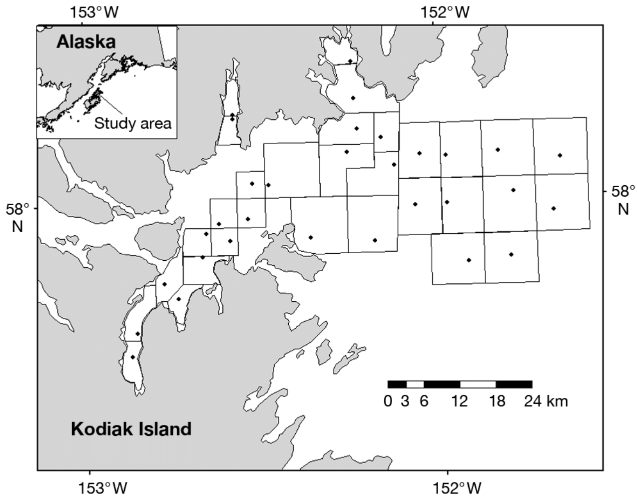


Fig. 1. Study location in Marmot Bay in the central Gulf of Alaska. The boxes indicate station boundaries; the solid dots represent the haul locations. One haul was made at each station during each of 5 sampling periods (see Table 1)

Table 1. *Gadus macrocephalus*, *Theragra chalcogramma*. Summary of sample sizes and fish lengths for cod and pollock in different sampling periods

	Sample size	Fish length (cm) Avg.	Range
24–29 Aug 1998			
Cod	136	62.5	26–86
Pollock	206	52.1	20–74
26–31 Oct 1998			
Cod	103	63.7	25–87
Pollock	185	48.7	9–87
7–17 Jan 1999			
Cod	135	64.3	10–95
Pollock	151	49.5	10–73
30 Mar–5 Apr 1999			
Cod	128	60.1	35–80
Pollock	164	50.5	24–67
19–23 Jun 1999			
Cod	103	62.8	37–84
Pollock	105	50.5	26–81
Overall			
Cod	605	61.4	10–95
Pollock	811	47.6	9–87

Data analysis

Calculations of diet overlap, niche width, diet richness, and diet evenness indices were made for each sampling period and for the entire study based on the sum of the prey weights of the individual fish. The combined prey items of both species were used to calculate the indices.

It is well known that both cod and pollock diets change with ontogeny (Dwyer et al. 1987, Yamamura et al. 2002, Yang et al. 2006, Poltev & Stominok 2008), so calculation of diet indices can be confounded if differing predator sizes are combined (Bolnick et al. 2002). Predator size distributions by sampling period were analyzed using a Kolmogorov-Smirnov test (Sokal & Rohlf 1995) to insure no significant differences existed in size distributions between periods when calculating diet evenness, niche width, and diet richness. Diet overlap was calculated for 3 different size classes of cod and pollock. Historical diet summaries (Yang 1993, Yang & Nelson 2000, Yang et al. 2006) were examined to identify the fish lengths at which shifts in diet occurred (Garrison & Link 2000).

The overlap by period between the diets of similarly sized cod and pollock were calculated using the Schoener similarity measure (Krebs 1999) as:

$$P_{jk} = \left[\sum_{i=1}^{n}(\text{minimum } p_{ij}, p_{ik})\right] \quad (1)$$

where P_{jk} is the proportion of overlap between species j and species k, p_{ij} is the proportion of the diet represented by i used by species j, p_{ik} is the proportion resource i of the total resources used by species k, and n is the total number of prey items considered. Percentage overlap has the advantage of ease of calculation and interpretation (Krebs 1999). Overlap >0.60 is considered biologically significant, overlap between 0.30 and 0.60 moderate, and overlap <0.30 low (Høines & Bergstad 1999, Guedes & Araújo 2008). A 2-sample t-test assuming unequal variances was used to determine the significance of the differences in interspecific differences in prey size.

Niche width of each species was calculated using Hurlbert's (1978) measure. He argues that the relative abundance of the prey resources, not only the proportions of the resource actually used, should be considered when calculating niche width. When proportional abundance is applied to prey use by species, the niche width can be calculated as:

$$B' = \frac{1}{\Sigma(p_j^2 / a_j)} \quad (2)$$

where B' is Hurlbert's niche width, p_j is the proportion of individuals using prey item j, and a_j is the proportion of the total prey items utilized consisting of prey item j. Variance of the estimate was calculated using the delta method (Krebs 1999). As described by Seber (1973), Smith (1982), and Krebs (1999), the delta method is a standard method for deriving standard errors based on the Taylor expansion (Odibat & Shawagfeh 2007).

Evenness and richness are 2 related components used to describe the diversity of resource use where richness is the number of resources being utilized and evenness is a measure of how equally the prey items are distributed between samples. With large sample sizes, a reasonable approximation of diet richness is simply a count of the number of prey items utilized (Krebs 1999). Evenness reaches a maximum value of 1 when the abundance values of all prey items are equally used by the population, indicating a generalist predation pattern.

$$E_{1/\hat{D}} = \frac{1/\hat{D}}{s} \quad \text{and} \quad \hat{D} = \Sigma p_i^2 \quad (3)$$

where $E_{1/\hat{D}}$ is Simpson's measure of evenness, s is the number of species in the sample, and p_i is the proportional abundance of each prey species. Values approaching zero can be interpreted as more specialized predation focusing on a limited range of prey items (Smith & Wilson 1996, Krebs 1999). In order to establish broad patterns of resource use, especially as it related to predation on crustaceans, evenness was calculated using the top 5 prey items of cod and pollock plus a grouping of all other prey items. The evenness value of the individual stomachs was used to calculate the variance of the estimate.

RESULTS

Prey composition

Cod diet overall contained a mixture of 59% benthic prey and 41% pelagic prey by weight, while pollock *Theragra chalcogramma* were limited to pelagic prey for 95% of their diet. Tanner crab *Chionoecetes bairdi* was the main prey item of cod, comprising from 20 to 45% of the diet (Fig. 2, Table 2), but they were virtually non-existent in pollock stomachs. The principal prey item of pollock was euphausiids. Those euphausiids that could be identified were primarily in the genus *Thysanoessa* (Fig. 2, Table 2). The proportion of pollock in the diets of both cod and pollock was similar at 13.5 and 15.0%, respectively, but pollock preyed on pollock almost entirely during the October sampling period, consuming fish which averaged 9.4 cm which corresponds to the size of young-of-the-year fish (Ciannelli et al. 1998). Cod preyed on pollock during all sampling periods and consumed fish that were in a broader size range, averaging 29.3 cm in length. Both species overall consumed fish other than pollock for approximately 15% of their diets, with pollock feeding mainly on Pacific sandlance, while cod fed largely on a variety of flatfish.

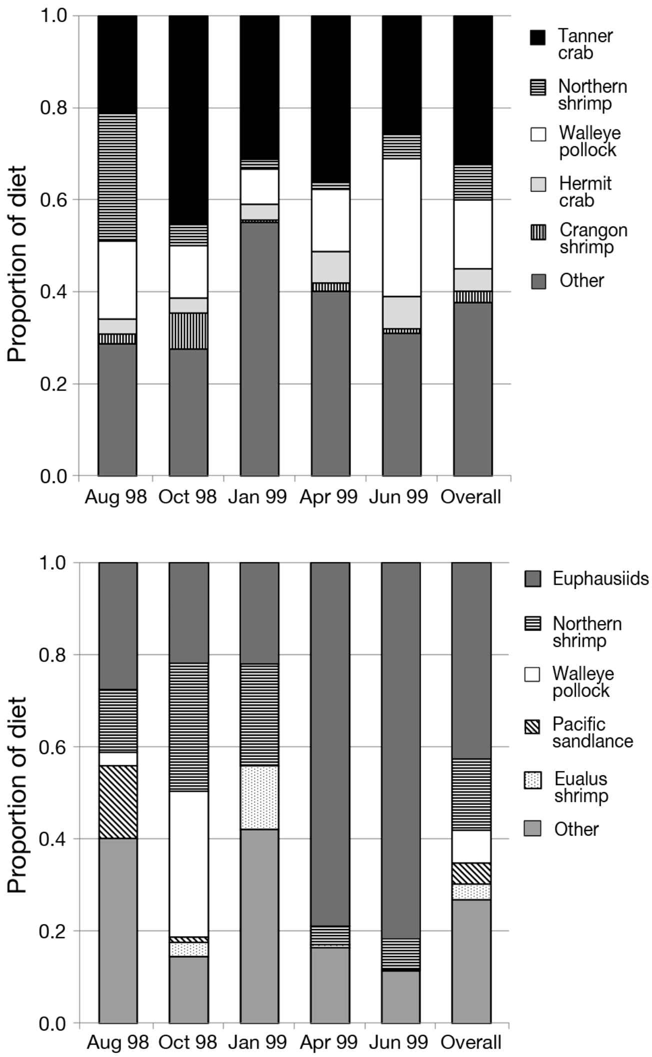


Fig. 2. *Gadus macrocephalus*, *Theragra chalcogramma*. Proportions by weight of the major diet items of cod (upper panel) and pollock (lower panel) by sampling period

Table 2. *Gadus macrocephalus*, *Theragra chalcogramma*. Percent weight of taxa and percent frequency of occurrence (FO) in the diets of cod and pollock. Only taxa which comprised >1% of the diet by weight are included

Taxon	Weight (%)	FO (%)
Cod diet		
Chionoecetes bairdi	28.3	56.9
Theragra chalcogramma	13.5	5.9
Pandalus eous	10.3	40.8
Paguridae	5.1	19.7
Crangon spp.	3.4	33.5
Caridea	2.7	19.0
Pleuronectidae	2.1	9.3
Atheresthes stomias	2.1	3.1
Aphroditidae	2.0	5.3
Lithodidae	1.9	0.4
Polychaeta	1.6	25.5
Hippoglossoides elassodon	1.6	3.4
Teleostei	1.3	11.6
Natantia	1.2	5.0
Reptantia	1.1	10.9
Pollock diet		
Thysanoessa sp.	20.1	12.7
Euphausiidae	16.0	57.7
Pandalus eous	15.3	37.4
Theragra chalcogramma	15.0	15.4
Thysanoessa spinifera	4.4	7.3
Ammodytes hexapterus	4.2	1.2
Hippolytidae	3.2	6.0
Eualus spp.	2.6	1.7
Caridea	2.5	6.1
Teleostei	1.9	4.4
Echiurus echiurus	1.5	1.1
Argis lar	1.5	0.8
Mysidacea	1.2	5.8
Crangon communis	1.1	2.6
Atheresthes stomias	1.1	0.3

The seasonal proportion of shrimp in the diet of cod and pollock showed very different patterns (Fig. 2, Table 3). During the August sampling period 47% of the cod diet by weight was shrimp, but the percentage of shrimp fell to <5% in the following periods. The proportion of shrimp in the pollock diet in August, November, and January was similar (range: 16 to 25%), but then declined when pollock concentrated on euphausiids in the April and June periods.

Overall, shrimp occurred less frequently in pollock diets than in cod diets. When pollock were consuming shrimp, however, shrimp constituted a much greater proportion of the prey items in their stomachs (Table 3). For example, in April 1999, 8% of cod were eating shrimp, which made up 6% of the stomach contents. Only 3.6% percent of pollock were eating shrimp during this period, but those shrimp represented 77% by weight of the stomach contents.

Niche indices

Cod diets (78 distinct prey items) contained greater prey richness than pollock diets(45 prey items), with 28 items shared by both species (Fig. 3). The diet overlap of cod and pollock was moderate for fish larger than 50 cm, but low in fish smaller than 50 cm (Fig. 4). Northern shrimp *Pandalus eous* was the main contributor to the diet overlap. Population niche width was significantly narrower in pollock than in cod overall (Fig. 3), indicating that cod were utilizing a broader spectrum of the available food resources than pollock.

Table 3. *Gadus macrocephalus*, *Theragra chalcogramma*. Percent of *Pandalus eous* in the diets of cod and pollock by frequency of occurrence (FO), percent of the overall diet by weight, and percent of the diet by weight of only those fish which were eating shrimp

Sampling period	FO (%) Cod	FO (%) Pollock	Diet weight (%) Cod	Diet weight (%) Pollock	Shrimp in stomach (%) Cod	Shrimp in stomach (%) Pollock
Aug 1998	81.1	9.2	47.0	16.9	53.0	68.6
Nov 1998	35.1	28.6	2.7	25.3	6.7	54.2
Jan 1999	25.6	2.0	4.0	22.3	16.8	38.3
Apr 1999	8.0	3.6	0.4	3.9	6.2	76.6
Jun 1999	10.9	12.0	3.7	6.9	38.4	27.8
Overall	43.5	14.0	11.6	14.7	36.1	50.0

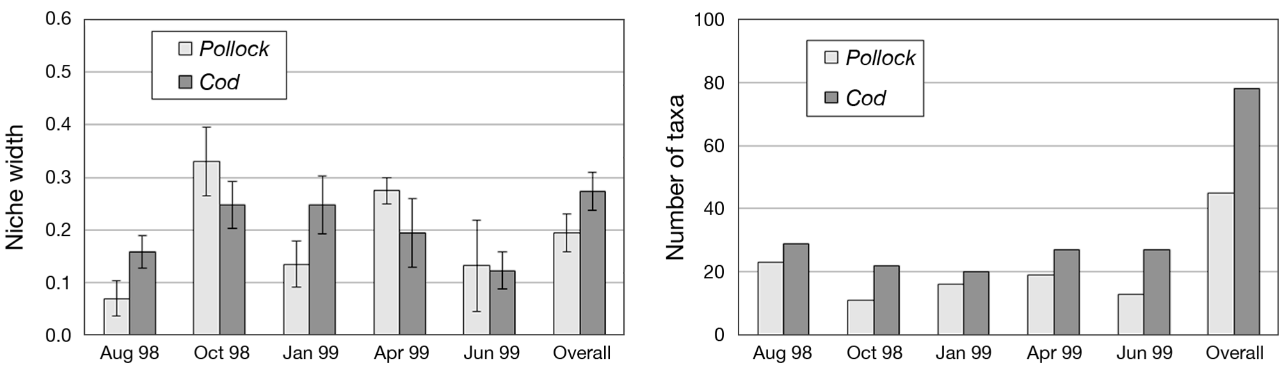
larger than 40 cm. Pollock gradually excluded their main food, euphausiids, from their diets at the largest fish sizes (Fig. 5). Shrimp, primarily northern shrimp, remained at approximately 35% by weight in the larger pollock diets, while the proportion of shrimp in cod diets declined with fish size to 5% in the largest cod (Fig. 5). The largest cod and pollock both consumed increasing proportions of pollock.

Cod and pollock also showed differing patterns of evenness of prey utilization. Simpson's measure of evenness for cod varied within a relatively small range from 0.49 to 0.58, while pollock diet evenness varied from 0.35 to 0.67, although the overall evenness measures for the 2 species were not significantly different (Fig. 3). The least even resource use occurred in April and June of 1999, when pollock were feeding almost exclusively on euphausiids (>80% of the diet).

Both cod and pollock changed their food habits with increasing size, but with somewhat different patterns. Tanner crab, the main food of cod, were consumed in relatively constant proportions by fish

DISCUSSION

Marmot Bay has a history of trawl surveys dating back to 1972; these have shown that cod and pollock coexist in all parts of the bay (Jackson 2005, Spalinger 2010). Both fish were found to consume a large variety of prey items, which is consistent with food habit studies in other parts of their range (Bailey & Dunn 1979, Albers & Anderson 1985, Kooka et al. 1998, Yamamura et al. 2002, Yang 2004, Napazakov 2008). A third of the prey items were shared by both species. The ability of these similar species to coexist appears to be at least partially based on differing foraging strategies. It is thought that the protruding



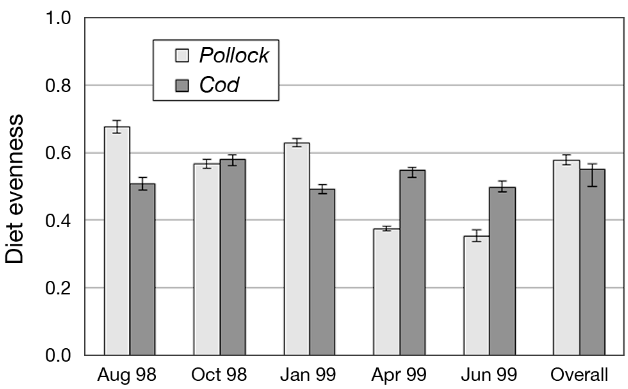


Fig. 3. *Gadus macrocephalus*, *Theragra chalcogramma*. Niche width, Simpson's measure of diet evenness, and diet richness of cod and pollock. Simpson's evenness index was calculated for the top 5 prey items, which, for Pacific cod, were *Chionoecetes bairdi*, *Pandalus eous*, *Theragra chalcogramma*, Paguridae, and *Crangon* spp. For walleye pollock the top 5 prey items were Euphausiidae, *Pandalus eous*, *Theragra chalco gramma*, *Ammodytes hexapterus*, and *Eualus* spp. Error bars represent the 95% confidence interval

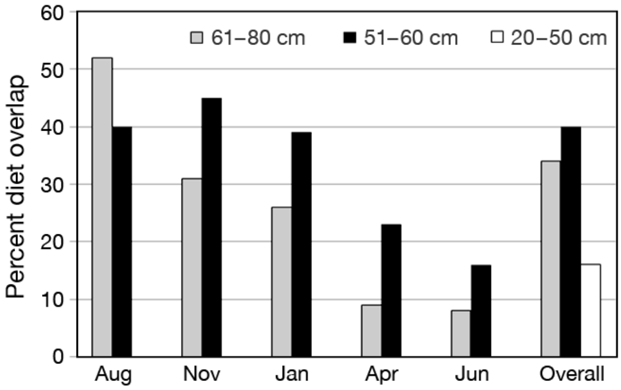


Fig. 4. *Gadus macrocephalus*, *Theragra chalcogramma*. Interspecific seasonal diet overlap between cod and pollock by fish size. Overlap of <30% is considered low; 30 to 60%, moderate; and >60%, high (Høines & Bergstad 1999, Guedes & Araújo 2008)

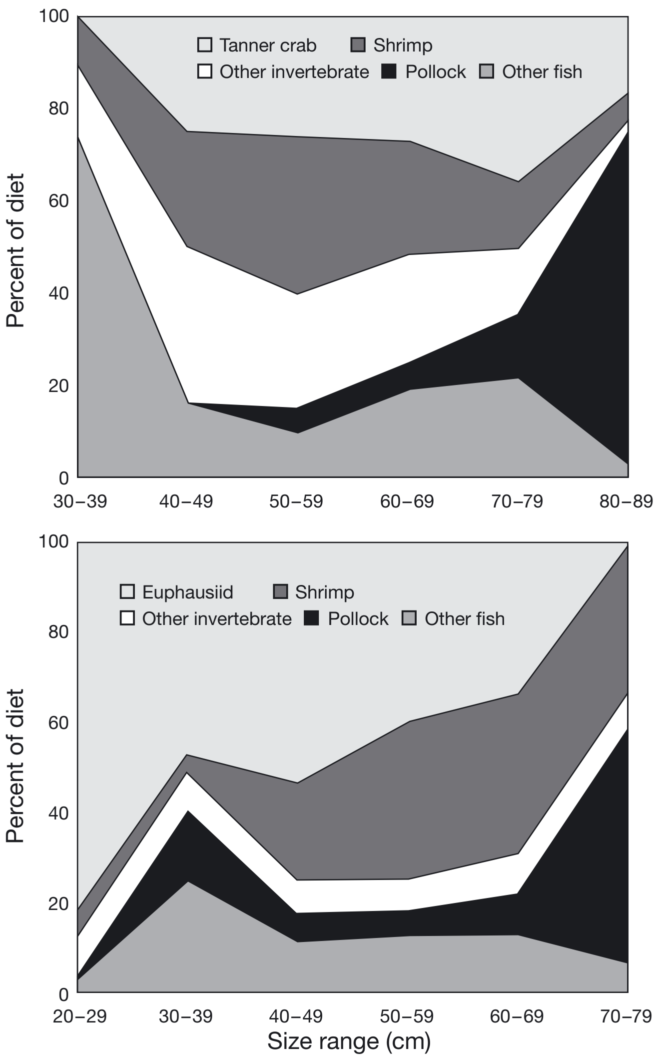


Fig. 5. *Gadus macrocephalus*, *Theragra chalcogramma*. Changes in diet by weight and fish size of cod (upper panel) and pollock (lower panel). Note differences in the size range of fish represented

lower jaw of pollock prevents them from effective benthic foraging, limiting them to a largely pelagic diet (Yamamura et al. 2002). Cod, however, are able to forage both benthically and pelagically. As larger fish, with a larger gape size, they have the ability to feed on a wider variety of prey items. While individual pollock tended to specialize on a single prey item, individual cod typically fed on a variety of prey items.

The present study confirms the findings of other studies that Tanner crab is a main prey item of cod during all seasons (Jewett 1978, Albers & Anderson 1985, Yang 2004, Yang et al. 2006, Poltev & Stominok 2008). At the same time, Tanner crab as a benthic species is virtually absent from pollock diets (Bailey & Dunn 1979, Clausen 1983, Dwyer et al. 1987, Yamamura et al. 2002, Yang 2004, Yang et al. 2006, Adams et al. 2007), although the gape size of pollock does not necessarily preclude them as a prey item. Pollock have a strong seasonal component to their diets, most notably with a spring focus on euphausiids. While euphausiids were preyed upon by pollock during all seasons, the concentration on euphausiids during the April and June sampling periods was likely due to the targeting of spawning aggregates of euphausiids which form in the northern Gulf of Alaska during these months (Pinchuk et al. 2008). Cod also preyed on euphausiids in large numbers during those periods, but the weight of euphausiids consumed was <1% of the diet. This study highlights the importance of sampling throughout the year to obtain a clear understanding of the overall diet patterns of these gadid predators.

Marmot Bay has been shown to be a productive marine environment, with species distributions that vary both temporally and spatially (Jackson 2005, Urban & Vining 2008, Spalinger 2010). The period of this study was no exception, as the North Pacific Ocean was in the midst of the 1998/1999 regime shift to a warmer environment (Curchitser et al. 2005), although it did not prove to be as strong or long lasting as the major shift in 1976/1977 (Litzow 2006). There have been no major trends in gadid populations, which have increased only slightly in recent years. There have been no strong trends either in Tanner crab or shrimp populations, which are near their 15 yr average. While there is some evidence that cod in Marmot Bay may regulate Tanner crab populations (Urban 2010), elsewhere in Alaska climate effects on crab larval survival have been used to explain crab recruitment variability (Zheng & Kruse 2006). Examination of the relationship between cod and shrimp biomass has supported the idea of the 'top-down' regulation of shrimp populations across the North Atlantic (Worm & Meyers 2003, Palsson & Bjornsson 2011). In Marmot Bay, however, there has actually been a slight positive correlation between shrimp biomass with cod and pollock biomass over the last 10 yr, so any conclusions about top-down regulation remain elusive. While the potential exists for cod to affect Tanner crab populations and for pollock and cod to impact shrimp populations, the interactions between climate, fishing, and food web dynamics in the Gulf of Alaska and other areas in the North Pacific Ocean are still poorly understood (Gaichas et al. 2011).

Both of these predators occupy a broad niche width but exhibit different foraging patterns. Cod are more generalist, with a diverse diet including relatively rare prey items, while individual pollock show a high level of specialization on a single prey category, for example, euphausiids or northern shrimp. Given their more diverse diet and ability to forage both benthically and pelagically, cod would be expected to be more resilient to changes in the marine community of Marmot Bay (Smith et al. 2011), while pollock could be more drastically affected by a collapse in the shrimp or euphausiid populations. The possibility remains, however, given the diversity of pollock prey items throughout their range, that changes in the marine community could make more prey species available to pollock.

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