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The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific

Jeffrey C. Drazen^{a,*}, Troy W. Buckley^b, Gerald R. Hoff^b

^a*Scripps Institution of Oceanography, University of California, San Diego, Marine Biology Research Division, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA*

^b*National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Seattle, WA 98115-0070, USA*

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Abstract

The diet of slope dwelling macrourid fishes in the eastern North Pacific is poorly known. We collected several hundred stomach samples to investigate the feeding habits of *Coryphaenoides acrolepis* and *Albatrossia pectoralis*, the two dominant slope dwelling macrourids off the continental United States. *Coryphaenoides acrolepis* exhibited a pronounced ontogenetic shift in diet. Specimens < 15 cm pre-anal fin length (PAF) consumed primarily polychaetes, amphipods, cumaceans and mysids, while larger individuals consumed increasingly larger, more pelagic prey such as fish, squid, and large crustaceans. Scavenging was also very important to specimens > 15 cm with scavenged food constituting approximately 20% of the weight of total prey and occurring in approximately 20% of fish 21–29 cm. *Albatrossia pectoralis* consumed primarily midwater fish and squid, and we believe that it feeds in the water column. There were significant differences between the diets of *A. pectoralis* and *C. acrolepis* suggesting some degree of niche separation between macrourid species on the continental slope of the eastern North Pacific. Both species are at the top of the food web on the upper continental slope and, because of their abundance, may exert significant pressures on their prey populations. © 2000 Elsevier Science Ltd. All rights reserved.

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* Corresponding author. Fax: + 001-619-534-7313.

E-mail address: jdrazen@ucsd.edu (J.C. Drazen).

1. Introduction

Macrourid fishes are among the dominant fishes in the deep sea (Marshall and Iwamoto, 1973; Stein and Percy, 1982; Wakefield, 1990; Merrett, 1992; Lauth, 1998). Many species are large and, in combination with their abundance, are potentially important apex predators in the deep-sea environment. Apex predators play a vital role in many communities by controlling prey populations, exerting selective pressure, and influencing general community dynamics. Despite their potentially important role, little is known of the feeding habits of most macrourids, primarily because of the difficulty of collection in the remote deep sea. Additionally, macrourids brought to the surface from great depths have a high frequency of stomach eversion as their large gas bladders expand with decreasing pressure.

Despite sampling problems, the diet compositions of five macrourid species in the eastern Pacific (Percy and Ambler, 1974; Hoff et al., 2000), seventeen species in the Atlantic (Haedrich and Henderson, 1974; Geistdoerfer, 1975; Mauchline and Gordon, 1984; Crabtree et al., 1991; Martin and Christiansen, 1997), and four species in the Mediterranean (Geistdoerfer, 1975; Macpherson, 1979) have been described in some detail. In these studies the problem of stomach eversion was overcome by capturing many fish, so that a reasonable subset would have intact stomachs. From these data, most macrourid species were described as generalist predators, but at least a few species were found to specialize to some degree on infaunal, epibenthic, or benthopelagic prey (Macpherson, 1979; Mauchline and Gordon, 1984, 1986).

Several species of macrourids have been photographed quickly arriving at bait, which suggests that these fish are also scavengers (Isaacs and Schwartzlose, 1975; Priede et al., 1991; Thurston et al., 1995). Studies of macrourid gut contents, from specimens collected in the eastern Pacific (Percy and Ambler, 1974) and the Atlantic (Haedrich and Henderson, 1974; Martin and Christiansen, 1997), showed that large specimens of several species consumed items of neritic origin and parts of squid and fish larger than themselves, further suggesting a scavenging lifestyle. It has been suggested that in the relatively food-poor deep sea, generalized feeding habits are common and scavenging may be an important means of meeting energy requirements (Dayton and Hessler, 1972; Haedrich and Henderson, 1974; Sedberry and Musick, 1978). A scavenging feeding mode also suggests a direct energetic link between the epipelagic zone and these deep-sea fishes. Consumption and later defecation of carcasses could redistribute large amounts of organic matter in this relatively food-poor environment (Dayton and Hessler, 1972; Priede et al., 1991, 1994). No studies to date have quantitatively assessed the importance of scavenging as a feeding mode for macrourids.

This study describes the feeding habits of *Coryphaenoides acrolepis* and *Albatrossia pectoralis*, two very common and abundant macrourids inhabiting the continental slope in the eastern North Pacific, addresses what factors affect their diets, and quantitatively determines the importance of scavenging in their diets. *Coryphaenoides acrolepis* typically is the most abundant macrourid on the continental slope of the contiguous United States and is distributed from Baja California to the Bering Sea and to Japan at depths between 600 and 2500 m (Iwamoto and Stein, 1974). *Albatrossia pectoralis* is another dominant macrourid species on the continental slope of the eastern North Pacific Ocean. This species is distributed from southern California to the Bering Sea and to Japan at depths between 200 and 2170 m, but it is more abundant north of California (Iwamoto and Stein, 1974; Novikov, 1970).

Despite their broad distributions and considerable relative abundance little is known of the feeding habits of *C. acrolepis* and *A. pectoralis*. Percy and Ambler (1974) examined the stomach contents of fewer than a dozen specimens of both species, and the diet of 33 specimens of *C. acrolepis* and 29 of *A. pectoralis* from off the coast of Oregon and Washington was described by Buckley et al. (1999). These sample sizes were insufficient to describe dietary breadth, ontogenetic diet shifts, and geographical variation in diet. The diet of *A. pectoralis* from the Bering Sea and Aleutian Islands was investigated from hundreds of samples, but only occurrence data was collected, limiting any meaningful conclusions about which prey were energetically important (Novikov, 1970).

2. Methods

2.1. Sample collection and processing

The majority of the stomach samples used in this study came from fish collected during the NMFS slope survey between 24 October 1997 and 24 November 1997. This survey employed a Nor'eastern bottom trawl with a 37.4 meter footrope to sample between 188 and 1260 m from Pt. Conception, California (34.5°N), to the US/Canadian border (48°N). All *C. acrolepis* and *A. pectoralis* were sorted from the catch and, when limited by time, random subsamples were examined. Fish with everted stomachs were discarded. Partial regurgitation was detected by looking for stomach content material caught in the mouth or on the gill rakers of the fish. Stomachs from fish that showed no signs of regurgitation were excised and placed in separate cloth sample bags that were immersed in 10% buffered formalin. Small fish were preserved whole as a group. The sex and pre-anal fin lengths (PAF) of all specimens were recorded.

In the laboratory, stomach samples were removed from formalin and soaked in water for one to two days before processing. Each stomach was cut open, and the food bolus was removed and weighed to the nearest 0.01 gram in the case of *C. acrolepis* and nearest 0.1 g for *A. pectoralis*. Small *C. acrolepis* consumed very small prey, which necessitated the higher measurement precision. The weight of food as a percent of body weight was calculated to give a quantitative estimate of fullness. Body weights were estimated from PAF–weight regressions (Lauth, 1998). After weighing, prey items were separated by prey taxon and state of digestion. The wet weight and number of individual prey were counted for each group. Prey from taxa that were difficult to identify were sent to appropriate taxonomists for specific identification or verification. Estimates of the size of squid prey were made using regressions based on beak size (Clarke, 1986; Wolff, 1984), and estimates of the size of fish were made from head lengths (Baxter, unpublished data). The digestive state of all prey items was noted to determine if net feeding had occurred.

In addition to the trawl sampling, *C. acrolepis* were collected from the San Diego Trough (1170 m) between June 1997 and November 1998 using a series of free vehicle tube traps. The trap array consisted of ten tube-shaped traps (Fig. 1). Each trap captured a fish by pulling it inside the tube via a spring-loaded hook and then closing a trap door. If a fish egested its stomach contents the trap retained the egested material. Upon recovery, the trap drained through holes fitted with 300 µm nitex screen. Some loose or very digested gut content material may have been

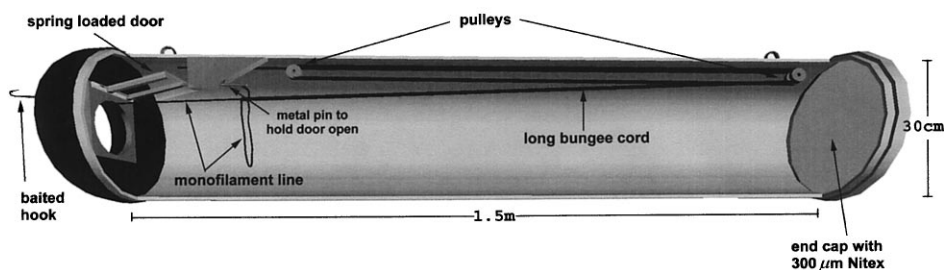


Fig. 1. Tube trap used to capture macrourids from the San Diego Trough.

lost through the screen, but all identifiable remains were retained and preserved in 10% buffered formalin. The stomach of each fish was removed, and any material remaining in the stomach was preserved with the trap material. These samples were analyzed in the same manner as the trawl samples.

2.2. Data analysis

Cumulative prey curves were used to determine if enough specimens had been sampled to accurately describe the diversity of the diet of each species (Cailliet et al., 1988). Curves were constructed by plotting the number of prey taxa versus cumulative number of stomachs. Stomach content data were sampled from the data set without replacement, and 500 iterations of this procedure were used to generate an average number of prey taxa for a given number of stomachs.

The percent frequency of occurrence (%FO), percent contribution to the total number of prey (%N), and percent contribution to the total weight of the prey (%W) were determined for each prey group. Often we were unable to identify digested remains beyond family or genera, which artificially increased the number of taxa (i.e. *Gnathophausia* sp. and *Gnathophausia ingens*). As a result, prey taxa were grouped into higher taxonomic categories for analysis. To help elucidate foraging behavior, prey taxa also were grouped into nine broad functional categories (infauna, small epifauna, large epifauna, micronekton, macronekton, fish, squid, scavenged material, and unidentified remains) based on known natural history information.

The effects of size, sex, depth, season and area of capture on the numeric and gravimetric composition of the diet were determined by comparing groups using a percent similarity index (PSI; Schoener, 1970; Hurlbert, 1978; Cailliet and Barry, 1979). The %FO, %N, and %W of groups also were compared using a Spearman nonparametric rank correlation test (Fritz, 1974). For the latter, many rare prey groups can drive the regression near the origin and lead to many correlations without biological meaning. To reduce the effect of rare species on the correlations only taxa that constituted greater than 10% FO, 5% N, or 5% W were included. Kruskal-Wallis ANOVA was used to compare differences in the number or weight of a particular prey category or in stomach fullness amongst groups. Mann Whitney *U*-tests were used to compare differences between two groups.

The diets of *C. acrolepis* and *A. pectoralis* were compared using the same methods between fish of the same size. To make sure the fish that we compared were foraging in the same locations we also compared only those specimens that were captured concurrently in the same trawls.

3. Results

3.1. General diet and size-related effects

Almost all of the approximately 14,000 macrourids captured during the slope survey were examined. *Coryphaenoides acrolepis* were captured from 605 to 1253 m and *A. pectoralis* from 611 to 1260 m. A total of 407 *C. acrolepis* and 304 *A. pectoralis* showed no signs of regurgitation and had food in their stomachs, so they were used in this diet analysis. Another 55 *C. acrolepis* and 312 *A. pectoralis* showed no signs of regurgitation but had empty stomachs. The tube traps deployed in the San Diego Trough (1170 m) captured 33 *C. acrolepis* with food and two *C. acrolepis* and one *A. pectoralis* with empty stomachs (no food present in the traps). Although the traps caught few fish, they were important because they captured most of the large specimens. Of the 407 *C. acrolepis* specimens captured from the trawls, only 24 were greater than 20 cm whereas all but two specimens captured in the tube traps were of this size.

The prey from the stomach contents of *C. acrolepis* were separated into 110 prey categories, and 67 categories were found in the *A. pectoralis* stomachs. These categories were placed into higher taxonomic groups creating 54 and 30 prey types respectively for the analysis (Tables 1 and 2).

Our prey accumulation curves allowed us to determine the adequacy of the sampling for a general description of diet. For *C. acrolepis*, the prey diversity for most size groups (see below) was well represented as indicated by each curve approaching an asymptote (Fig. 2a). However, for the two largest size groups few specimens were available and the diet may not be as comprehensively described. The steepness and potential asymptote increase with size for *C. acrolepis*, but prey diversity appears to be low for the largest size class. For *A. pectoralis*, prey diversity was much lower than for *C. acrolepis* (Fig. 2b). The prey accumulation curves for 13–15 cm ($n = 15$) and 26–41 cm ($n = 17$) *A. pectoralis* do not level off, suggesting the diet breadth of these groups may not be very well described (Fig. 2b).

We attempted to determine seasonal variation in the diet of *C. acrolepis* from our collections in the San Diego Trough, but inadequate sample sizes, 5–9 specimens per collection period, precluded a meaningful analysis.

To assess the effects of size on the diet of each species, samples were grouped by PAF. After testing 2, 3, 4, and 5 cm size groups, we selected roughly 5 cm categories, yielding six groups for *C. acrolepis* and four groups for *A. pectoralis* (Tables 1 and 2). This grouping allowed sample sizes sufficient for robust statistical tests while providing enough groups to examine size-related changes in diet. For each of these size groups the diets of males and females were significantly correlated ($p < 0.01$), indicating similar diets, so sex was not considered a factor for the rest of the analysis.

The range of means of *C. acrolepis* stomach fullness by size group was 0.65–1.04% of body weight (bw), and the means were not significantly different (ANOVA, $p = 0.63$; Table 1), but diet composition changed dramatically with size. Using either the numerical or gravimetric composition of the prey taxa PSI values typically declined as the difference in fish size increased, indicating a decline in food overlap (Table 3). The diets of all neighboring size groups and of fish 2–20 cm apart were significantly correlated ($p < 0.05$) with regard to frequency of occurrence and relative number. However, when relative weight was used the only significant correlations were between 2–5 cm and 6–10 cm fish and between 16–20 cm and 26–29 cm fish (Table 3). The changes in diet with size can be seen with a variety of taxa (Fig. 3). Microcrustaceans (amphipods, calanoids,

Table 1
Percentage frequency of occurrence (FO), percentage of the total number of prey (N) and percentage of the total weight of the prey (W) for each size category (PAF) of *C. acrolepis*^a

Size class (PAF)	Prey category	Group	2–5 cm			6–10 cm			11–15 cm			16–20 cm			21–25 cm			26–29 cm		
			% FO	% N	% W	% FO	% N	% W	% FO	% N	% W	% FO	% N	% W	% FO	% N	% W	% FO	% N	% W
Nematoda		Infaua				1.01	0.04	0.00				1.33	0.09	0.10	2.33	0.25	0.14			
Polychaeta		Infaua	28.92	2.69	10.69	60.61	4.29	18.83	56.59	6.85	16.65	36.00	4.60	4.65	4.65	0.75	0.36			
		s. epi.				4.04	0.53	0.60	1.55	0.09	0.02	2.67	0.18	0.02						
Gastropoda		Infaua	1.20	0.10	0.03	1.01	0.04	0.00	5.43	0.45	0.90	4.00	0.36	0.04						
Bivalvia		Infaua										1.33	0.09	0.01						
Scaphopoda		l. epi.																		
Cephalopoda		Squid				5.05	0.48	0.06	12.40	1.00	0.55	14.67	1.17	1.79	9.30	1.24	2.78	27.27	4.41	0.28
remains																				
Unidentified squid beaks		Squid				15.15	0.92	0.42	37.21	5.99	1.04	48.00	8.39	0.85	53.49	12.69	1.23	27.27	8.82	0.47
<i>Chiroteuthis</i> sp.		Squid										5.33	0.36	0.07	2.33	0.50	0.06			
Cranchiidae		Squid							0.78	0.05	0.15	2.67	0.27	0.07	2.33	0.25	0.09	9.09	2.94	0.45
Gonatidae		Squid										9.33	0.72	1.86	4.65	1.49	0.04			
<i>Histeoteuthis</i> sp.		Squid										2.67	0.18	14.72				9.09	1.47	21.93
<i>Ocototeuthis</i> sp.		Squid										9.33	1.26	7.59	4.65	0.50	0.03	9.09	1.47	0.07
Octopoda		Squid				1.01	0.48	0.02	2.33	0.41	0.26	2.67	0.54	0.04	2.33	0.75	0.01			
<i>Vampyroteuthis infernalis</i>		Squid							4.65	0.27	0.13	10.67	1.17	0.15	16.28	2.49	0.71			
Unidentified		Unident	85.54	7.45	21.87	81.82	3.68	20.99	78.29	4.72	7.34	52.00	3.52	1.67	60.47	6.47	1.54	36.36	5.88	1.11
Crustacean remains																				
Ostracoda		Micro				1.01	0.04	0.01	0.78	0.05	0.00									
Copepoda		Micro										1.33	0.09	0.00						
Calanoida		Micro	31.33	8.39	5.93	20.20	5.25	1.62	9.30	0.68	0.03	8.00	1.08	0.01	4.65	0.50	0.01			
Harpacticoida		Infaua							0.78	0.05	0.00									
Leptostraca		Micro				1.01	0.04	0.01	1.55	0.09	0.01									
Mysidacea		Micro	56.63	9.83	11.72	65.66	9.37	5.31	57.36	15.92	2.23	32.00	5.77	0.31	9.30	1.74	0.03			
<i>Gnathophausia</i> sp.		Macro										5.33	0.36	3.94	27.91	3.48	7.09	36.36	5.88	6.52
Cumacea		Micro	28.92	12.63	5.25	33.33	18.91	2.08	42.64	9.80	0.40	28.00	4.15	0.04	6.98	1.74	0.01			
Tanaidacea		s. epi.	1.20	0.10	0.01															
Isopoda		s. epi.	10.84	1.97	3.73	19.19	2.76	3.77	19.38	4.94	3.17	13.33	14.97	1.75	4.65	5.47	0.86	18.18	2.94	0.03
Amphipoda		Micro	78.31	39.03	23.34	88.89	34.50	9.87	65.12	22.49	2.38	50.67	19.48	0.49	20.93	8.46	0.13			
Euphausiacea		Micro	4.82	0.52	0.63	5.05	0.31	0.34	10.85	1.09	0.28	22.67	2.80	0.31	6.98	1.00	0.01			
Unidentified Decapoda remains		Unident				1.01	0.04	0.01	5.43	0.32	0.78	4.00	0.27	0.46	11.63	1.24	0.04	9.09	1.47	0.04
Unidentified shrimp		Unident	2.41	0.21	0.80	10.10	0.48	1.81	5.43	0.54	0.54	4.00	0.27	0.37	4.65	0.50	0.30	27.27	4.41	0.21
Sergestidae		Macro							2.33	0.14	0.63	6.67	0.63	0.15						
<i>Bentheogenemema</i> sp.		Macro													2.33	0.25	0.65			

Table 2
Percentage frequency of occurrence (FO) of the total number of prey (N) and of the total weight of the prey (W) for each size category (PAF lengths) of *A. pectoralis*^a

Size class (PAF) Prey category	Group	13–15 cm			16–20 cm			21–25 cm			26–41 cm		
		% FO	% N	% W	% FO	% N	% W	% FO	% N	% W	% FO	% N	% W
Nematoda	Infauna				0.52	0.52	0.01						
Cephalopod remains	Squid	6.67	6.45	9.02	1.04	0.34	0.01	1.25	0.36	0.03			
Unidentified squid beaks	Squid	46.67	45.16	22.54	56.77	43.28	2.25	46.25	35.23	1.13	29.41	11.90	0.05
<i>Aburropsis</i> sp.	Squid				1.04	0.34	0.01						
Cranchiidae	Squid				0.52	0.17	0.65	2.50	0.71	3.61			
Gonatiidae	Squid	13.33	12.90	8.03	24.48	17.93	76.95	21.25	7.12	36.24	11.76	4.76	11.29
<i>Histeoteuthis</i> sp.	Squid				1.56	0.52	0.03	1.25	0.36	0.00			
<i>Octopoteuthis</i> sp.	Squid				4.69	1.55	3.98	10.00	3.20	14.62			
<i>Vampyroteuthis infernalis</i>	Squid	6.67	3.23	0.90	3.65	1.55	0.14	22.50	8.54	2.22	5.88	2.38	0.04
Unidentified Crustacean remains	Unident.	6.67	3.23	1.80	4.17	1.38	0.04	12.50	3.56	0.12			
Mysidacea	Micro				0.52	0.52	0.01	1.25	0.71	0.01	11.76	4.76	0.01
<i>Gnathophausia</i> sp.	Macro				3.13	1.03	3.75	5.00	1.42	0.84			
Isopoda	s.epi							1.25	0.36	0.05	5.88	2.38	0.00
Amphipoda	Micro	6.67	3.23	8.12	4.17	1.90	0.07	3.75	1.07	0.02			
Euphausiacea	Micro				0.52	0.17	0.01	1.25	0.36	0.00	5.88	2.38	0.00
Unidentified shrimp	Unident.				0.52	0.17	0.01	1.25	0.36	0.00			
Sergestidae	Macro				2.60	1.21	1.75	2.50	0.71	0.50	5.88	2.38	0.08
Pasiphaeidae	Macro												
Hippolytidae	Lepi	6.67	3.23	4.51									
<i>Stereomastis sculpita</i>	Lepi				0.52	0.17	0.70						
Ophiuroidea	Lepi				0.52	0.17	0.00	2.50	0.71	0.01			
Asciacea	Lepi										5.88	2.38	0.97
Fish remains	Fish	20.00	9.68	9.02	31.77	14.48	2.52	48.75	18.15	13.15	82.35	50.00	12.89
midwater fish	Fish				7.29	2.41	3.64	10.00	2.85	10.10			
<i>Coryphaenoides</i> sp.	Fish				0.52	0.17	0.48				5.88	2.38	1.07
<i>Merluccius productus</i>	Fish							3.75	1.07	9.75	5.88	2.38	5.01
Scavenged material	Scav.							2.50	0.71	14.42	5.88	2.38	67.77
Unidentified prey	Unident.	6.67	3.23	0.90	2.08	0.69	0.54	1.25	0.36	0.04			
Unidentified organic material	Unident.	20.00	9.68	35.17	23.96	7.93	2.07	35.00	9.96	2.78	5.88	2.38	0.52
Sediment	Unident.				3.65	1.38	0.41	7.50	2.14	0.35	17.65	7.14	0.25
Mean stomach wt (% body wt)		0.02	±	0.02	0.40	±	1.95	0.83	±	2.13	0.88	±	2.57
Total stomachs with food (empty)		15 (27)			192 (226)			80 (50)			17 (9)		
Total number of prey items		31			580			281			42		
Total prey weight							713.58			954.94			491.95
PSI		24	28	1.11	32	17		50	41		36	38	

^a Prey categories were grouped as described in the methods section. The column “group” identifies the functional group that each prey category was assigned to (abbreviations are as for Table 1). Percent similarity indices (PSI) are shown at the bottom of the table for comparisons with *C. acrolepis* of the same size.

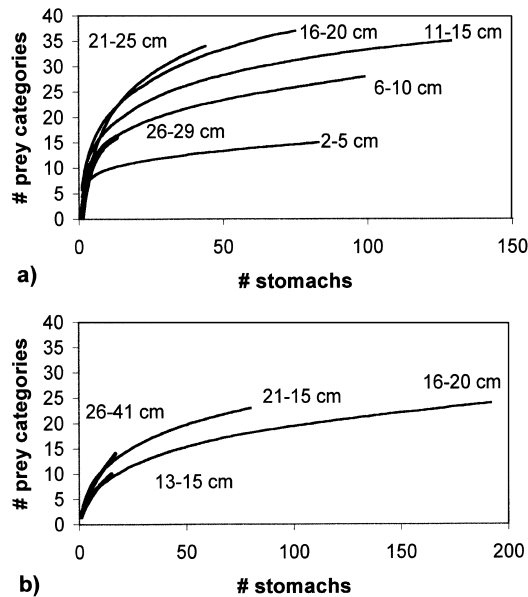


Fig. 2. Cumulative prey taxon curves for each size group of (a) *C. acrolepis* and (b) *A. pectoralis*.

cumaceans, and mysids) declined in frequency (Fig. 3a) while fish, squid and the large bathypelagic mysid *Gnathopausia* increased in frequency with size (Fig. 3b). Juvenile tanner crabs, *Chionoecetes* sp. (carapace width 5.0–16.2 mm), isopods, euphausiids, and polychaetes all showed the greatest frequency of occurrence in medium sized fish between 6 and 20 cm (Fig. 3c). These trends are generally reflected in the relative weight of each prey taxon. The relative weight of microcrustaceans declines (Fig. 3d), but epifaunal isopods also follow this trend (Fig. 3f). Polychaetes and *Chionoecetes* sp. have peaks in relative weight for intermediate-sized fish, and while euphausiids had a greater frequency for 11–15 cm fish, their contribution by weight is consistently minimal (Fig. 5f). The contribution by weight of fish, squid, *Gnathopausia* sp., and scavenged material all increased with size (Fig. 3e), but these changes are somewhat sporadic compared to the smooth changes seen in frequency of occurrence (Fig. 3b).

The range of means of *A. pectoralis* stomach fullness by size group was 0.02–0.88% bw (Table 2). Variances were very large, and the means were not significantly different (ANOVA, $p = 0.24$), but diet composition exhibited some change with size. Again PSI declined as the size difference between the groups increased (Table 3). With respect to frequency of occurrence and relative number the diets of 13–25 cm individuals were not statistically different ($p < 0.05$). No two groups showed a significant correlation with each other when compared using relative weight (Table 3). The frequency of occurrence of the major prey groups does not change with size in *A. pectoralis* as much as for *C. acrolepis*. However, it is apparent that the relative frequency of unidentified squid declines somewhat in larger *A. pectoralis* at the same time that the frequency of occurrence of fish prey increases (Table 2). The relative frequency of scavenged material also increased with size while that of midwater fishes and *Vampyroteuthis infernalis* was greatest for 21–25 cm fish. The relative weight

Table 3
PSI between size groups for both species^a

PAF	2–5	6–10	11–15	16–20	21–25	26–29	PAF	13–15	16–20	21–25	26–41
<i>C. acrolepis</i>											
2–5	■	85	68	51	37	25 % number	<i>A. pectoralis</i>	13–15	■	80	31 % number
6–10	68	■	71	55	36	25		16–20	16	■	38
11–15	39	48	■	72	52	36		21–25	16	■	46
16–20	21	22	42	■	61	42		26–41	18	35	■
21–25	10.71	18	47	55	■	65			% weight		
26–29	5.26	7.46	30	63	66	■					
	% weight										

^a Indices comparing the numbers of prey are above and indices comparing the weight of prey are below the diagonal. Shaded values indicate that the diet of the two groups was significantly correlated ($p < 0.05$). Bordered values indicate that the diet of the two groups was significantly negatively correlated.

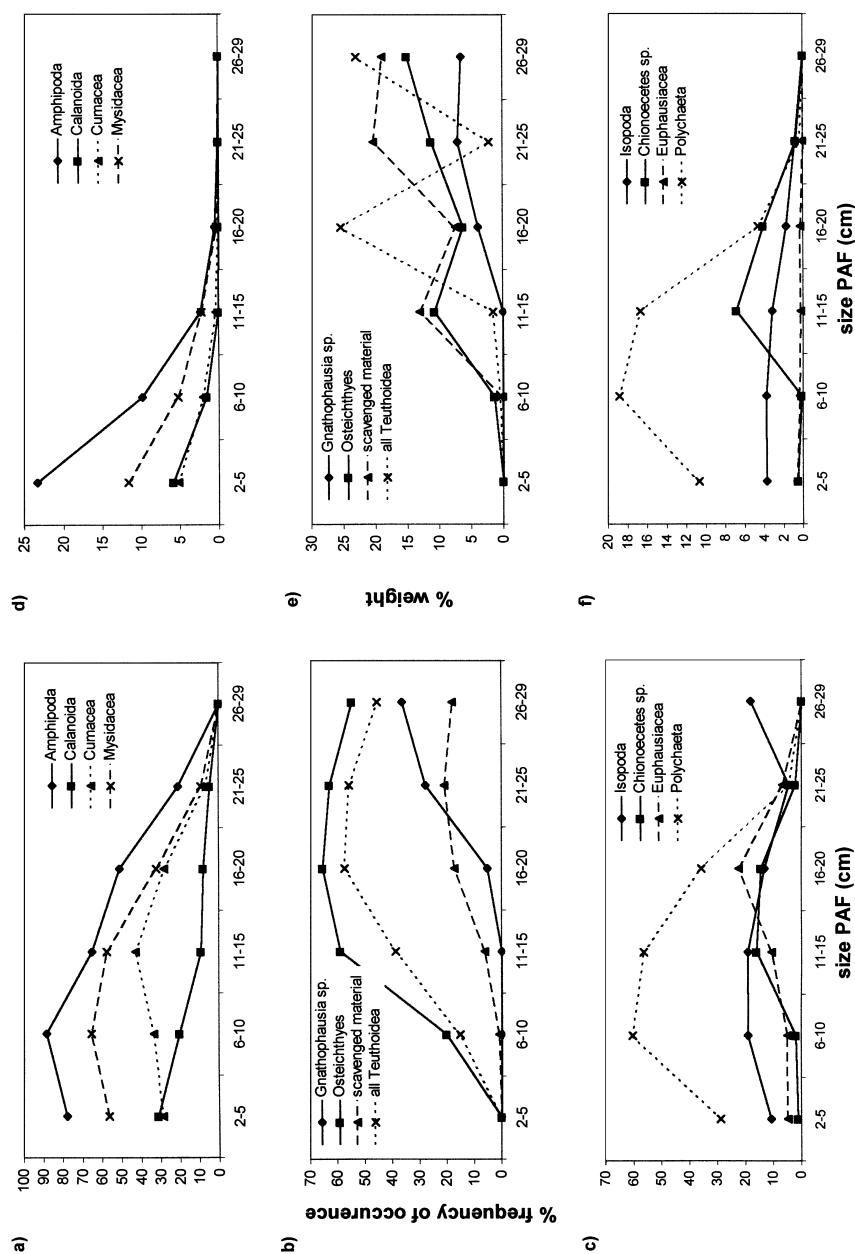


Fig. 3. Size-related changes in the frequency of occurrence (%FO) and weight (%W) of major prey taxa of *C. acrolepis* are shown for (a) groups whose %FO declines, with size, (b) groups whose %FO increases with size, (c) groups whose %FO peak at intermediate sizes and ((d)–(e)) those groups corresponding changes in %W. Note that the data are categorical but were presented as lines to clearly show changes in prey composition.

of prey taxa generally did not change with size. The exceptions are the exceedingly high contribution of gonatid squid to 16–20 cm fish and the high contribution of scavenged material for the largest size group of *A. pectoralis* (Table 2). These data are the result of a diet punctuated by occasional large prey items as evidenced by the variability in the mean stomach content weight (Table 2). Two very large gonatid squid were found in the stomachs of two 16–20 cm fish and two very large skulls (head lengths 11 and 14 cm) of *Merluccius productus*, Pacific hake, were found in two *A. pectoralis*, 24 and 30 cm PAF. The hake skulls were determined to be fisheries offal by the presence of cleanly severed vertebrae at the base of the skull.

3.2. Functional groups

Distinct changes with size occurred in the functional types of prey consumed by *C. acrolepis*. The functional groups to which the prey categories were assigned are given in Tables 1 and 2. The smallest *C. acrolepis* predominantly preyed upon micronekton and infauna (Fig. 4a–c). The primary micronekton are amphipods, small mysids, cumaceans and calanoid copepods. Cumaceans are normally infaunal (Gage and Tyler, 1991), but identification of the specimens from this study showed that the individuals consumed by *C. acrolepis* were almost entirely males equipped with appendages for swimming, suggesting that few were picked out of the sediments (L. Watling, pers. comm.). The infauna group consisted primarily of polychaetes, which were difficult to identify. The most common identifiable polychaetes were onuphids (C. Martin and L. Harris, pers. comm.), tube-dwelling polychaetes that often protrude above the sediment surface (Fauchald and Jumars, 1979). Onuphids represented ~10% of the numbers and weight of polychaetes and were assigned to the small epifauna functional group. Infauna and micronekton declined in importance with predator size at the same time that larger, often more mobile prey such as macronektonic crustaceans, fish, and squid became predominant. These trends are evident from both the frequency of occurrence and the relative weight of the taxa (Fig. 4a–c). The relative frequency of small epifauna, primarily isopods, remains fairly constant with fish size (Fig. 4b) but the frequency of large epifauna, such as crabs and large benthic shrimp increases (Fig. 4a). The weight contribution of small epifauna remains consistent up to 16–20 cm *C. acrolepis* where it begins to decline. The relative weight of large epifauna increase slightly with fish size and then declines again with fish > 20 cm (Fig. 4c).

Scavenged material appeared in the diet of *C. acrolepis* in specimens > 10 cm. Its frequency of occurrence and relative weight both increase with increasing fish size (Fig. 4a and c). Scavenged material was composed of a variety of food items that were most likely not consumed as living prey. Such material included (1) fishery offal, (2) epipelagic fishes (mainly clupeids but also *Scomber japonicus*) whose vertical depth range is far above that of either macrourid species, (3) fish and squid that were determined by the size of their remains to be as large or larger than the fish that ate them, (4) overboard material such as broccoli, cantaloupe, and onion peels, and (5) algae. The latter two components made up a relatively small fraction of this category.

The diet of *A. pectoralis* was dominated by fish and squid (Fig. 4d–f). Squid were consistently frequent and dominated the diet by weight for all sizes except for the largest fish (26–41 cm PAF), where scavenged material becomes the most important, primarily due to a large scavenged hake head. The relative frequency of fish prey increased with predator size, but the relative weight remained fairly constant with size (Fig. 4d and f). With the exception of a single nematode, no

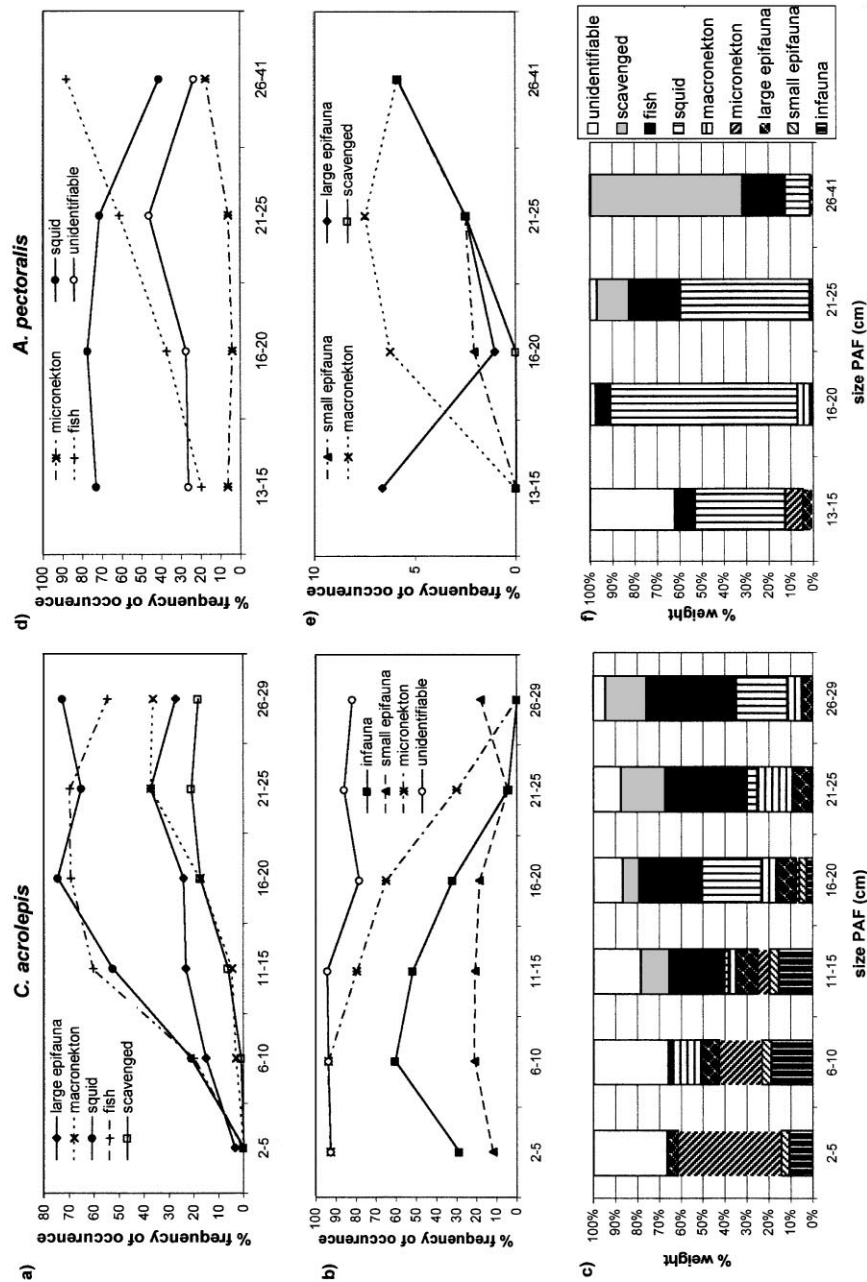


Fig. 4. Size-related changes in diet composition of *C. acrolepis* and *A. pectoralis* using functional groups. (a) Functional groups that increase in %FO with size, (b) functional groups that decline or remain fairly similar in %FO with size, and (c) changes in the gravimetric composition of the functional groups for *C. acrolepis*. (d) %FO of common functional groups (%FO > 10%), (e) %FO of uncommon functional groups (FO < 10%), and (f) changes in the gravimetric composition of the functional groups for *A. pectoralis*.

infaunal prey were found. The frequency of micronekton increased somewhat with fish size, but the relative weight of this group did not show a concurrent increase, and both epifaunal and nektonic groups remained consistently low in relative frequency and weight (Fig. 4e and f).

3.3. Regional and depth related effects

We divided our samples into 7 groups to investigate the effects of the area of capture and depth on the diet of *C. acrolepis* and *A. pectoralis*. Regionally, four areas were used from south to north with boundaries chosen based on their general importance in delineating the ranges of many prey

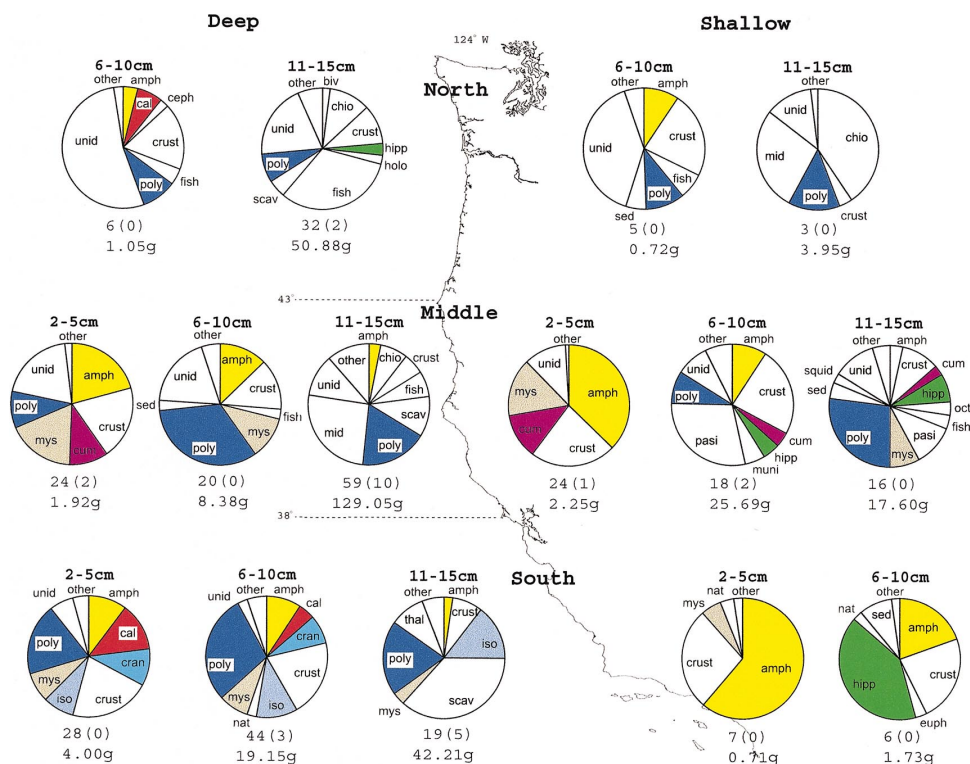


Fig. 5. Gravimetric diet composition of 2–15 cm *C. acrolepis* segregated by area and depth. Numbers of full stomachs, empty stomachs (in parentheses), and total prey weight are given below each pie chart. Prey categories referred to in the text are highlighted. Prey categories are abbreviated as follows; Amphipoda — amph, Ascidacea — ascid, Bivalvia — biv, Calanoida — cal, Cephalopod remains — ceph, *Chionoecetes* sp. — chio, *Coryphaenoides* sp. — cory, Crangonidae — cran, Cranchiidae — cranch, unidentified Crustacean remains — crust, Cumacea — cum, Euphausiacea — euph, fish remains — fish, *Gnathophausia* sp. — gnat, Gonatidae — gon, Hippolytidae — hipp, *Histioteuthis* sp. — hist, Holothuroidea — holo, Isopoda — iso, *Lithodes couesi* — lith, *Merluccius productus* — merl, midwater fish — mid, *Munidopsis* sp. — muni, Mysidacea — mys, unidentified shrimp (Natantia) — nat, Octopoda — oct, *Octopoteuthis* sp. — octop, other prey — other, Pasiphaeidae — pasi, *Pleuroncodes planipes* — pleur, Polychaeta — poly, scavenged material — scav, sediment — sed, unidentified squid beaks — squid, *Stereomastis sculpia* — ster, Thaliacea — thal, unidentified organic material — unident, *Vampyroteuthis infernalis* — vamp.

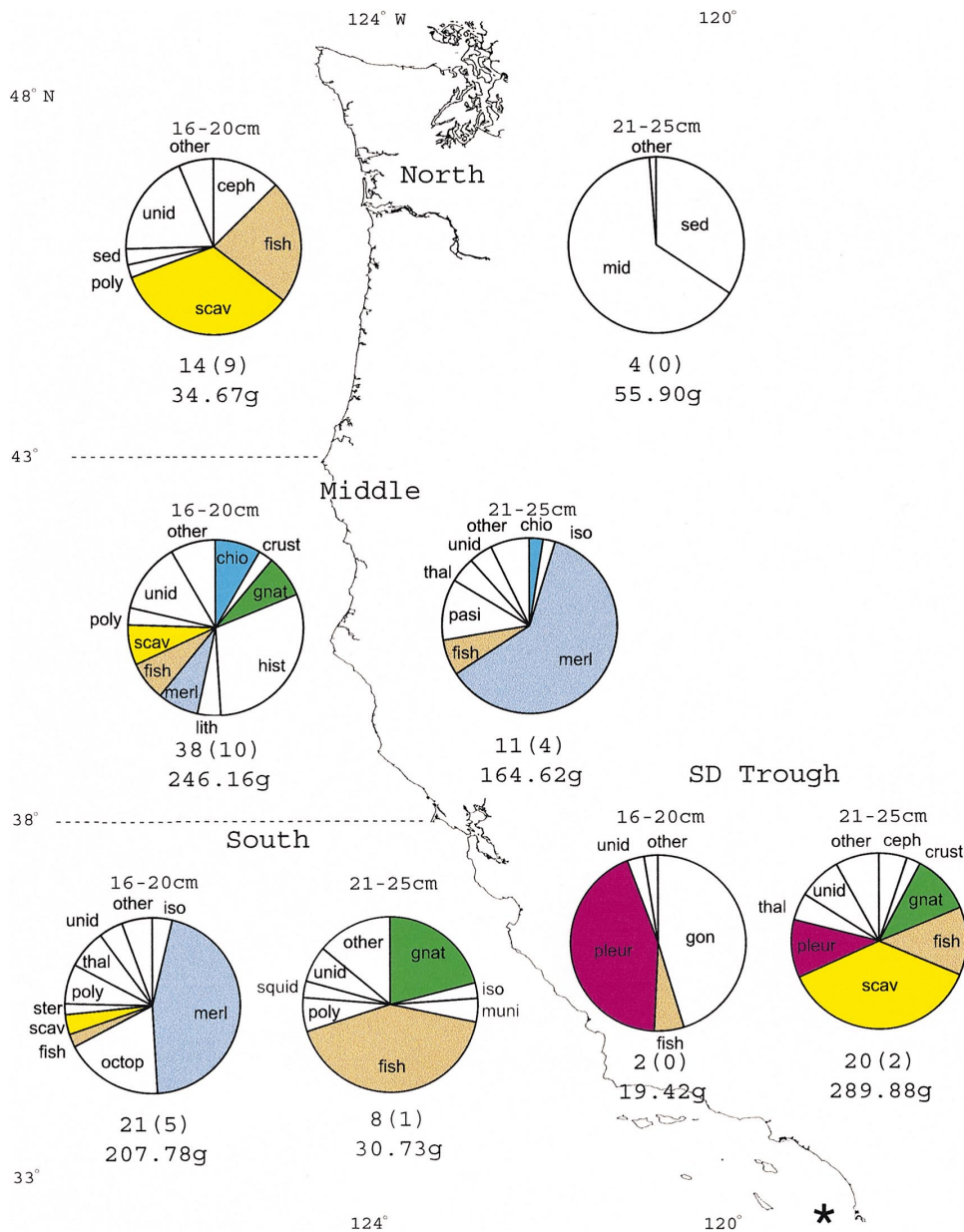


Fig. 6. Gravimetric diet composition of 16–25 cm *C. acrolepis* segregated by area and depth. Numbers of full stomachs, empty stomachs (in parentheses), and total prey weight are given below each pie chart. Prey categories referred to in the text are highlighted. A star indicates the position of the San Diego Trough. See Fig. 5 for a list of abbreviations for prey taxa.

species (Figs. 5–7). The San Diego (SD) Trough at approximately 32°40'N, where we collected fish using free-vehicle fish traps, was the first area. The southern area ranges from Point Conception to 38°N at San Francisco Bay. The middle area extends north from San Francisco Bay to Cape Blanco off the Oregon coast at 43°N. The northern area extends north from Cape Blanco to the

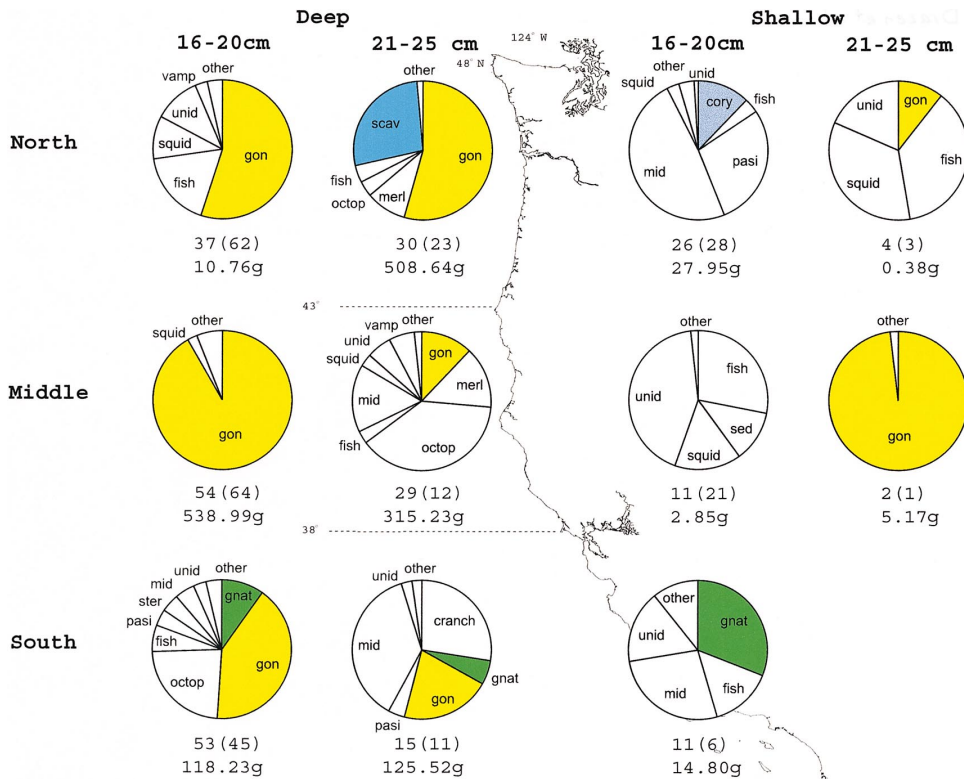


Fig. 7. Gravimetric diet composition of 16–25 cm *A. pectoralis* segregated by area and depth. Numbers of full stomachs, empty stomachs (in parentheses), and total prey weight are given below each pie chart. Prey categories referred to in the text are highlighted. See Fig. 5 for a list of abbreviations for prey taxa.

Strait of Juan de Fuca at approximately 48°N. We further divided our sampling area into two broad depth zones, from 605–900 m (shallow) and 901–1260 m (deep). These two zones were chosen as they roughly divided our depth range in half and because we found an absence of *C. acrolepis* (with or without intact stomachs) between 800 and 900 m. In order to account for differences in diet between fish of different size only fish in the same size group were compared across areas and depths.

Few clear regional or depth related trends in diet were found for *C. acrolepis*. It should be noted that when regionally comparing the diet of large fish all but one of the 26–29 cm *C. acrolepis* were captured in the SD Trough. PSI using %N showed generally high values between neighboring groups (i.e. fish from northern and middle areas or deep southern to shallow southern areas) with no obvious trend. Weight composition was considerably more variable between groups. For 2–10 cm fish, calanoid copepods and polychaetes were generally more important in the diet of deep dwelling fish, while amphipods were less predominant (Fig. 5). Statistically polychaete biomass was greater at depth only in 2–5 cm and 6–10 cm fish from the southern region ($p < 0.01$) and amphipod biomass was only significantly greater at shallower depths for 2–5 cm and 11–15 cm fish from the southern and middle regions respectively (Mann-Whitney U tests; $p < 0.05$). Hippolytid

shrimp were consumed primarily at shallow stations whereas crangonids were consumed only at depth in the southern region (Fig. 5). Regional trends in the gravimetric composition of the diet included the majority of cumaceans being consumed in the middle region and the majority of isopods were consumed in the southern region (Fig. 5). Mysids were not eaten in the northern region (Fig. 5). *Chionoecetes* sp. and fish prey were more prevalent in the diet of large fish captured in the north, but this was significant only for 16–20 cm fish (Mann-Whitney *U* tests; $p < 0.01$; Figs. 5 and 6). Most of the *Gnathophausia* sp. captured were in 21–29 cm fish from the southern and SD Trough regions (Fig. 6, Table 1) and all *Pleuroncodes planipes* were consumed by fish from the SD Trough (Fig. 6, Table 1). *Merluccius productus* was prevalent in the diet of 16–20 cm *C. acrolepis* from the southern region and in 21–25 cm specimens from the middle region. Scavenged material was prevalent for 16–20 cm fish in the northern region and for 21–29 cm from the SD Trough.

There were no significant differences in the mean stomach fullness of *C. acrolepis* between areas and depths except for 6–10 cm fish (ANOVA, $p > 0.05$). For this size group the mean stomach fullness of fish from shallow depths in the middle area was 1.54% bw, significantly higher than fullnesses of 0.16–0.72% bw for fish from the other areas and depths (Mann Whitney *U* test, $p < 0.01$). In addition, fish from shallow depths in the southern region had a greater stomach fullness, 0.67% bw, compared to fish captured from either shallow or deep water (0.16 and 0.24% bw, respectively) in the northern region ($p < 0.01$).

While the diet of trapped *C. acrolepis* from the SD Trough had some differences in prey composition we also wanted to determine whether this method sampled the total stomach contents differently than trawling. To test this we compared the average stomach fullness between SD Trough *C. acrolepis* and trawl caught specimens and found no significant difference (Mann Whitney *U*-test; $p = 0.55$). We also compared the proportions of empty and full stomachs for 21–25 cm fish between trawl and trap caught specimens but found no significant difference (Chi-square test, $p = 0.85$). Even if potential differences in stomach eversion with fish size are ignored and all fish between 16 and 25 cm are compared, there was no significant difference in the proportions of full and empty stomachs ($p = 0.43$).

Albatrossia pectoralis appeared to consume fish and squid regardless of where it was captured although some differences in the gravimetric composition of their diet between depths and regions were found. Since few of the smallest and largest fish were captured, robust comparisons could be made only for 16–20 and 21–25 cm fish and differences in gravimetric composition between regions were highly skewed by several very large prey items. For instance, in the deep middle region gonatid squid composed 92% of the weight of the prey of 16–20 cm fish but most of this was two large squid. Similarly, for 21–25 cm PAF fish one of the two fish captured at shallow depths in the middle region had consumed a juvenile gonatid squid, which dominated the weight of this group's diet. Consequently, while gonatids appeared to be gravimetrically more important in the diet of both size groups of *A. pectoralis* captured at depth (Fig. 7) these differences were not significant (Mann-Whitney *U*-test, $p > 0.05$). Nevertheless, a significant correlation using the gravimetric composition of the diets was found between 16 and 20 cm fish from the deep northern and deep middle regions ($p < 0.01$) indicating overall diet similarity. These fish had diets primarily composed of gonatid squid (Fig. 7). In addition, *Coryphaenoides* sp. (including one ~ 4 cm *C. acrolepis*) were consumed only by *A. pectoralis* from shallow depths in the northern region and scavenged remains were only eaten by fish captured at deep stations in the northern region (Fig. 7). *Gnathophausia* sp.

was consumed only in the southern region (Fig. 7). We also examined differences in mean stomach fullness between depths and regions for both size groups, but the high variance in stomach fullness precluded any significant differences (ANOVA, $p > 0.05$).

3.4. Comparison of macrourids

The diets of similarly sized *C. acrolepis* and *A. pectoralis* were compared. The PAF–weight relationships of the two species are similar suggesting that using PAF to compare fish sizes is valid (Lauth, 1998). In general, the diet of *C. acrolepis* was much more diverse than that of *A. pectoralis* with 5 to 18 more prey categories depending on which sized fish were compared (Fig. 2; Tables 1 and 2). The stomach fullness of *A. pectoralis* was much more variable than that of *C. acrolepis*, punctuated by infrequent but large prey items. Generally, PSI values suggested that there was a moderate amount of overlap, and there were no significant correlations in diet ($p > 0.05$; Table 2). Most of the specimens of these two species were captured concurrently from 50 hauls. When the diets of *C. acrolepis* and *A. pectoralis* were compared from specimens taken only from these hauls, there still were no significant correlations ($p > 0.05$). At 11–20 cm *C. acrolepis* still consumed a variety of microcrustaceans and polychaetes (Table 1) while *A. pectoralis* of the same size consumed almost exclusively fish and squid (Table 2). The diet of specimens > 20 cm was much more similar (PSI up to 50) with both *C. acrolepis* and *A. pectoralis* consuming large quantities of fish, various squid, and scavenged food. However, the relative importance (rank) of these prey groups differed between the macrourids so no significant correlation in diet was found (Tables 1 and 2). When functional groups were considered for specimens > 20 cm, we found that *C. acrolepis* still consumed more macronektonic crustaceans and large epifaunal prey than *A. pectoralis* (Fig. 4).

4. Discussion

4.1. Diet of *Coryphaenoides acrolepis*

We believe that *C. acrolepis* stomach samples collected with trawls and free vehicle fish traps were comparable. While prey composition varied between trap and trawl captured samples, these differences were most likely due to the geographic range of prey species. For instance, *Pleuroncodes planipes* is a species that is almost never found north of Point Conception, hence its exclusive occurrence in fish captured from the SD Trough (Boyd, 1967). Furthermore, there were no significant differences in average stomach fullness as a percent of body weight or the proportions of empty and full stomachs between trap and trawl collected samples.

For *C. acrolepis* a pronounced ontogenetic shift in feeding habits was found. The smallest individuals foraged over the bottom consuming polychaetes and various epifaunal and hyperbenthic crustaceans (Table 1). It was been hypothesized that the general morphology of macrourids with a long and broad anal fin was an adaptation for head down swimming so that they could “root in the ooze” (Marshall and Bourne, 1964; McClellan, 1972). A variety of species primarily within the genus *Coelorrhynchus* and *Nezumia* have been found to prey heavily on infaunal organisms (McClellan, 1972; Macpherson, 1979; Mauchline and Gordon, 1984; Marques and

Almeida, 1998; Hoff et al., 2000). Small *C. acrolepis* from this study frequently consumed infauna, but this type of prey never exceeded 20% of the weight of prey. This suggests that infauna is less important to *C. acrolepis* than species in the genera *Coelorhynchus* and *Nezumia* and that instead of rooting in the ooze, they forage on top of the sediments or in the water column just above.

With increasing size, *C. acrolepis* consumed progressively larger, more pelagic prey and for the most part did not consume infaunal organisms. Squid, fish and large crustaceans were the dominant prey of specimens > 15 cm; however, they still foraged over the bottom as indicated by the presence of large epifaunal prey (Fig. 4) and sediment (Table 1). Similar results were found for 33 specimens examined from off the coast of Oregon and Washington with polychaetes and small crustaceans dominating the bulk of the diet of 5–9 cm individuals and squid and fish becoming more important with increasing size (Buckley et al., 1999). We also found that their diet diversified with size increasing from 15 to 42 prey categories between the smallest size group and 15–20 cm fish. This trend can be seen also in the cumulative prey curves as the steepness of curves becomes greater for larger fish (Fig. 2a). Part of this apparent increase in prey diversity likely may be due to our inability to identify the small prey (various microcrustaceans) of small specimens past coarse taxonomic levels. However, 14 of the 15 prey categories for 2–5 cm fish also occurred in all larger predator sizes through 16–20 cm and 12 of the 15 prey types occurred through 21–25 cm fish, while new prey types were found in each larger size category.

The ontogenetic shifts in diet of *C. acrolepis* were similar to that of several other species of macrourids. The diet of *Coryphaenoides armatus* also shifts with the size of the fish from small epibenthic prey to large fish and squid and is quite diverse (Percy and Ambler, 1974; Haedrich and Henderson, 1974; Campbell et al., 1980; Mauchline and Gordon, 1984; Martin and Christiansen, 1997). *Coryphaenoides rupestris* from the North Atlantic also appears to have similar ontogenetic shifts in diet with an increase in diet diversity and a greater amount of pelagic prey in the stomachs of larger fish (Mauchline and Gordon, 1984; Houston and Haedrich, 1986). While other species may not exhibit the same general diet, many still exhibit an ontogenetic diet shift from epibenthic or infaunal prey to more pelagic organisms (Percy and Ambler, 1974; Mauchline and Gordon, 1984; Crabtree et al., 1991). The decrease in the frequency of occurrence of small prey with increasing predator size may be due to an increasing distance between gill rakers and a larger buccal cavity as has been shown for several pelagic predators (Magnuson and Heitz, 1971). In addition, changes in foraging behaviour may be associated with increasing locomotory ability as was illustrated by the largest specimens being caught in baited traps up to 20 m off the bottom but not in trawls.

There were some regional and depth related shifts in the gravimetric composition of the diet of *C. acrolepis*. Considering the relatively generalized diet of *C. acrolepis*, we believe that regional shifts probably reflect regional variation in prey availability. When examining depth related trends in diet it is important to note that *C. acrolepis* has a maximum depth distribution of 2500 m, considerably greater than our collection methods allowed us to sample (Iwamoto and Stein, 1974). In our study, *C. acrolepis* > 15 cm were captured from 936–1253 m while smaller fish were captured from 604–1253 m. A “bigger-deeper” trend in *C. acrolepis* has been documented before at the depths that we sampled and it has been suggested that macrourids have pelagic larvae that settle along the continental slope and juveniles that migrate down-slope as they grow (Stein and Percy, 1982). It has been hypothesized that one reason for such distributions is that larger fish can

swim more efficiently between food patches as the distance between the patches increases with depth (Polloni et al., 1979). If this were true then small fish would experience greater foraging success at shallower depths and we should see a greater amount of food in their stomachs, but this was the case only for 6–10 cm fish from the middle region, San Francisco Bay to Cape Blanco. The gravimetric composition of the prey varied significantly by depth for 2–5 cm and 11–15 cm fish and it appears that amphipods were more available as prey at shallower depths. Further, in the southern region, polychaetes were more important in the diet of 2–10 cm fish collected at deep stations. It appears that while the availability of different prey may shift with depth, small *C. acrolepis* generally manage to consume on average the same amount of food regardless of depth. Our diet data do not help explain a shallower depth distribution in small *C. acrolepis*.

4.2. Diet of *Albatrossia pectoralis*

Size related differences in the diet of *A. pectoralis* were not pronounced but a smaller size range was available (Table 3). Very small individuals (< 10 cm) rarely are captured in trawls, and no specimens less than 10 cm were captured during the 1997 survey (Lauth, 1998). It has been hypothesized that juvenile *A. pectoralis* are pelagic (Novikov, 1970; Cohen et al., 1990). These small individuals would be expected to have food habits different from the larger *A. pectoralis* we sampled simply on the basis of mouth size. The relative weight of the prey taxa between the four size groups in this study was never correlated, but this likely results from the nature of their stomach contents rather than from true differences in feeding behavior. Often the stomach contents were the remains of prey but occasionally larger, less digested prey were found. This led to a high variance in the weight of each prey taxon and mean stomach fullness.

Albatrossia pectoralis primarily feeds in the water column, only occasionally consuming benthic animals. Squid consistently made up the majority of their diet and this was affected little by the depth or region of capture. The most common squids consumed were gonatids, primarily *Gonatus* sp. and *Gonatopsis borealis*, both of which have considerable vertical ranges but are generally considered meso- or bathypelagic to depths of 2000 m (Nesis, 1982). Two common bathypelagic squid in the stomach contents were *Octopoteuthis deletron* and *Vampyroteuthis infernalis* (Nesis, 1982; Hunt, 1996). Almost all of the identifiable fish that *A. pectoralis* consumed were deep pelagic or hyperbenthic species such as *Chauliodus macouni*, *Chiasmodon* sp., bathylagids, myctophids, alepocephalids, and *M. productus*. Not many of these fish have daily vertical migrations that could bring them in close proximity to the bottom where they could have been eaten, but the absence of benthic fish suggests that they were consumed somewhere in the water column. The occurrence of sediment is also considerably lower for this species than for *C. acrolepis* (Table 2).

Other studies are in accordance with the interpretation that *A. pectoralis* forages in the water column (Okamura, 1970). An examination of 29 specimens from the eastern North Pacific showed pelagic prey such as squid, the bathypelagic mysid *Gnathophausia*, pelagic Pasiphaeid shrimp and fishes to be most important (Buckley et al., 1999). From occurrence data, specimens examined from the Bering Sea were found to consume primarily mesopelagic fishes, squid, and shrimp (Novikov, 1970).

The tissue composition of *A. pectoralis* also suggests a midwater lifestyle. The white muscle of this species is approximately 92% water, which is likely an adaptation to increase buoyancy without the metabolic costs of buoyant lipids or a gas bladder and further suggests that this species

is adapted to moving vertically throughout the water column (Drazen, in preparation). While the tissue composition is indicative of a midwater lifestyle it suggests a relatively inactive predator. Typically fish with gelatinous tissues are rather sedentary as they have low muscle fiber density and low metabolic enzyme concentrations (Sullivan and Somero, 1980; Siebenaller et al., 1982). The diet of these animals includes very active squid such as gonatids, which are difficult to capture in trawls because of net avoidance. It seems unlikely that a watery fish such as *A. pectoralis* would have the capacity to pursue such active prey and perhaps *A. pectoralis* avoids aerobically active pursuit by ambushing its prey. An ambush foraging strategy may not be needed to explain their diet because large squid only make up $\sim 7.5\%$ of the number of squid consumed. The remainder of the prey squid are not all identified but most of the beaks were quite small (lower rostral length < 3.0 mm) indicating generally small squid (Clarke, 1986). There is considerable variability between species in the relationship between beak size and mantle length, but for the most commonly consumed group, the gonatids, a 3 mm beak corresponds to a mantle length of approximately 8.5 cm and a weight of 20 g (Wolff, 1984; Clarke, 1986). It is plausible that *A. pectoralis* could pursue and consume squid of this size.

It may not be uncommon for some species of macrourids to forage in the water column far above the seafloor. *Coryphaenoides filifer* also has been shown to consume primarily midwater prey (Pearcy and Ambler, 1974) and has been captured as much as 500 m above the bottom in midwater (Pearcy, 1976). In the North Atlantic, *C. rupestris* has been captured 270–1440 m above the bottom (Haedrich, 1974) and in the Pacific, *C. armatus* has been captured up to 685 m above bottom (Smith et al., 1979) and *C. yaquinae* up to 1000 m above bottom (Smith et al., 1992). Even a few *C. acrolepis* have been captured 1000 m above the bottom (Iwamoto and Stein, 1974; Simenstad et al., 1977; J. Childress, unpublished data).

4.3. The importance of scavenging

The presence of scavenged material in the diet of macrourids has been noted with some regularity (Haedrich and Henderson, 1974; Percy and Ambler, 1974; Stein, 1985; Martin and Christiansen, 1997) and their attraction to artificial “food-falls” has been studied in detail (Isaacs and Schwartzlose, 1975; Dayton and Hessler, 1972; Thurston et al., 1995; Mahaut et al., 1990; Priede et al., 1994; Jones et al., 1998). Yet quantification of the importance of scavenged material in the diet has been elusive. Close examination of the prey items in this study has allowed us to determine a conservative minimum estimate of its importance. For *C. acrolepis* the frequency of occurrence and contribution by weight of this material can be as high as 20% (Fig. 6, Table 1). However, it is of little importance to fish 2–10 cm probably because they cannot fit such large parcels in their mouths, and perhaps they avoid food falls because carrion attracts predators that could eat them. For *A. pectoralis* the frequency of occurrence of scavenged material was low but the relative weight was approximately 68% for 26–41 cm PAF fish (Fig. 7, Table 2). It should be noted that there were only 17 specimens in this size group and only one of them had a large hake skull in its stomach (Fig. 4). The weight composition of a small sample size can be greatly affected by a single large prey item; therefore this high %W of scavenged material may not be typical for this group.

Our estimate of the importance of scavenged material in the diet is a conservative one because other prey might have been included in the list of scavenged food. There were several squid prey

that were large but smaller than the predator. Using regressions from their beaks, we estimate that six specimens had mantle lengths approximately equal to the PAF of the fish that ate them and weighed between 20 and 48% of the predator weight (Clarke, 1986). In addition to these items the mud crab *Pleuroncodes planipes* could have been scavenged. *Pleuroncodes planipes* feeds almost exclusively on phytoplankton from the surface to 500 m off Baja California where it can form dense aggregations in midwater from the surface to about 300 m (Boyd, 1967; Auroles-Gamboa, 1992). All of the *C. acrolepis* whose stomachs contained this species were captured in the San Diego Trough at a depth of approximately 1200 m, much deeper and farther north than *P. planipes* typically occurs. It is difficult to determine if these crabs were alive on the bottom or in deep midwater when they were consumed or if they simply died and sank to the bottom. Boyd (1967) found that this species was primarily pelagic until it reached 26 mm carapace length. The specimens from the stomachs of *C. acrolepis* had a carapace length of 15–26 mm, so most of the specimens that were preyed upon could have been epipelagic but several of the larger specimens were easily within Boyd's size range for benthic habits. Unfortunately no bottom photographs of the area could be found during this time period to see if *P. planipes* was residing at depth.

Regardless of whether *P. planipes* and the six squid are included, scavenged material constitutes a significant component of the diet of *C. acrolepis* > 20 cm. *Corphaenoides acrolepis* can follow odor plumes to locate food falls and it quickly arrives at artificially placed carcasses (Isaacs and Schwartzlose, 1975; Dayton and Hessler, 1972; Smith and Hessler, 1974; Smith, 1985) showing that it is adapted to find such food. Our data suggest that either surface-derived food parcels are common along the continental slope or that *C. acrolepis* is quite successful at locating the few parcels that are available or perhaps both. Considering the quantity of carrion in the diet of this species and its relatively high density along the continental slope, the quantity of carrion eaten by these fish could be considerable. However, the degree of scavenging by *C. acrolepis* may not be typical among deep-sea fish. Merrett and Haedrich (1997) have noted that instances of scavenging are relatively rare and the majority of deep-sea fish are not attracted to bait and many of those that are do not feed on it. So whether carrion constitutes a large, previously unrecognized fraction of the downward flux of energy into the deep sea remains equivocal.

4.4. Comparison of the diet of macrourid species and other slope dwelling predators

The more specialized diet of *A. pectoralis* was not correlated to that of *C. acrolepis* and similarity in diet between these species was not high (Table 2). *Coryphaenoides acrolepis* > 15 cm are typically found only below 900 m but *A. pectoralis* has a broader depth distribution with specimens captured as shallow as 550 m (Lauth, 1998). It is conceivable that such low diet overlap could be the result of different depth distributions. But, most of our specimens were captured together (50 out of 83 trawls) and most specimens over 15 cm were captured in the same depth range of 900 to 1250 m. Even when we restricted our analysis to specimens from trawls that captured both species, we found no significant correlations between their diets ($p > 0.05$). While both species were captured on the bottom, *A. pectoralis* appears to feed higher in the water column than *C. acrolepis*, thus reducing diet overlap.

The diets of *Nezumia liolepis* and *N. stelgidolepis* have been described from specimens collected during the 1997 NMFS slope survey (Hoff et al., 2000). These data allow us to compare their diets

to that of *C. acrolepis* of similar size from this study and further assess diet partitioning of eastern Pacific slope-dwelling macrourids. The diet of *N. liolepis* (3.9–8.4 cm PAF) was dominated by amphipods, shrimp (primarily benthic hippolytids), polychaetes, and mysids (Hoff et al., 2000). This is very similar to the diet of 2–15 cm *C. acrolepis*. *Nezumia liolepis* were caught between 581 and 1247 m overlapping in distribution with *C. acrolepis*, so these two species could compete for food resources. However, the gravimetric composition of their prey species differs. *Nezumia liolepis* consumed more hippolytid shrimp and fewer polychaetes than *C. acrolepis*. *Nezumia liolepis* is not commonly captured but often it occurs in large numbers and Hoff et al. (2000) suspect that it may associate with steep rocky substrate, which could contribute to differences in the availability of prey taxa. *N. stelgidolepis* (3.6–8.5 cm) had a diet very similar to that of *N. liolepis* and 2–15 cm *C. acrolepis* with amphipods, mysids, shrimps, and crabs being dominant (Hoff et al., 2000). However it is doubtful that *N. stelgidolepis* utilizes the same food resources as other macrourids because it occurs much shallower, on the upper continental slope between 285 and 555 m.

Other studies have suggested diet partitioning in macrourids. McClellan (1972) demonstrated that variation in head morphology was indicative of different foraging strategies with fish in the genera *Coelorinchus* and *Mataeocephalus* feeding on benthos and bathygadine species feeding on pelagic prey. Other studies have also shown differences in diet with different species feeding either on infauna, epifauna, or pelagic prey (Pearcy and Ambler, 1974; Macpherson, 1979) and that species consuming similar types of prey can have differing depth distributions (Mauchline and Gordon, 1984). Our data and these studies support the hypothesis that macrourid fishes are not restricted to simple opportunism in the food-poor deep sea but that some specialization can occur both in where they forage and upon what they prey.

Coryphaenoides acrolepis and *A. pectoralis* are near the top of the food web because they have a diet similar to other large fishes on the continental slope and have few predators. Other large, abundant fishes in this environment include *Anoplopoma fimbria*, *Sebastolobus altivelis* and *S. alascanus*. The diet of *A. fimbria* consists of large crustaceans, cephalopods, and fish including many juvenile *Sebastolobus* sp. (Conway, 1967; Caillet et al., 1988; Buckley et al., 1999). *Anoplopoma fimbria* also has been photographed at artificial food-falls (Smith, 1985) and scavenged material (fisheries offal) has been noted as part of their diet (Buckley et al., 1999). *Sebastolobus alascanus* has a diet dominated by benthic fishes, crabs and shrimps (Buckley et al., 1999). *Sebastolobus altivelis* exhibits an ontogenetic shift in diet from polychaetes and amphipods to mainly crabs, shrimps and fishes (Buckley et al., 1999). These diets are roughly similar to those of *C. acrolepis* and *A. pectoralis*. These macrourids have few known predators. Beaked whales eat them (Walker and Mead, in preparation) and the holotype of *C. acrolepis* came from the stomach of a northern fur seal, *Callorhinus ursinus* (Gill and Townsend, 1897).

Coryphaenoides acrolepis and *A. pectoralis* have the 7th and 8th highest biomass of the demersal fish species captured on the continental slope during 1997 with biomass estimates of 6.31 and 5.60 kg/ha, respectively. These biomass estimates are averaged across all areas and depths (183–1280 m). If only the 1098–1280 m depth stratum is considered then these two species rank 1st and 3rd in biomass with 22.33 and 19.22 kg/ha (Lauth, 1998). Given these large estimates of population biomass, macrourids could exert a significant influence on their prey populations. However, reliable estimates of feeding rates would be required to calculate the magnitude of such effects.

5. Conclusions

Our study has provided the first comprehensive analysis of the diets of *C. acrolepis* and *A. pectoralis*, the two dominant macrourids on the upper slope of the continental United States. The diet of *C. acrolepis* is relatively generalized. A pronounced ontogenetic shift from polychaetes and microcrustaceans to larger, more pelagic prey such as fish, squid, and large crustaceans was noted. Regional and depth related variation in the gravimetric composition of the prey likely reflects variation in prey availability. The diet of *A. pectoralis* was not as general as that of *C. acrolepis* and was dominated by midwater fish and squid regardless of depth or region. It is likely that this species forages primarily in the water column.

We provide the first quantitative estimate of the importance of scavenging in a macrourid fish. Scavenged material made up approximately 20% of the total weight of prey for *C. acrolepis* > 20 cm and occurred in approximately 20% of the fish examined. We consider this estimate a conservative one and several potentially scavenged organisms were not included in this prey category. This large estimate implies that scavenged material is more than an incidental component of the diet and suggests a significant link between surface waters and the deep sea at least for this species.

Some diet partitioning occurred between macrourids on the continental slope of the eastern North Pacific. *Coryphaenoides acrolepis* and *A. pectoralis* exhibited moderate diet overlap and their diets were not significantly correlated. *Nezumia liolepis* had a diet similar to that of *C. acrolepis* < 15 cm but consumed more hippolytid shrimp and fewer polychaetes. *Nezumia stelgidolepis* was distributed much shallower than the other macrourids and likely does not utilize the same food resources. Furthermore, *C. acrolepis* and *A. pectoralis* are among the top predators on the upper continental slope and because they are relatively abundant they likely have large impacts on their prey populations.

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References

- Aurolles-Gamboa, D., 1992. Inshore-offshore movements of pelagic red crabs, *Pleuroncodes planipes* (Decapoda, Anomura, Galatheididae) off the Pacific coast of Baja California Sur, Mexico. *Crustaceana* 62 (1), 71–84.

- Boyd, C.M., 1967. The benthic and pelagic habitats of the red crab, *Pleuroncodes planipes*. Pacific Science 21, 394–403.
- Buckley, T.W., Tyler, G.E., Smith, D.M., Livingston, P.A., 1999. Food habits of some commercially important groundfish species off the coasts of California, Oregon, Washington, and British Columbia. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC 102, p. 173.
- Cailliet, G.M., Barry, J.P., 1979. Comparison of food array overlap measures useful in fish feeding habit analysis. In: Lipovsky, S.J., Simenstad, C.A. (Eds.), Gutshop' 78, Fish Food Habit Studies; Proceedings of the Second Pacific Northwest Technical Workshop, University of Washington Division of Marine Resources, Washington Sea Grant Report WSG-WO-79-1, pp. 67–69.
- Cailliet, G.M., Osada, E.K., Moser, M., 1988. Ecological studies of sablefish in Monterey Bay. California Fish and Game 74 (3), 132–153.
- Campbell, R.A., Haedrich, R.L., Munroe, T.A., 1980. Parasitism and ecological relationships among deep-sea benthic fishes. Marine Biology 57, 310–313.
- Clarke, M.R., 1986. A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford, pp. 273.
- Cohen, D.M., Inada, T., Iwamoto, T., Scialabba, N., 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis No. 125, Vol. 10. Rome, FAO.
- Conway, J.B., 1967. Food relationships and general population biology of the sablefish, *Anoplopoma fimbria*, and Pacific hake, *Merluccius productus*. MS Thesis, San Diego State College.
- Crabtree, R.E., Carter, J., Musick, J.A., 1991. The comparative feeding ecology of temperate and tropical deep-sea fishes from the western North Atlantic. Deep-Sea Research 38 (10), 1277–1298.
- Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Research 19, 199–208.
- Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review 17, 193–284.
- Fritz, E.S., 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 1, 210–214.
- Gage, J.D., Tyler, P.A., 1991. Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Victoria, Australia, pp. 504.
- Geistdoerfer, P., 1975. Ecologie alimentaire des Macrouridae. Ph.D. Thesis, University of Paris VI.
- Gill, T., Townsend, C.H., 1897. Diagnoses of new species of fishes found in Bering Sea. Proceedings of the Biological Society of Washington, Vol. 11, pp. 231–234.
- Haedrich, R.L., 1974. Pelagic capture of the epibenthic rattail *Coryphaenoides rupestris*. Deep-Sea Research 21, 977–979.
- Haedrich, R.L., Henderson, N.R., 1974. Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. Deep-Sea Research 21, 739–744.
- Hoff, G.R., Buckley, T.W., Drazen, J.C., Duncan, K.M., 2000. Biology of *Nezumia liolepis* and *Nezumia stelgidolepis* from the west coast of North America. Journal of Fish Biology, in press.
- Houston, K.A., Haedrich, R.L., 1986. Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. Marine Biology 92, 563–574.
- Hunt, J.C., 1996. The behaviour and ecology of midwater cephalopods from Monterey Bay: submersible and laboratory observations. Ph.D. Thesis. University of California, Los Angeles.
- Hurlbert, S.H., 1978. The measurement of niche overlap and some relatives. Ecology 59 (1), 67–77.
- Isaacs, J.D., Schwartzlose, R.A., 1975. Active animals of the deep-sea floor. Scientific American 233, 85–91.
- Iwamoto, T., Stein, D.L., 1974. A systematic review of the rattail fishes (Macrouridae: Gadiformes) from Oregon and adjacent waters. Occasional Papers of the California Academy of Sciences 111, 1–79.
- Jones, E.G., Collins, M.A., Bagley, P.M., Addison, S., Priede, I.G., 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. Proceedings of the Royal Society of London, Series B 265, 1119–1127.
- Lauth, R.R., 1998. The 1997 Pacific west coast upper continental slope trawl survey of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, and length composition. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-98, pp. 284.
- Macpherson, E., 1979. Ecological overlap between macrourids in the western Mediterranean Sea. Marine Biology 53, 149–159.

- Magnuson, J.J., Heitz, J.G., 1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fishery Bulletin* 69, 361–370.
- Mahaut, M.L., Geistdoerfer, P., Sibuet, M., 1990. Trophic strategies in carnivorous fishes: their significance in energy transfer in the deep-sea benthic ecosystem (Meriadzek Terrace — Bay of Biscay). *Progress in Oceanography* 24, 223–237.
- Marques, M., Almeida, A.J., 1998. Notes on the biology of *Nezumia sclerorhynchus* and *Nezumia aequalis* (Gadiformes: Macrouridae) from the Algarve slope, Northeast Atlantic. *Cybiurn* 22 (1), 21–29.
- Marshall, N.B., Bourne, D.W., 1964. A photographic survey of benthic fishes in the Red Sea and Gulf of Aden, with observations on their population density, diversity and habits. *Bulletin of the Museum of Comparative Zoology. Harvard University* 132 (2), 223–244.
- Marshall, N.B., Iwamoto, T., 1973. Family macrouridae. In: Cohen, D.M. (Ed.), *Fishes of the Western North Atlantic*, Part 6. Sears Foundation for Marine Research, Yale University, pp. 496–665.
- Martin, B., Christiansen, B., 1997. Diets and standing stocks of bathypelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. *Deep-Sea Research I* 44 (4), 541–558.
- Mauchline, J., Gordon, J.D.M., 1984. Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* 81, 107–121.
- Mauchline, J., Gordon, J.D.M., 1986. Foraging strategies of deep-sea fish. *Marine Ecology Progress Series* 27, 227–238.
- McClellan, T., 1972. Feeding strategies of the macrourids. *Deep-Sea Research* 24, 1019–1036.
- Merrett, N.R., 1992. Demersal ichthyofaunal distribution in the abyssal eastern North Atlantic, with special reference to *Coryphaenoides (Nematonurus) armatus* (Macrouridae). *Journal of the Marine Biological Association of the United Kingdom* 72, 5–24.
- Merrett, N.R., Haedrich, R.L., 1997. *Deep-Sea Demersal Fish and Fisheries*. Chapman & Hall, London.
- Nesis, K.N., 1982. *Cephalopods of the World*. Light and Food Industry Publishing House, Moscow (Translated from Russian by Levitov, B.S., T.F.H. Publications, Neptune City).
- Novikov, N.P., 1970. Biology of *Chalinura pectoralis* in the North Pacific. In: Moiseev, P.A. (Ed.), *Soviet Fisheries Investigations in the North-East Pacific*, Part 5 (in Russian). Proceedings of the All-Union Science Research Institute of Marine and Fisheries Oceanography (VINRO) Vol. 70, and Proceedings of the Pacific Science Research Institute of Fisheries and Oceanography (TINRO), Vol. 72, pp. 304–331 (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, 1972).
- Okamura, O., 1970. Studies on the macrourid fishes of Japan: morphology, ecology, and phylogeny. *Report of the USA Marine Biological Station* 17 (1-2), 1–179.
- Pearcy, W.G., 1976. Pelagic capture of abyssobenthic macrourid fish. *Deep-Sea Research* 23, 1065–1066.
- Pearcy, W.G., Ambler, J.W., 1974. Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Research* 21, 745–759.
- Polloni, P., Haedrich, R., Rowe, G., Clifford, C.H., 1979. The size-depth relationship in deep ocean animals. *Internationale Revue der gesamten Hydrobiologie* 64, 39–46.
- Priede, I.G., Bagley, P.M., Smith Jr, K.L., 1994. Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides (Nematonurus) armatus* in the eastern North Pacific Ocean. *Limnology and Oceanography* 39 (2), 279–285.
- Priede, I.G., Bagley, P.M., Armstrong, J.D., Smith Jr, K.L., Merrett, N.R., 1991. Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. *Nature* 351, 647–649.
- Schoener, T.W., 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408–418.
- Sedberry, G.R., Musick, J.A., 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. *Marine Biology* 44, 357–375.
- Siebenaller, J.F., Somero, G.N., Haedrich, R.L., 1982. Biochemical characteristics of macrourid fishes differing in their depths of distribution. *Biological Bulletin* 163, 240–249.
- Simenstad, C.A., Isakson, J.S., Nakatani, R.E., 1977. Marine fish communities. In: Merritt, M.L., Fuller, R.G. (Eds.), *The Environment of Amchitka Island, Alaska*. U.S. Energy Research and Development Administration, TID 267-12, pp. 451–492.
- Smith, C.R., 1985. Food for the deep-sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina Basin floor. *Deep-Sea Research* 32 (4), 417–442.

- Smith Jr, K.L., White, G.A., Laver, M.B., McConnaughey, R.R., Meador, J.P., 1979. Free vehicle capture of abyssopelagic animals. *Deep-Sea Research* 26A, 57–64.
- Smith Jr, K.L., Hessler, R.R., 1974. Respiration of benthopelagic fishes: *in situ* measurements at 1230 meters. *Science* 184, 72–73.
- Smith Jr, K.L., Kaufmann, R.S., Edelman, J.L., Baldwin, R.J., 1992. Abyssopelagic fauna in the central North Pacific: Comparison of acoustic detection and trawl and baited trap collections to 5800 m. *Deep-Sea Research I* 39, 659–685.
- Stein, D.L., 1985. Towing large nets by single warp at abyssal depths: methods and biological results. *Deep-Sea Research* 32 (2), 183–200.
- Stein, D.L., Pearcy, W.G., 1982. Aspects of reproduction, early life history, and biology of Macrourid fishes off Oregon. U.S.A. *Deep-Sea Research I* 29 (11A), 1313–1329.
- Sullivan, K.M., Somero, G.N., 1980. Enzyme activities of fish skeletal muscle and brain as influenced by depth of occurrence and habits of feeding and locomotion. *Marine Biology* 60, 91–99.
- Thurston, M.H., Bett, B.J., Rice, A.L., 1995. Abyssal megafaunal necrophages: latitudinal differences in the eastern North Atlantic Ocean. *Internationale Revue der gesamten Hydrobiologie* 80 (2), 267–286.
- Walker, W., Mead, J.G., Food habits of Bairds beaked whales off the Pacific coast of central Japan and southern Sea of Okhotsk, in preparation.
- Wakefield, W.W., 1990. Patterns in the distribution of demersal fishes on the upper continental slope off central California with studies on the role of ontogenetic vertical migration in particle flux. Ph.D. Thesis, University of California, Scripps Institution of Oceanography, San Diego.
- Wolff, G.A., 1984. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. U.S. Department of Commerce, NOAA Technical Report, NMFS 17, 50pp.