Bypassing the abyssal benthic food web: Macrourid diet in the eastern North Pacific inferred from stomach content and stable isotopes analyses

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Abstract

Deep-sea fishes prey on benthic fauna and scavenge on the carcasses of surface-living animals. Few studies have addressed the relative importance of each trophic pathway. Recent documentation of inter-decadal fluctuations in macrourid densities in the abyssal Pacific, related to changing food supplies, hastens the need for information. We conducted stomach content and stable isotope analyses of two abyssal macrourids, carrion sources, and benthic prey, collected concurrently at 4100 m off California. Squid and fishes were the most frequent prey for *Coryphaenoides armatus,* with small crustaceans numerous in the diet of small specimens. The diet of *Coryphaenoides yaquinae* included more benthic prey such as crustaceans, polychaetes, and the holothuroid *Protankyra brychia*. Carrion was present in both species and it was 69% of the mass of food of large *C. armatus.* Carrion $\delta^{15}N$ values were comparable to those in abyssal deposit feeders, but carrion was relatively enriched in ^{13}C, giving it a unique isotopic signature compared to benthic prey sources. The highest $\delta^{13}C$ and $\delta^{15}N$ values were observed in benthic shrimps and large polychaetes. The two macrourids had intermediate values, with *C. armatus* having slightly but significantly lower $\delta^{15}N$ relative to *C. yaquinae*. Results of isotope mass balance suggest that carrion was the most important prey resource for both species but to a lesser extent in *C. yaquinae*. These two species bypass the conventional phytodetritus-based abyssal food web for much of their nutrition. Their population dynamics may be tied more closely to fluctuations in epipelagic nekton populations through fishing effects and direct climatic forcing on top trophic levels.

The top predators at abyssal depths are primarily fishes, and there are two trophic pathways that they can exploit. Despite the difficulties of sampling, many studies have investigated their diets and have found a diversity of feeding habits ranging from infaunal browsing to active predation on large nekton (Gartner et al. 1997). By consuming deep-sea prey, the fishes are ultimately dependent upon an allochthonous food supply in the form of phytodetritus generated in surface waters. In simplified terms, phytodetritus is consumed by deposit feeders, which in turn are consumed by primary carnivores, and so on to the top trophic positions including many fishes. However, an alternative trophic pathway exists. Many deep-sea fishes are attracted to cameras baited with pelagic carrion (Priede and Bagley 2000) and a few studies have noted carrion in their diets (Haedrich and Henderson 1974; Pearcy and Ambler 1974; Bjelland et al. 2000). This trophic pathway is rarely quantified (Drazen et al. 2001). Scavenging on the sunken carcasses of epipelagic nekton bypasses the conventional benthic food web, although the beginning of each path shares primary production in surface waters. The relative importance of these two trophic pathways remains uncertain. Understanding whether deep-sea fish populations are more closely tied to benthic or epipelagic food supplies is critical for understanding how anthropogenic influences such as fishing and climate change will affect deep-sea ecosystems.

Recently, long time-series investigations on the abyssal plains have documented shifts in animal abundances and size frequencies (Billett et al. 2001; Ruhl and Smith 2004; Bailey et al. 2006), providing insight into possible climate change effects on deep-sea ecosystems. Inter-decadal fluctuations in the abundance of two abyssal macrourids, *Coryphaenoides armatus* and *Coryphaenoides yaquinae*, have been described (Bailey et al. 2006). These species are abundant on the abyssal plains of the eastern North Pacific Ocean and dominate the benthic fish fauna under the California Current (Pearcy et al. 1982; Cailliet et al. 1999). *C. armatus* is common at depths of 2000–4300 m and *C. yaquinae* from 3400 to at least 5800 m (Wilson and Waples 1983). These two species are thought to compose the top trophic position in the food web at an abyssal station (Sta. M) where the benthic ecosystem has been studied extensively (Smith and Druffel 1998). It was hypothesized that the shifts in their abundance resulted from migrations in response to regional changes in food supply. The abundance of epibenthic megafauna, consisting mainly of echinoderms, was used as the food supply index (Bailey et al. 2006). Some information is available on the diet of these species (Haedrich and Henderson 1974; Pearcy and Ambler 1974; Martin and Christiansen 1997) and they are attracted to baited cameras (Priede and Bagley 2000). However, the diet of neither macrourid species has been described from this site, hampering the identification of causal relationships.

In order to understand more accurately the role of macrourids in the food web at abyssal depths and their population responses to food supply, it is important to know their trophodynamics. Samples are expensive to collect in the deep sea, and macrourids have gas bladders that expand upon retrieval to the surface, causing regurgitation or stomach eversion. As a consequence of limited recovery of gut contents, classic stomach examination was augmented by stable isotope analyses. Stable isotopes offer a complementary perspective but have rarely been used on deep-sea fishes. Only one study has been made previously on abyssal fishes (Iken et al. 2001). Stable isotope analyses can infer trophic level (TL) and can discriminate between different sources of food (West et al. 2006). Whereas stomach contents can provide a description of recent meals, stable isotopic compositions integrate the signatures of different prey consumed over much longer periods of time. Isotopic values for a species can be interpreted only in light of the isotopic values of potential prey sources (Post 2002). Thus, isotopic compositions of potential benthic prey and carrion sources also were examined, resulting in the first isotopic data for abyssal animals in the Pacific. The goals of the present study were to describe the diets of *C. armatus* and *C. yaquinae* at Sta. M and to assess the importance of carrion relative to benthic prey, each representing a different trophic pathway.

Methods

Sample collection—All samples were collected at a study site in the eastern North Pacific at ~4100 m (Sta. M). For a complete description of the physical and biological characteristics of this station *see* Smith and Druffel (1998). In brief, this site is located 220 km west of Point Conception, California, on the Monterey Abyssal Fan, and lies underneath the California Current. The bottom is relatively flat with sediments composed of fine silt and clay. Particulate matter fluxes to the seafloor show a distinct seasonal periodicity following a similar pattern in surface water productivity.

Particulate matter fueling the bottom of the food web at Sta. M was sampled in two ways. First, sinking particulate organic matter (POM) was collected in a sediment trap moored 50 m above the seafloor. The mooring collected material in cups from May to August 2006 with a 10-d resolution. Stable isotopic values for each of the 13 cups were averaged. Surface sediments (0–2.5 mm) were collected from three sediment push cores taken with the DSV Alvin in August 2006.

Macrourids, *C. armatus*, and *C. yaquinae* were sampled using baited traps, longlines, and trawls from 1995 to 2006. Each specimen was measured, weighed, and sexed. Macrourids have fragile tail tips that can be broken off naturally or during capture, so length in all cases is pre-anal fin length (PAFL). All specimens were examined for stomach content analysis. Stomachs from specimens that showed no signs of eversion or regurgitation were excised and preserved in 10% buffered formalin. All animals were inspected for net or bait feeding. Only two fish from trawls met our criteria for sampling and only one of these had food in its stomach. It was concluded that net feeding had not occurred because most prey were digested. In traps, the macrourids could not consume bait because it was protected by a screen. Squid (*Illex* sp. or *Loligo opalescens*) used for bait on longlines was cut into square pieces that were easily recognized in stomach contents and were excluded from the analysis.

Tissue samples from macrourids and from a variety of other megafauna (potential prey) were collected during a cruise in August 2006. Animals that were known to be prey from preliminary stomach content analysis were chosen. Species that were abundant in the environment but absent or rare in the macrourid diet (i.e., echinoderms and anemones) were also selected for comparison. Megafauna were collected primarily with the DSV *Alvin*. Slurp guns or scoops were employed so that relatively fragile animals could be collected gently and intact. They were placed in insulated boxes for ascent to the surface. Macrourids and more robust megafauna were also collected with a 12.3-m semi-balloon otter trawl. Upon retrieval to the surface, specimens that showed little or no signs of damage were rinsed free of any adhering sediment and placed on ice. Tissues or whole animals (sediment and digested material removed from the guts) were placed in cryovials and frozen in liquid nitrogen. Additional macrourids were captured using a free-vehicle baited trap. Macrourid white muscle tissue from under the first dorsal fin was dissected free, placed in cryovials, and frozen in liquid nitrogen. Common epipelagic nekton such as *Merluccius productus*, *Trachurus symmetricus*, and gonatid and ommastrephid squids are potential carrion sources, and they were sampled using conventional fishing gear in surface waters. Squid dorsal

mantle muscle was sampled in a similar fashion to fish tissues. All samples were stored at $-80°C$ in the laboratory.

Stomach content analysis—Stomach content analysis followed the procedures described in Drazen et al. (2001). All food items were identified to the lowest taxonomic level possible, counted, and weighed to the nearest 0.01 g. The weight of food as a percentage of body weight was calculated to give a quantitative estimate of fullness. Prey from taxa that were difficult to identify were sent to appropriate taxonomists for specific identification or verification. Cephalopod beaks were identified using published keys (Clarke 1986) and with the help of taxonomic experts. The percentage frequency of occurrence (%FO), percentage contribution to the total number of prey (%N), and percentage contribution to the total weight of the prey (%W) were determined for each prey group. An index of relative importance (IRI = [%W + %N] × %FO) was used and subsequently converted to a proportion of the total IRI values for the species. To simplify the diet data, address unevenness in taxonomic identification of prey, and facilitate comparisons of general feeding modes, prey taxa were grouped into broad categories (Polychaeta, Cephalopoda, small Crustacea, Decapoda [crabs and shrimps], Echinodermata, miscellaneous invertebrate prey [those that did not fit into any of the other prey groupings], Teleostei, carrion, and unidentifiable remains) in a similar fashion to Drazen et al. (2001).

Isotope analysis—Samples for isotope analysis were oven-dried (60°C) and homogenized to a fine powder with a ceramic mortar and pestle. Invertebrate samples, particularly echinoderms and crustaceans, contain a large amount of skeletal calcium carbonate, which can bias $\delta^{13}C$ values of the organic tissues of the animal (Post 2002). As a result, all invertebrate samples were acidified with 12 mol L^{-1} HCl in an acid-fuming container, and dried again prior to isotope measurement. Nitrogen and carbon isotopic compositions were measured in a Finnigan ConFloII/Delta Plus mass spectrometer coupled to a Carla Erba NC2500 Elemental Analyzer. All values are reported relative to international standards (atmospheric N_2 for nitrogen and Vienna Pee Dee Belemnite [V-PDB] for carbon) using conventional notation. Comparisons between species' isotope values were done using Mann-Whitney U-tests.

A multiple source isotope mass balance mixing model was used to assess the relative importance of different prey or prey groups (Phillips and Gregg 2003). This model uses the distinct isotopic values of the various prey to determine the range of all possible source contributions to the macrourid diet. We considered contributions from all potential prey items for which isotopic data were available, whether or not they were found in the stomachs of the macrourids. Phylogenetically and isotopically similar species were grouped prior to analysis to reduce the number of variables in the model. We used an increment of 2% and a tolerance of ±0.1‰ and assumed 0.5‰ enrichment for ^{13}C and 2.5–3.0‰ enrichments for ^{15}N (Vanderklift and Ponsard 2003)—that is, we applied the model first by

assuming 0.5‰ and 2.5‰ shifts in $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and then assuming 0.5‰ and 3.0‰ increases in $\delta^{13}C$ and $\delta^{15}N$ values, respectively. We report the feasible contributions of prey to the macrourids' diets at the 1–99 percentile range using the full range of possible solutions from all model results. Model results for the diet of *C. yaquinae* were also evaluated at an increment of 2% and a tolerance of ±0.1‰, assuming 0.5‰ and 2.5‰ shifts in $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

Results

Stomach contents—Forty-two rattail specimens showed no signs of stomach eversion or regurgitation and were used in the present analysis of food habits: 31 *C. armatus* and 11 *C. yaquinae*. *C. armatus* ranged in size from 15 to 34 cm PAFL. Sample sizes were small, preventing statistical comparisons. However, ontogenetic changes in diet are well known in macrourids (Pearcy and Ambler 1974; Drazen et al. 2001), and because the size range of the *C. armatus* examined was large, specimens were divided into two groups (≤20 cm and >20 cm PAFL), yielding roughly equal numbers in each group. The *C. yaquinae* ranged in size from 12.5 to 19 cm PAFL, a similar size range to the small *C. armatus*. Forty-three prey categories were found, representing 413 total prey items from both species (Table 1).

The diets of small and large *C. armatus* were diverse but with relatively few frequently occurring prey categories. Also, only a few prey categories represented more than 10% of the prey items or 10% of the prey weight. Seventy-five percent of the IRI value of small *C. armatus* was amphipods and unidentified fishes (Teleostei). Copepods were 10% of IRI. Unidentified fishes comprised ~50% of IRI for large *C. armatus*, with 9–11% each *Gonatopsis borealis*, unidentified squid, and *T. symmetricus*. The stomach contents of *C. yaquinae* were different from those of both sizes of *C. armatus* in that they contained on average much more material (as a percentage of body weight, Table 1) and more unidentifiable digested contents. Notably, unidentified polychaetes and *Protankyra brychia* had greater %IRI values and unidentified fish remains lower %IRI in comparison to *C. armatus*.

The diet data were also analyzed by broadly classifying the prey into groups (Table 2). The groups to which prey were assigned are given in Table 1. Small *C. armatus* and *C. yaquinae* had similar proportions of several prey groups, including small amounts of carrion. However, *C. yaquinae* had greater %FO, %N, and %W of polychaetes and echinoderms whereas small *C. armatus* had higher proportions of cephalopods, fishes, and a large miscellaneous invertebrate (*Pyrosoma*). In contrast, carrion comprised 69.2% of the mass of prey of large *C. armatus*. Despite its gravimetric importance, carrion was a small numerical proportion of the prey (13.2%), reflecting the large size of the carrion items, but it was consumed by 40% of the large *C. armatus* examined. These trends were also evident in the %IRI of each prey group.

Several sources of carrion were identified (Table 1). Some carrion was identified because it consisted of animals

Table 1.   Prey consumed by *Coryphaenoides armatus* and *Coryphaenoides yaquinae* as a function of the percentage frequency of occurrence (%FO), of the total number of prey (%N), and of the total weight of the prey (%W). Total numbers of fish, total number of prey, and total prey weight are given at the bottom of the appropriate columns. The column labeled ''Group'' refers to the broad prey group to which that prey was assigned (poly, Polychaeta; ceph, Cephalopoda; carr, carrion; dec, Decapoda (crab and shrimps); scrus, small Crustacea; echino, Echinodermata; tel, Teleostei; misc, miscellaneous invertebrate prey; unident, unidentifiable remains).*

Prey category	Group	*C. yaquinae*				*C. armatus* ≤20 cm				*C. armatus* >20 cm			
		%FO	%N	%W	%IRI	%FO	%N	%W	%IRI	%FO	%N	%W	%IRI
Polychaeta													
Nereidae/Dorvilleidae	poly	0.00	0.00	0.00	0.0	6.25	0.93	0.13	0.1	0.00	0.00	0.00	0.0
Paradiopatra sp.	poly	9.09	0.68	1.36	0.3	0.00	0.00	0.00	0.0	13.33	3.77	2.42	1.7
Polynoidae	poly	9.09	0.68	11.78	1.6	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Travisia sp.	poly	27.27	2.74	2.34	1.9	12.50	0.93	0.39	0.2	0.00	0.00	0.00	0.0
Unident. Polychaeta	poly	63.64	8.90	14.09	20.2	25.00	1.87	0.73	0.9	13.33	3.77	0.05	1.0
Cephalopoda													
Vampyroteuthis infernalis	ceph	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0	13.33	3.77	0.09	1.0
Cirrate Octopoda	ceph	9.09	0.68	0.03	0.1	18.75	1.40	0.43	0.5	0.00	0.00	0.00	0.0
Onychoteuthis borealojaponica	ceph	9.09	0.68	0.01	0.1	12.50	0.93	0.66	0.3	13.33	3.77	0.55	1.2
Berryteuthis anonychus	ceph	0.00	0.00	0.00	0.0	6.25	0.47	0.01	0.0	13.33	3.77	0.02	1.0
Galiteuthis phyllura	ceph	9.09	0.68	0.36	0.1	0.00	0.00	0.00	0.0	6.67	1.89	0.36	0.3
Gonatus pyros	ceph	0.00	0.00	0.00	0.0	6.25	0.47	0.10	0.1	6.67	1.89	0.02	0.3
Gonatopsis borealis	ceph	9.09	0.68	0.14	0.1	0.00	0.00	0.00	0.0	33.33	9.43	4.30	9.3
G. borealis carrion	carr	9.09	0.68	1.69	0.3	12.50	0.93	0.91	0.3	20.00	5.66	6.22	4.8
Chiroteuthis sp.	ceph	0.00	0.00	0.00	0.0	6.25	0.47	7.97	0.8	0.00	0.00	0.00	0.0
Unident. squid	ceph	9.09	0.68	0.00	0.1	31.25	2.80	3.41	2.8	26.67	16.98	2.70	10.7
Crustacea													
Shrimp	dec	18.18	1.37	10.71	3.0	6.25	0.47	0.65	0.1	0.00	0.00	0.00	0.0
Euphausiacea	scrus	9.09	1.37	0.26	0.2	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Lepas sp.	carr	0.00	0.00	0.00	0.0	6.25	4.21	2.82	0.6	0.00	0.00	0.00	0.0
Amphipoda	scrus	72.73	30.14	1.14	31.4	50.00	35.51	1.68	26.6	13.33	3.77	0.01	1.0
Isopoda	scrus	36.36	4.79	0.51	2.7	6.25	0.47	0.02	0.0	0.00	0.00	0.00	0.0
Copepoda	scrus	36.36	10.27	0.06	5.2	25.00	27.57	0.17	9.9	0.00	0.00	0.00	0.0
Mysida	scrus	9.09	0.68	0.05	0.1	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Ostracoda	scrus	9.09	0.68	0.00	0.1	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Tanaidacea	scrus	9.09	0.68	0.01	0.1	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Munidopsis sp.	dec	0.00	0.00	0.00	0.0	6.25	0.47	3.05	0.3	0.00	0.00	0.00	0.0
Unident. Crustacea	unident	36.36	2.74	1.39	2.1	37.50	3.27	1.36	2.5	20.00	5.66	0.07	2.3
Echinodermata													
Holothuroidea	echino	18.18	1.37	7.19	2.1	6.25	0.47	0.24	0.1	0.00	0.00	0.00	0.0
Protankyra brychia	echino	54.55	17.81	5.62	17.6	18.75	2.34	2.87	1.4	0.00	0.00	0.00	0.0
Misc. invertebrates													
Bathysiphon sp.– Foraminifera	misc	0.00	0.00	0.00	0.0	6.25	0.47	0.11	0.1	6.67	1.89	0.03	0.3
Pyrosoma	misc	0.00	0.00	0.00	0.0	6.25	0.47	18.85	1.7	0.00	0.00	0.00	0.0
Priapulida	misc	9.09	0.68	0.99	0.2	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0
Unident. gelatinous prey	unident	9.09	1.37	0.29	0.2	6.25	0.47	1.99	0.2	0.00	0.00	0.00	0.0
Teleostei													
Merluccius productus	carr	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0	6.67	1.89	29.30	4.2
Trachurus symmetricus	carr	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0	13.33	5.66	33.69	10.7
Unident. Teleostei	tel	72.73	8.22	1.98	10.2	87.50	12.15	28.01	50.3	66.67	24.53	12.12	49.8
Sponge spicules		9.09	0.68	0.31	0.1	6.25	0.47	0.06	0.0	0.00	0.00	0.00	0.0
Plant remains		0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.0	6.67	1.89	0.00	0.3
Mud		18.18		1.99		6.25		0.01		13.33		0.01	
Charcoal/wood		0.00		0.00		0.00		0.00		6.67		1.66	
Unident. material	unident	100.0		35.72		75.00		23.36		33.33		6.36	
Totals		11	146	87.1		16	214	86.4		15	53	260	
Mean stomach weight (% body weight)			1.9±2.1				0.8±0.9				0.7±0.8		

* %IRI, index of relative importance; Misc., miscellaneous.

Table 2. Diet of *Coryphaenoides armatus* and *Coryphaenoides yaquinae* using broad prey groups. Diet is expressed as a function of the percentage frequency of occurrence (%FO), of the total number of prey (%N) and of the total weight of the prey (%W).

Prey group	C. yaquinae				C. armatus ≤20 cm				C. armatus >20 cm			
	%FO	%N	%W	%IRI	%FO	%N	%W	%IRI	%FO	%N	%W	%IRI
Polychaeta	72.73	13.01	29.56	21.9	31.25	3.74	1.25	1.4	26.67	7.55	2.47	2.7
Cephalopoda	45.45	2.74	0.51	1.0	62.50	5.14	12.15	9.5	73.33	41.51	8.05	36.3
Small Crustacea	72.73	48.63	2.03	26.1	56.25	63.55	1.87	32.4	13.33	3.77	0.01	0.5
Decapoda	18.18	1.37	10.71	1.8	12.50	0.93	3.69	0.5	0.00	0.00	0.00	0.0
Echinodermata	63.64	19.18	12.81	14.4	18.75	2.80	3.11	1.0	0.00	0.00	0.00	0.0
Teleostei	72.73	8.22	1.98	5.2	87.50	12.15	28.01	30.9	60.00	24.53	12.12	21.9
Carrion	9.09	0.68	1.69	0.2	12.50	5.14	3.74	1.0	40.00	13.21	69.21	32.9
Misc. invertebrates	18.18	0.68	0.99	0.2	18.75	0.93	18.96	3.3	6.67	1.89	0.03	0.1
Unidentified	100.0	4.11	37.40	29.4	75.00	3.74	26.72	20.1	46.67	5.66	6.43	5.6

* %IRI, index of relative importance; Misc., miscellaneous.

that do not have vertical distributions deep enough to bring them into contact with the macrourids. These prey included the barnacle *Lepas* sp., which colonizes floating debris in the open ocean; parts of large jack mackerel, *T. symmetricus*, an epipelagic carangid fish common in the California Current (Brodeur et al. 2003); and Pacific hake, *M. productus*. Pacific hake have a depth range extending to 1000 m (Miller and Lea 1972), but this is not deep enough to encounter the macrourids, even when considering that these species may migrate as much as 1000 m above bottom (Smith et al. 1992). Many squid species have poorly documented vertical ranges, but broadly gonatids, cranchiids, and onychoteuthids occupy the upper 2000 m of the water column or less (Roper et al. 1984; Nesis 1997). In 18 years of time-lapse photography and camera sled transects, squid have never been observed on the seafloor at Sta. M. (K. Smith unpubl.). However, to be conservative squid were considered to have been eaten as carrion if, based on beak lower rostral length to mass regressions (Clarke 1986; Walker et al. 2002), the squid mass was equal to or greater than 50% of the mass of the rattail that consumed it. It does not seem likely that a macrourid could actively attack and consume a squid half its size. Gonatid squid brood a large mass of their eggs in midwater to depths of 2000 m, possibly for a duration of ~6–9 months (Seibel et al. 2005). While brooding they are relatively immobile, do not feed, and could be attacked. In this way a rattail might successfully prey on a gonatid squid; however, the largest amount of food found in a rattail stomach amounted to 14% of its body weight (J. Drazen unpubl.), far less than our 50% threshold. More likely, egg-brooding squid die after their eggs hatch and, because of depleted lipid reserves, sink to the seafloor (Nesis 1997). Using the 50% mass threshold, six macrourids contained squid that were considered carrion. All of these squid were the gonatid *G. borealis*. They ranged in size from 1140 to 1460 g or from 59% to 161% of the rattail mass. Smaller specimens were not considered as carrion using the rationale described above; therefore, Table 1 divides this species into *G. borealis* and *G. borealis* carrion.

Isotope analyses—Isotope values in this study ranged from 8.6‰ (POM) to 19.7‰ (*Travisia* sp.) for $\delta^{15}N$ and from −21.7‰ (POM) to −16.8‰ (*Travisia* sp.) for $\delta^{13}C$

(Fig. 1). POM had a similar $\delta^{13}C$ value to sediments and was depleted in ^{15}N relative to sediments by ~0.8‰. The $\delta^{15}N$ and $\delta^{13}C$ values for the benthic animals, excluding the carrion sources and amphipods (*see* below) were highly correlated ($\delta^{15}N = 50.72 + 1.85 \times \delta^{13}C$; $n = 16$, $r^2 = 0.89$, $p < 0.001$).

The isotope ratios of 13 species of benthic megafauna were determined ($n = 1$–5) and they generally fell on a line from the bottom left to the upper right of Fig. 1. A cluster of taxa were found at ~15‰ $\delta^{15}N$ and −20‰ $\delta^{13}C$ values. This included the tube-dwelling onuphid polychaete *Paradiopatra* sp., the holothuroids *Abyssocucumis abyssorum* and *Peniagone vitrea*, and the ophiuroids *Ophiura bathybia* and *Ophiacantha* sp. Assuming a trophic enrichment factor for $\delta^{15}N$ of 3.0‰ and that the POM would represent TL 1 in this system, this cluster of echinoderms was at TL ~3, representing omnivores or secondary consumers. The holothurian, *P. brychia*, had much higher isotopic values (TL = 3.9) than the other echinoderms and was similar to the galatheid crab *Munidopsis* sp. and the anemone *Bathyphellia australis*. The highest isotopic values were exhibited by the large predatory aphroditid polychaete *Laetmonice* sp., an unidentified benthic caridean shrimp, and a large burrowing opheliid polychaete *Travisia* sp. The amphipods (Lysianassidae) had a highly negative $\delta^{13}C$ signature and did not fall on the general line with the rest of the benthic megafauna. The C:N ratio of the amphipods was 7.6, about twice that of the other megafauna, indicating a high lipid content. Lipid synthesis favors incorporation of ^{12}C; thus, lipid-rich organisms have very low $\delta^{13}C$ values (Post et al. 2007), to the point of obscuring food web effects.

Isotopic values for several sources of carrion were obtained, and they were distinct from those of the benthic fauna (Fig. 1). The epipelagic fishing efforts at the station in August 2006 resulted in the capture of Humboldt squid *Dosidicus gigas*. In addition to squid, the stomach content analysis identified hake and jack mackerel as carrion. Therefore, isotopic values for hake, *M. productus* ($n = 6$), and jack mackerel, *T. symmetricus* ($n = 44$), from the California Current were taken from the literature (Miller et al. unpubl.). Data for three juvenile hake collected off central California are also presented (Kim et al. unpubl.). The
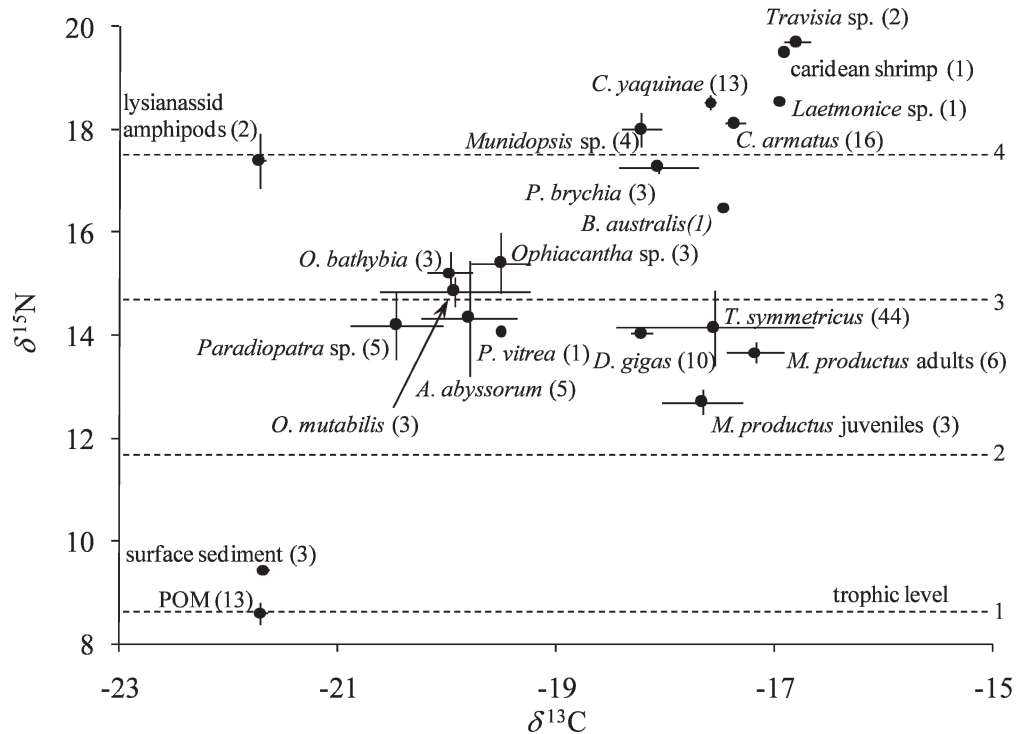
Fig. 1. Carbon and nitrogen isotopic compositions of *C. armatus* and *C. yaquinae*, other megafauna, surface sediments (0–0.25 cm), and POM (from sediment trap 50 m above bottom) at Sta. M. Means and standard errors are shown with sample sizes in parentheses. Dotted horizontal lines represent TLs based on $\delta^{15}N$, assuming that the values for POM are TL 1, and a trophic enrichment factor of 3.0 (*see* text).

$\delta^{15}N$ values of these epipelagic nekton (white muscle or mantle) were some of the lowest in the study and similar to the benthic echinoderms (Fig. 1). On the other hand, $\delta^{13}C$ values were much less negative than values for the echinoderms.

$\delta^{15}N$ and $\delta^{13}C$ values of *C. armatus* were 18.1‰ ± 0.08‰ and −17.4‰ ± 0.09‰ ($n = 16$, mean ± SE) and were 18.5‰ ± 0.14‰ and −17.6‰ ± 0.06‰ ($n = 13$) for *C. yaquinae*, placing both species near the top of the range (TL 4.2–4.3), but lower than two large polychaetes and an unidentified caridean shrimp (Fig. 1). Size-related differences in the isotopic composition of *C. armatus* were investigated by regression and by comparing the ≤20 cm PAFL group ($n = 8$) to the >20 cm PAFL group ($n = 8$), but in both cases no significant effect of size was found ($p > 0.05$). Values for the two macrourid species were significantly different from each other ($p < 0.05$). However, these differences were small in relationship to the spectrum of isotopic values for all benthic megafauna (Fig. 1).

An isotope mixing model was applied to examine the potential contributions of different types of prey (Table 3). The deposit-feeding echinoderms were grouped (except for the isotopically distinct holothuroid *P. brychia*) and represented by their average isotopic value ($\delta^{15}N$ 14.77‰ and $\delta^{13}C$ −19.75‰). The same was done for the epipelagic nekton, representing potential carrion ($\delta^{15}N$ 13.64‰ and $\delta^{13}C$ −17.66‰) and the large polychaetes ($\delta^{15}N$ 19.13‰ and $\delta^{13}C$ −16.88‰).

Conservatively using the 1–99 percentile ranges gave wide ranges in the possible contributions of each group, but allowed for comparisons of the relative importance of different prey. In *C. armatus* carrion was the only prey group with a minimum feasible contribution greater than 0% and had the highest maximum contribution (Table 3). The anemone *B. australis* had the next highest maximum potential contribution of 50%, with the remaining benthic prey groups much less. The relative ranking of each group's potential contribution was the same for *C. yaquinae*. However, carrion had a lower range of feasible contribution to the diet and the benthic prey had higher contributions than in *C. armatus*. The model was also run with *B. australis* removed (*see* discussion below). This resulted in a slightly greater feasible contribution of several benthic prey groups for both macrourid species and a considerable increase in the minimum contribution of carrion (Table 3).

Discussion

Diet from stomach contents—The diet of *C. armatus* consisted primarily of fish and cephalopods regardless of size, with small crustaceans more numerous in smaller fish and carrion comprising greater than half the mass of the diet of larger animals. Off the coast of Oregon (1974) and in the north Atlantic (Haedrich and Henderson 1974; Martin and Christiansen 1997) *C. armatus* diet shifted from a predominance of benthic prey to a diet of fishes and squids at larger sizes, similar to our results. Martin and Christiansen (1997) found large numbers of lysianassid amphipods in smaller specimens just as in our data. These studies all found carrion, such as squid, or other scavenged material, such as oranges, onion peels, algae, and plastic, in the stomachs of *C. armatus*. However, this is the first study to quantify its gravimetric importance. Although, we have a small sample size, our

Table 3. Results of stable isotope mixing model calculations (IsoSource; Phillips and Gregg 2003) showing the distribution of feasible contributions from each source to the diet of *Coryphaenoides armatus* and *Coryphaenoides yaquinae*. Values shown in parentheses are the feasible contributions from each source to the diet of these macrourids, including anemone (*see* explanation in text). Prey have been corrected for trophic fractionation of 0.5‰ for $\delta^{13}C$ values and 2.5–3.0‰ for $\delta^{15}N$ values. Values shown are the 1–99 percentile ranges for these distributions using a 2% increment and 0.1‰ tolerance.

	C. armatus	*C. yaquinae*
Potential prey	Feasible contribution of prey (%)	Feasible contribution of prey (%)
Lysianassid Amphipoda	0–8 (0–8)	0–12 (0–12)
Paradiopatra sp.	0–14 (0–14)	0–22 (0–22)
Echinodermata	0–18 (0–18)	0–28 (0–28)
Shrimp	0–28 (0–24)	0–30 (0–26)
Predatory Polychaeta	0–28 (0–26)	0–32 (0–28)
Munidopsis sp.	0–30 (0–26)	0–38 (0–34)
Protankyra brychia	0–38 (0–32)	0–46 (0–42)
B. australis	(0–50)	(0–56)
Carrion	44–70 (28–68)	28–58 (10–56)

estimate of 69.2% of the mass of food of large *C. armatus* is very large. Pearcy and Ambler (1974) classified prey of *C. armatus* as benthic or pelagic, the latter including a variety of mesopelagic or bathypelagic shrimps, fishes, and squids. Some of these prey may have been consumed alive and the authors indicate only that some were very likely carrion because of their shallow distributions or, in the case of squids, very large size. For *C. armatus,* their pelagic fraction was 61–100% of the mass of prey in animals 30 cm total length (13 cm PAFL) or larger. This matches our largest size category, but we found that for smaller *C. armatus*, 15–20 cm PAFL, only 3.74% of the mass of prey was carrion. Fishes and cephalopods, the main taxonomic groups of carrion, had the highest %IRI values for small *C. armatus* (Table 2). Because of the conservative nature of our classification of these items as carrion, it is likely that we have underestimated the importance of this food type.

The diet of *C. yaquinae* consisted of more infaunal and epifaunal prey and lacked the large contributions by fishes, squid, and carrion seen in either small or large *C. armatus* (Table 1). The small sample sizes for this species do make interpretations of the data difficult. %IRI values can be skewed by low sample sizes because of their sensitivity to %FO. For the broad prey groups, however, the differences between the fishes are reflected in the other three diet metrics (Table 2). In addition, 15 specimens captured off northern California at 4300 m consumed a variety of benthic invertebrates such as polychaetes and amphipods, similar to the present results (Stein 1985).

Ontogenetic shifts in diet probably account for most of the differences in feeding between the two macrourid species. Ontogenetic changes in diet are common in fishes, including macrourids (Pearcy and Ambler 1974; Drazen et

al. 2001). *C. armatus* and *C. yaquinae* may partition food resources by having different depth distributions (Wilson and Waples 1983) and, where they overlap, by having different size frequency distributions. *C. yaquinae* is smaller than *C. armatus* at Sta. M (Drazen 2007) and larger individuals may be found deeper or farther into the Pacific gyre. It is well known that *C. armatus* individuals are "bigger–deeper," attaining their largest sizes at abyssal depths (Collins et al. 2005).

Isotopic signatures of potential prey—Abyssal systems are fueled by the allochthonous transport of organic material from surface waters. At Sta. M there is a seasonal pulse of organic matter lagging the surface spring phytoplankton bloom by a few months (Baldwin et al. 1998). This food is utilized by sediment-dwelling macrofauna such as foraminiferans and harpacticoid copepods (Drazen et al. 1998; Sweetman and Witte 2008). The activity of many deposit-feeding echinoderms also increases in response (Kaufmann and Smith 1997) and tracer studies indicate that they consume phytodetritus (Lauerman et al. 1997). Long-term fluctuations in echinoderm abundances and size frequencies correlate with the vertical flux of phytodetritus (Ruhl and Smith 2004; Ruhl 2007). The $\delta^{13}C$ and $\delta^{15}N$ values of POM collected 50 m above bottom and surface sediments are the lowest isotopic signatures measured in this study, as would be expected for the base of the food web. $\delta^{13}C$ and $\delta^{15}N$ values of the benthic animals and basal organic matter (POM and surface sediments) were strongly correlated, indicating that the photosynthetically derived organic matter is the base of this abyssal food web, as found in other isotope studies of bathyal (Polunin et al. 2001) and abyssal (Iken et al. 2001) environments.

The only echinoderm found in the stomachs of *C. armatus* and *C. yaquinae* in the North Pacific (Table 1; Pearcy and Ambler 1974) is the vermiform burrowing holothuroid *P. brychia* (Lauerman et al. 1996). Its isotopic signature was much higher than that of the rest of the echinoderms, indicative of a higher TL and perhaps a different biology. Macrourids do not eat many echinoderms (Pearcy and Ambler 1974; Stein 1985; Martin and Christiansen 1997) even though they are very abundant and dominate the epibenthic megafauna in most abyssal habitats and at this site (Lauerman et al. 1996). This suggests that macrourids may actively avoid them because of their low caloric density and high carbonate content (Billett 1991) or because of toxicity or distastefulness (Stonik et al. 1999). Absence of echinoderms in acidic macrourid stomachs is probably not an artifact resulting from rapid digestion, because carbonate-rich ophiuroids are most of the few echinoderms found (Pearcy and Ambler 1974; Drazen et al. 2001).

The isotopic signatures of the three species of epipelagic nekton were distinct from the abyssal benthic fauna because the abyssal food web may have an isotopic baseline that is enriched in ^{15}N compared to that in the epipelagic ocean. It has been shown that sinking particulate matter can have $\delta^{15}N$ values 3–4‰ higher than that of suspended particulate nitrogen, or phytoplankton, in surface waters, or $\delta^{15}N$ values similar to the deep nitrate pool (Altabet et

al. 1999). This is partly the result of sinking material, including zooplankton fecal pellets, molts, etc., in addition to dead phytoplankton (Montoya et al. 2002). The composition of seafloor phytodetritus at Sta. M varies temporally but does include such material, including large numbers of phaeodarian radiolarians and zooplankton mucous webs (Beaulieu and Smith 1998). Bacteria colonize sinking particles, and it is feasible that phytodetritus could become enriched in ^{15}N relative to surface-water suspended particulate nitrogen through this metabolic processing of the organic material. However, studies of the $\delta^{15}N$ values of sinking particulate matter below the photic zone find small increases or no change with depth (Wu et al. 1999). A ^{15}N enrichment of the phytodetritus relative to phytoplankton is consistent with the relatively low $\delta^{15}N$ values for large epipelagic nekton. Their TL is certainly higher than indicated in Fig. 1, based on the POM collected in deep sediment traps as TL 1. The more positive $\delta^{13}C$ values for these animals are more difficult to explain. Although we sampled muscle tissue of the epipelagic nekton vs. whole benthic deposit feeders, their C:N ratios were similar, suggesting that the lipid contents in these organisms were roughly similar. Regardless of the mechanism, epipelagic nekton as potential carrion have an isotopic signature different than most of the macrourids' benthic prey. The nekton have significantly lower $\delta^{15}N$ values than the trophically similar species in the benthic food web. This could impart lower than expected $\delta^{15}N$ values in the macrourids compared to other species that do not eat carrion.

Rattail diet inferred from stable isotope analyses—The isotopic values of the two macrourid species suggest, at first, a trophic position lower than that of large predaceous polychaetes and a benthopelagic caridean shrimp. This is a surprising result, particularly in light of the diet data (Tables 1, 2), which suggest that they are the top predators in their habitat eating shrimp and large polychaetes. However, when the isotopic values of the carrion are considered, it becomes clear that the macrourids' isotopic compositions represent a mix between relatively enriched benthic prey and relatively depleted epipelagically derived carrion. Indeed, results of isotopic mass balance revealed that carrion is the most important trophic category (Table 3).

Results from the isotopic mixing model corroborate the stomach content findings in most cases, but with a notable exception. Generally, the isotope mass balance mixing model results indicate that carrion was very important, and it was found to comprise a major fraction of the mass in large *C. armatus* stomachs. *P. brychia*, predaceous polychaetes, crabs, and shrimp contributed less to the diet than carrion but more than echinoderms, tube-dwelling polychaetes, and amphipods—results similar to the gravimetric contributions to stomach contents. However, what contrasted was the importance of the anemone *B. australis*. This species was initially chosen because it was considered very unlikely prey and a good comparison to known prey. Most fishes do not consume cnidarians because of the nematocysts and associated

toxins. Fishes that specialize in eating cnidarians often have pharyngeal mills and other morphological adaptations (Haedrich 1967) that are not present in the macrourids. The isotope mixing model simply calculates the relative contribution of isotopic entities such as *B. australis*. When *B. australis* is removed from the mixing model, the relative contributions of carrion increase, suggesting an even greater importance of this type of food to the macrourids.

Both macrourid species have similar isotopic compositions relative to benthic and epipelagic prey sources. Their average $\delta^{13}C$ values are within analytical precision, but the $\delta^{15}N$ value of *C. armatus* is significantly lower (0.4‰), possibly because of a greater amount of carrion (relatively low $\delta^{15}N$ values; Fig. 1) in its diet, as suggested by stomach content data. The mixing model results also suggested a slightly smaller contribution of carrion and higher contributions of benthic prey for *C. yaquinae*, but the model differences are small relative to those suggested by the stomach content analysis. Our sample sizes for stomach contents, which provide only a snapshot of food habits, are small, but general trends are clear and are corroborated by previous studies (Pearcy and Ambler 1974; Stein 1985). Nevertheless, the isotopic results suggest that a full comparison of diet between these two species will require additional concurrently collected stomach samples.

Our results suggest that these abyssal macrourids bypass the abyssal benthic food web (Fig. 2). Both isotopic and diet data indicate that they feed on benthic fauna and are abyssal top predators. However, a considerable fraction of their nutrition is derived from feeding on large, higher-TL animals from the epipelagic food web. In the abyssal North Atlantic, several top predatory fishes, including *C. armatus*, had $\delta^{15}N$ values indicative of a TL lower than many benthic invertebrates such as polychaetes, asteroids, and hexactinellid sponges (Iken et al. 2001). Scavenging is a likely explanation, and we suggest that bypassing the benthic food web by abyssal fishes may be common. Consumption of carrion by deep-sea fishes has been known for a long time. Many studies have photographed a diversity of fishes and invertebrates at bait falls in the deep sea (Priede and Bagley 2000), but whether the observations represented simple opportunism in a food-poor environment or an important trophic mode remained uncertain. What is new here is that, for at least some of these species, carrion is a significant source of nutrition, probably more important than benthic prey from their own habitat.

The benthic community in the eastern abyssal Pacific is supported by allochthonous inputs of organic matter, and different types of inputs fuel different levels of the food web. Both carrion and phytodetritus are ultimately produced by primary production in surface waters (Fig. 2). A classical food web with sinking phytodetritus as its base supports the sediment infauna and many benthic invertebrates. However, abyssal macrourids consume the allochthonous supply of nekton carcasses for much of their nutrition, thus bypassing the classic phytodetrital food web. As a result, the populations of these abyssal fishes are weakly linked to benthic
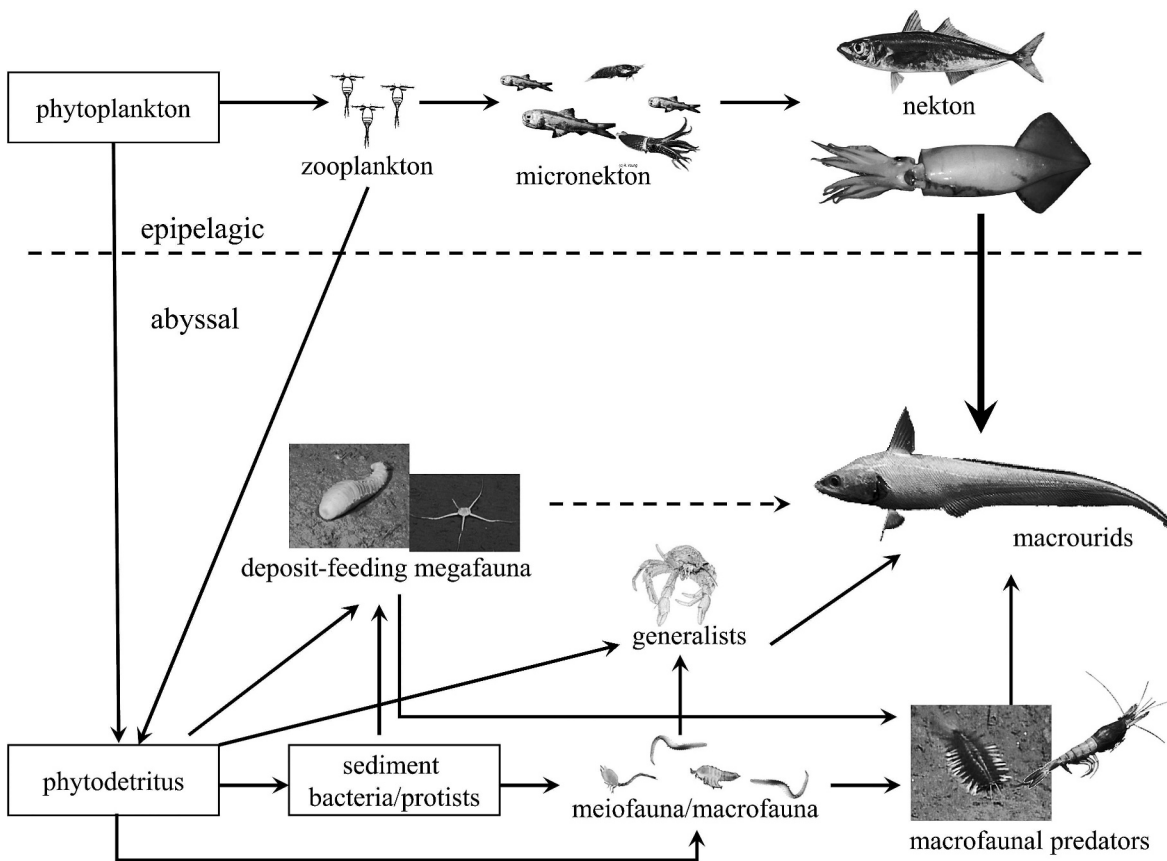
Fig. 2. Simplified trophic pathways from primary production to macrourid fishes at Sta. M. The classical phytodetrital pathway and its bypass by the allochthonous input of carrion are illustrated. For pathways leading to the macrourids, more important paths are indicated by thick arrows and minor ones are indicated by dotted lines. The image of the jack mackerel was provided by the International Game Fish Association.

community dynamics and more strongly linked to processes affecting the epipelagic nekton. Previous work has focused on linking benthic community dynamics to climate processes that affect phytodetrital flux (Smith and Kaufmann 1999; Ruhl and Smith 2004; Bailey et al. 2006). Changes in surface water productivity that influence phytodetrital flux will affect the entire epipelagic ecosystem through bottom-up forcing. However, epipelagic nekton populations in the Pacific have experienced reductions and changes in community composition related to fishing (Sibert et al. 2006; Zeidberg and Robison 2007) and climate change (Brodeur et al. 2003). There is currently no commercial fishing in the abyss, but pelagic fisheries generate bycatch, and the discards could fuel abyssal fish populations. Alternatively, reductions in nekton biomass could negatively affect abyssal fish populations and/or generate an increase in predation pressure on benthic populations. Climate-related changes in epipelagic nekton distributions or composition could also change carrion flux. The trophic links established in this study suggest that a future understanding of abyssal fish dynamics should include a consideration of epipelagic nekton populations and the anthropogenic forces affecting them.

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