J.C. Drazen

Energy budgets and feeding rates of *Coryphaenoides acrolepis* and *C. armatus*

Abstract This study develops energy budgets and esti-mates feeding rates for two macrourid fishes, *Coryphae-noides acrolepis*, dominant in the bathyal eastern North Pacific, and the abyssal cosmopolitan species, *Corypha-enoides armatus*. Daily energy expenditure by *C. acrolepis* was nearly twice that of *C. armatus*. *C. acrolepis* allocated nearly equal amounts of energy to metabolism and growth. Once sexual maturity was reached reproduction became the dominant energetic cost. Either these costs are necessary to retain adequate numbers of eggs and larvae on the continental slopes, or this fish does not reproduce on an annual basis and the calculated costs are an overestimate. *C. armatus* allocated relatively more energy to metabolism than growth. It may be semelp-arous, and this strategy would be of great energetic savings in its food-poor but stable environment. Indi-vidual daily ration for *C. acrolepis* decreased from 0.31% to 0.07% of body weight (BW) and for *C. armatus* from 0.12% to 0.02% BW with increasing fish length. These rates are substantially lower than those for fishes living in cold waters on the continental shelves. The population feeding rates for *C. acrolepis* ranged from 0.8 to 15 kg km^{-2} day^{-1} and for *C. armatus* from 5 to 2,800 g km^{-2} day^{-1}. The scavenging behaviour of *C. acrolepis* was used to investigate the role of carrion as a food supply to the deep-sea benthos. It was estimated that the carrion eaten by *C. acrolepis* is equivalent to 0.04 mg C m^{-2} day^{-1} or only 0.2–0.4% of the average small particulate flux.

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J.C. Drazen
Scripps Institution of Oceanography, University of California,
San Diego, Marine Biology Research Division,
9500 Gilman Drive, La Jolla, CA 92093-0202, USA

E-mail: jdrazen@ucsd.edu

Present address: J.C. Drazen
Monterey Bay Aquarium,
Research Institute (MBARI), 7700 Sandholdt Rd,
Moss Landing, CA 95039-9644, USA
e-mail: jdrazen@mbari.org

Carrion consumption is important for scavengers like *C. acrolepis*, but it is not an important component of the carbon flux into the deep-sea benthic environment.

Introduction

Many studies of the diet and feeding habits of demersal deep-sea fishes have been performed (reviewed by Gartner et al. 1997; Merrett and Haedrich 1997). These studies indicate that some macrourid fishes, among the dominant fishes in the deep sea (Marshall and Iwamoto 1973; Stein and Pearcy 1982; Wakefield 1990; Merrett 1992; Lauth 1998), are among the top predators (Mauchline and Gordon 1984; Martin and Christiansen 1997; Drazen et al. 2001). Top predators play a vital role in many communi-ties by controlling prey populations, exerting selective pressure and influencing general community dynamics. In addition to diet information, quantitative estimates of predatory impacts require feeding rates. Feeding rates of deep-sea organisms are also needed to quantitatively construct food-web and biogeochemical models.

Currently, almost no data are available for approxi-mating feeding rates of any demersal deep-sea fish. Al-though limited in scope, two types of data exist, those that infer meal frequency and others that estimate av-erage daily rations. Meal frequency for macrourids, *Anoplopoma fimbria* and some other deep-sea fish is thought to be low, with long intervals between feeding bouts (Smith and Hessler 1974; Smith 1978; Sullivan 1982). These hypotheses are based on indirect evidence. For example, neutral lipid concentrations of the mac-rourid *Coryphaenoides armatus* suggest this fish could go without feeding for up to 200 days (Smith 1978).

Two methods to estimate average daily ration have been used for deep-sea studies. Macpherson (1985) was the first to estimate feeding rates (defined here as average daily ration) in deep-sea demersal fish. He used the gastric evacuation method (reviewed in Bromley 1994). Gastric evacuation is the rate at which food is moved from the

stomach to the intestine, and must be determined under controlled laboratory conditions, making it impossible to determine for most deep-sea fishes. Therefore, Macpherson (1985) used evacuation rates from shallow-living cod and estimated the feeding rate of the bathyal macrourid *Coelorhynchus fasciatus* to be between 0.55% and 2.15% of body weight per day (BW day^{-1}). Koslow (1996) has recently attempted to calculate the daily ration of several benthopelagic, benthic and seamount-associated deep-sea fishes using energy budgets. An energy budget assumes that the energy consumed in food must be spent by the fish in production (growth), reproduction, metabolism, or lost as wastes (Brett and Groves 1979; Gerking 1994). Koslow (1996) estimated the feeding rate of macrourids to be between 0.05% and 0.10% BW day^{-1}. However, he did not include any size scaling relationships to estimate changes in feeding rates and energetic partitioning with the length of the fish.

Energy budgets can also be used to assess energetic strategies. Koslow (1996) compared energy partitioning between seamount-associated and benthopelagic deep-sea fishes. He found that seamount-associated fishes had relatively higher total energy expenditures which were the result of greater metabolic rates. These fishes encounter high and variable currents, and an active locomotory capacity is required to maintain their position in the water column. Despite their high energy use, these fishes had slow growth, comparable to that of the benthopelagic species. Comparisons of meso- and bathypelagic fishes also suggest differences in energy partitioning. Bathypelagic species have very low metabolic rates and higher growth rates in comparison to mesopelagic species (Childress et al. 1980). Bathypelagic species may not require good locomotory capacities in their dark environment, so instead they invest energy in growth, to increase the size range of potential prey they could eat and reduce predation risk.

The present study constructs energy budgets and estimates feeding rates for two of the dominant macrourids in the North Pacific, *Coryphaenoides acrolepis* and *C. armatus*. Since earlier efforts (Koslow 1996), new data on the diet (Drazen et al. 2001) and growth (Andrews et al. 1999) of *C. acrolepis* have been presented, allowing for a more accurate energy budget with fewer assumptions. Furthermore, an effort is made to scale the energy budgets to the size of the fish. The energy budgets allow an examination of energy partitioning in benthopelagic fishes to see what, if any, adaptations exist to their environment. For the first time, consumption rates for major prey groups are determined and the importance of *C. acrolepis* and *C. armatus* in deep-sea food webs is assessed.

The model

Energy budgets

Energy budgets were modelled using the equation below and scaled to the length of the fish.

$$0.8 \times \text{consumption } (C) = \text{metabolism } (M) + \text{growth } (G) + \text{reproduction } (R) \quad (1)$$

It was assumed that 80% of the food consumed was used in metabolism, growth, or reproduction and that the remaining 20% was lost as wastes (Brett and Groves 1979). Table 1 lists the values used for each component (M, G and R) and the source for the data. All units were converted to kilojoules for the models.

Metabolic rates were estimated from in situ respirometer measurements (Smith and Hessler 1974; Smith 1978), and the scaling coefficients come from a regression between fish weight and respiration using data for both species (mass range: 0.5–1.8 kg; Smith and Brown 1983). A factor of 19.4 kJ l^{-1} O$_2$ was used to convert respiratory rates to metabolic energy consumption. The growth of *C. acrolepis* was described using a von Bertalanffy growth function (Andrews et al. 1999). Age was estimated by counting rings in otolith thin sections and validated using a radiometric technique. Growth information was converted from increases in length to increases in mass, using length-to-mass regressions (Table 1). The energy density of each species was determined from proximate composition data (Drazen 2002) and was then used to estimate the energy (kJ) required for each gram of body mass added. The growth rates of *C. armatus* have been estimated using counts of otolith rings (Wilson 1988), but there is no validation of the annual periodicity of these rings and the ages estimated are considerably younger than those of any other deep-sea fish. Therefore, *C. armatus* growth (von Bertalanffy parameters, k and L_{inf}) was estimated from *C. acrolepis* growth. L_{inf}, the asymptotic size of the species, was estimated from the known maximum lengths of the fish. Fish collected in my studies and by Stein and Pearcy (1982) suggest a maximum length of 34 cm pre-anal fin length (PAF). The growth coefficient, k, is more difficult to determine. *C. armatus* lives at abyssal depths, much deeper than the slope-dwelling *C. acrolepis* (Iwamoto and Stein 1974). The abyssal environment is characterised by lower temperatures and lower food supply than the continental slope (Gage and Tyler 1991). Therefore, it was assumed that *C. armatus* growth could not be faster than that of *C. acrolepis* (it is likely to be slower), and k was assigned a value one-half that of *C. acrolepis*. The resulting growth curves for both species are given in Fig. 1.

Reproductive output was modelled differently for each of the species. Conflicting studies show that reproduction may be seasonal (Matsui et al. 1990) or continuous in *C. acrolepis* (Drazen 2002). There is no information available about what proportion of the population spawns each year. It was assumed that all adult animals spawned and reproductive expenditure equalled gonad weight [gonadosomatic index (GSI)×body mass] multiplied by the energy density of the eggs every year. The energy density of ripe *C. acrolepis* eggs has not been measured, but it is probably similar to that of *C. rupestris* from the North Atlantic, because these macrourids both have large eggs with a large oil droplet (Stein and Pearcy 1982; Grigor'ev and Serebryakov 1983). The proximate composition of ripe eggs (Craik and Harvey 1987) was converted to energy density using the following conversion factors: 23.85 kJ g^{-1} protein, 36.4 kJ g^{-1} lipid and 17.15 kJ g^{-1} carbohydrate (Childress et al. 1990). *C. armatus* has a very high fecundity in comparison to other macrourids. Despite extensive collections, only one ripe and no post-spawning *C. armatus* have been captured, suggesting that this species is semelparous (Stein 1985). Therefore, growth of the fish throughout its life also represents the growth of its gonads, which are spent once before the fish dies. Energy for gonad development may be accumulated in the liver as it is for many other fish (Love 1970). The liver of *C. armatus* enlarges dramatically with total fish mass (hepatosomatic index (HSI) up to 18%) and is very high in lipid (Stein and Pearcy 1982; Drazen 2002). The growth of this energy-dense organ is reflected in the increasing energy density with size (Table 1). Much of this energy could be expended in gonad development or reproductive behaviours (mate location, migration, etc.) just prior to spawning.

Table 1 *Coryphaenoides* spp. Sources of data for energetic parameters and feeding rate models. Energy budgets take the form of 0.8×consumption = metabolism + growth + reproduction (Brett and Groves 1979). Reproductive information comes from several sources; von Bertalanffy growth parameters (k, L_{inf} and t_0) are shown. See "The model – Energy budgets" for derivation of growth in *C. armatus* (*PAF* pre-anal fin length; *GSI* gonadosomatic index)

Parameter	*C. acrolepis*		*C. armatus*	
	Value	Source	Value	Source
Respiration	2.4 ml O_2 kg^{-1} h^{-1}	Smith and Hessler (1974)	2.7–3.7 ml O_2 kg^{-1} h^{-1}	Smith (1978)
Metabolic scaling	2.85 ± 5.0 $wt^{-0.35 \pm 0.08}$	Smith and Brown (1983)	2.85 ± 5.0 $wt^{-0.35 \pm 0.08}$	Smith and Brown (1983)
Growth	$k = 0.041 \pm 0.01$	Andrews et al. (1999)	$k = 0.0205$	Estimated – present study
	$L_{inf} = 27.2 \pm 2.6$ cm PAF, $t_0 = 0.25$		$L_{inf} = 34.0$ cm PAF, $t_0 = 0.25$	
Energy density	4.39 ± 0.046 kJ g^{-1}	Drazen (2002)	$0.19 \pm 0.091 \times PAF^{0.63 \pm 0.16}$	Drazen (2002)
Length-weight	$wt = 0.2555 \pm 0.045 \times PAF^{2.697 \pm 0.058}$	R.R. Lauth (unpublished data)	$wt = 0.129 \pm 0.029 \times PAF^{2.944 \pm 0.068}$	Drazen (unpublished data)
Reproduction	GSI = 12.8–14.5, maturity at ~16 cm PAF	Stein and Pearcy (1982); Matsui et al. (1990); Drazen (2002)	Semelparous?	Stein (1985); Drazen (2002)
Energy density of eggs	5.23 kJ g^{-1}	Craik and Harvey (1987)	5.23 kJ g^{-1}	Craik and Harvey (1987)

Feeding rates

The dietary analysis for *C. acrolepis* was taken from Drazen et al. (2001) and for *C. armatus* from Pearcy and Ambler (1974). Both of these studies provide the gravimetric composition of the diet and ontogenetic differences in diet. The broad prey categories of each study were used because they should reflect the general feeding habits of the fishes and should not be as affected by specific changes in prey composition. For convenience the diet of each species is listed in Table 2. The percent contribution of each prey type given by Pearcy and Ambler (1974) are percentages of identifiable prey. These have been adjusted to account for the unidentifiable portion. Each species exhibits pronounced ontogenetic shifts in diet, so feeding rates were calculated for each size class in the diet studies to facilitate determination of taxon-specific feeding rates. The size classes given in Pearcy and Ambler (1974) were converted from total length (TL) to PAF (TL = 12.743 + PAF×2.364, $r^2 = 0.96$, $n = 88$; Drazen, unpublished data).

The energy budgets give estimates of feeding rates in kilojoules. To convert these units to wet mass of prey, the energy density of the prey must be determined (Table 2). Energy densities derived from bomb calorimetry were taken from representative taxa collected primarily on the continental slope (Steimle and Terranova 1988; Dauvin and Joncourt 1989). The average energy density of the diet was calculated as a weighted average of the energy densities of each prey type according to its gravimetric contribution. Multiplying the feeding rate (kJ $fish^{-1}$ day^{-1}) by the energy density of the diet (kJ g^{-1}) yields the feeding rate in grams per fish per day. Feeding rate was also expressed as a proportion of body weight. Feeding rates for each prey type were calculated for each size class of fish as the product of the total feeding rate and gravimetric contribution to the diet. For these calculations, I used the median body weight and feeding rate from the energy budgets for each size class.

Population feeding rates, the average daily consumption by all members of the population in a given area, were also calculated for total prey and for each prey type. These feeding rates are simply the product of the density of individuals in a size class and the individual feeding rate. The data on population density and structure (size-frequency) of *C. acrolepis* was taken from Wakefield (1990) and Lauth (1998), for depths between 600 and 1,600 m on the continental slope of the contiguous United States. Density estimates ranged from 4,900 to 9,390 fish km^{-2}. The population density of *C. armatus* was taken from several sources using data in both the North Pacific and North Atlantic between 2,300 and 5,200 m (Pearcy et al. 1982; Cailliet et al. 1999; Merrett 1992).
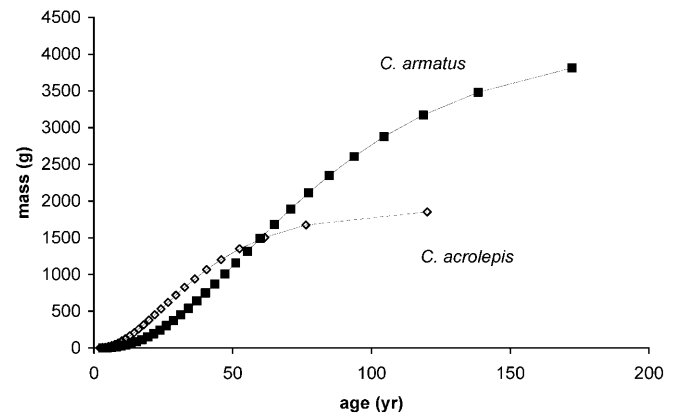

Fig. 1 *Coryphaenoides* spp. Von Bertalanffy growth function for *C. acrolepis* (Andrews et al. 1999) converted to mass growth. Growth parameters are: $k = 0.041$, $L_{inf} = 27.2$ and $t_0 = 0.25$. The growth of *C. armatus* is plotted for comparison. Growth parameters are: $k = 0.0205$, $L_{inf} = 34.0$ and $t_0 = 0.25$ (Table 1)

Density estimates ranged from 250 to 1,971 fish km^{-2}. Population structure was from Stein and Pearcy (1982) over the same depth range (same sampling as in Pearcy et al. 1982).

Model error

Minimum and maximum values or standard errors for model parameters were incorporated to generate a range of values for feeding rate estimates. For instance, the standard errors associated with metabolism, growth parameters, and minimum and maximum values for GSI, and the standard deviation of the energy density of the diet are all incorporated to give minimum and maximum feeding rates (g $fish^{-1}$ day^{-1}). Population feeding rates also have minimum and maximum values derived from the range in individual feeding rates and the range in population densities. This method gives a conservative and broad range of values, because the errors in each parameter in the energy budgets are additive and for the calculation of feeding rate they are multiplicative.

Table 2 *Coryphaenoides* spp. Gravimetric composition of the diets of *C. acrolepis* and *C. armatus* and energy densities (kJ g^{-1} wet wt; mean $\pm$ SD) used for each prey type. Data from Pearcy and Ambler (1974) are corrected for the contribution of unidentifiable food. Total lengths (*TL*) of *C. armatus* were converted to pre-anal fin length (*PAF*) as described in "The model – Feeding rates". Energy data are from Steimle and Terranova (1988), except for micro-nekton which are from Dauvin and Joncourt (1989). The taxon for which the actual energy density comes from is given. The energy density of unidentifiable prey and miscellaneous prey is estimated as the average of all prey types for *C. acrolepis*. For consistency this value is also used for *C. armatus* (*PAF* pre-anal fin length; *TL* total length)

Prey type	Size class						Energy density	Taxon in original reference
C. acrolepis – Drazen et al. (2001)								
	2–5 cm PAF	6–10 cm PAF	11–15 cm PAF	16–20 cm PAF	21–25 cm PAF	26+ cm PAF		
Infauna	10.69	18.84	15.53	2.81	0.36	0.00	4.23 $\pm$ 1.06	Polychaetes
Small epifauna	3.75	4.37	4.01	3.39	0.20	0.03	4.64 $\pm$ 1.97	Benthic decapods
Large epifauna	5.04	8.47	10.11	8.94	8.56	5.02	4.64 $\pm$ 1.97	Benthic decapods
Micronekton	46.88	19.22	5.33	1.16	0.19	0.00	5.08 $\pm$ 0.30	Amphipods
Macronekton	0.00	13.04	3.25	7.10	15.89	6.52	5.07 $\pm$ 2.74	Pelagic decapods
Squid	0.00	0.51	2.12	27.14	4.93	23.21	4.68 $\pm$ 2.52	All squid
Fish	0.00	1.36	24.98	28.71	36.95	40.75	5.87 $\pm$ 2.13	Benthic and pelagic fish
Scavenged	0.00	0.01	13.03	7.42	20.24	18.87	6.30 $\pm$ 1.45	Shelf-living pelagic fish
Unidentifiable	33.65	34.18	21.64	13.33	12.69	5.60	5.06	–
C. armatus – Pearcy and Ambler (1974)								
	100–299 mm TL 4–12 cm PAF	300–399 mm TL 13–16 cm PAF	400–499 mm TL 17–21 cm PAF	500–599 mm TL 22–25 cm PAF	>600 mm TL 26+ cm PAF			
Holothurians	0.68	9.75	6.64	0.95	0.00		1.01 $\pm$ 0.30	Holothurians
Ophiuroids	0.00	0.00	0.00	0.00	0.00		2.13 $\pm$ 0.53	Ophiuroids
Polychaetes	1.70	0.00	0.00	0.00	0.00		4.23 $\pm$ 1.06	Polychaetes
Benthic rustaceans	12.92	1.30	0.83	0.00	0.00		4.64 $\pm$ 1.97	Benthic decapods
Pelagic crustaceans	2.72	7.80	2.49	0.95	4.60		5.07 $\pm$ 2.74	Pelagic decapods
Crustacean remains	10.88	5.85	4.15	0.00	0.00		4.86	Average of benthic and pelagic decapods
Cephalopods	0.34	29.25	49.80	89.30	0.92		4.68 $\pm$ 2.52	Squid
Fishes	0.00	2.60	16.60	2.85	86.48		5.87 $\pm$ 2.13	Benthic and pelagic fish
Miscellaneous	4.76	8.45	2.49	0.95	0.00		5.06	
Unidentifiable	66.00	35.00	17.00	5.00	8.00		5.06	

Model results

Energy budgets

Energy budgets indicate that total daily energy expenditure is greater for *Coryphaenoides acrolepis* than *C. armatus* (Fig. 2). In the smallest *C. acrolepis* the budget is evenly divided between metabolism and growth. As the fish increase in length, metabolism continues to increase at a greater rate than growth. *C. armatus* growth is always less than metabolism even at the smallest sizes. Growth declines with fish length, as is typical in almost all fish (Brett and Groves 1979). The sudden jump in total expenditure of *C. acrolepis* at 16 cm PAF is due to the introduction of reproductive costs, which are very large, exceeding metabolism and growth. I could not find information describing what proportions of the population reached maturity at various sizes, which would be required to create a smooth increase in the proportion of reproductive costs. Instead, it has been reported that *C. acrolepis* are mature at 16 cm PAF (Matsui et al. 1990). Thus, I introduced reproductive costs at this size resulting in a sudden increase in total energy expenditure. As stated above, *C. armatus* may be semelparous, so reproductive costs can be viewed as part of growth. The absence of yearly reproductive costs in *C. armatus* greatly reduces its total daily energy expenditure.

Energy expenditure was also expressed as lifetime totals (Fig. 2). The lifetime expenditure is greater for *C. acrolepis* due to reproductive costs. *C. armatus* grows
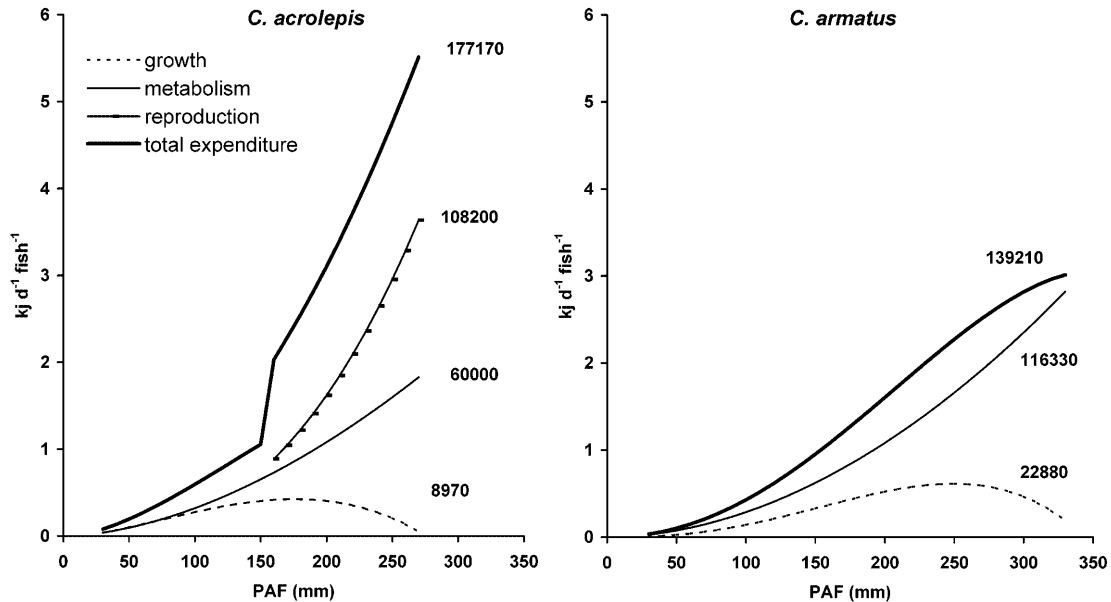
Fig. 2 *Coryphaenoides* spp. Daily energy budgets are presented as a function of size (*PAF* pre-anal fin length). Total daily expenditure is the sum of metabolism, growth and reproduction, and it is 80% of the feeding rate (see "The model – Energy budgets"). The lifetime expenditures derived from each function are given at the right of each panel (in kJ)

almost twice as large as *C. acrolepis*, resulting in larger lifetime growth cost. Its lifetime metabolic cost is greater because of its larger size (higher daily metabolic cost; Fig. 2) and its long life-span. The absence of annual reproductive costs saves considerable energy.

Feeding rates

The average energy density of the diet was only moderately different between species and size classes (Table 3). Most of the prey groups had similar caloric densities, except for the echinoderms (Table 2).

Feeding rates were expressed in several ways (Table 3). Rates from the energy models (kJ) are the median values for each size class. The range of values is quite large due to the many uncertainties in the model. Individual feeding rates are expressed as grams consumed by a fish per day. Feeding rates are also expressed as a proportion of body weight (BW) and decrease from 0.31% to 0.07% BW day^{-1} for *C. acrolepis* and from 0.12% to 0.02% BW day^{-1} for *C. armatus*, with increasing fish size. This reflects declining mass-specific growth and metabolism (Brett and Groves 1979; Jobling 1994).

Population feeding rates (the product of population density and individual feeding rate) for *C. acrolepis* were almost 18 times higher than those of *C. armatus* (Table 4). The population of *C. acrolepis* on the continental slope consumes approximately 2.7 kg km^{-2} day^{-1} of prey, whereas *C. armatus* on the continental rise and abyssal plain consumes only 156 g km^{-2} day^{-1} of prey. Again, the range in values is considerable given the range in rates from the energy budgets and the range in

observed population densities, particularly for *C. armatus*. The considerably reduced rates for *C. armatus* are the product of both much lower population densities and lower individual feeding rates. The population feeding rates of both species are maximal near the middle of the size range for the species. This is the result of increasing individual consumption with size and subsequent declines in the density of large fish (Stein and Pearcy 1982; Wakefield 1990). The feeding rates on specific prey groups or taxa are also calculated as the product of the population feeding rate and the gravimetric composition of the diet (Table 2). These rates show that *C. acrolepis* prey most heavily on squid, fish and scavenged food. *C. armatus* feed most heavily on squid and fish. Even though micronekton and infauna are the dominant prey of small fish, they are relatively less important to the population as a whole. This is due to the relatively low individual feeding rates for small fish (Table 3). Note that no data on the population density of very small (2–5 cm PAF) *C. acrolepis* were available in the literature.

Discussion

Evaluation of the energy budgets

The partitioning of the energy budgets is fairly similar to generalized budgets for shallow-living, carnivorous fishes. In most cases it is assumed that 20% of the food consumed is excreted, and, of the remainder, 75% is used for metabolism in adult fish (Brett and Groves 1979). Metabolism ranges from 65% to 94% of the energy expenditure of *Coryphaenoides armatus* (Fig. 2). In *C. acrolepis*, metabolism accounts for between 50% and 60% of the budget, but drops to 35% once reproduction begins.

Energy budgets for North Atlantic cod, shallow-living and well-studied relatives of the macrourids, are also

Table 3 *Coryphaenoides* spp. Estimated individual feeding rates of *C. acrolepis* and *C. armatus*. Energy density (mean ± SD) is the weighted average of the prey (see "The model – Feeding rates"). Feeding rates (kJ fish^{-1} day^{-1}) are median values for the size range taken from the energy budgets. Minimum and maximum feeding rates include ranges in energy budgets and energy density of prey

Size		Feeding rate (kJ fish^{-1} day^{-1})			Dietary energy density (kJ g^{-1}) Mean ± SD	Individual feeding rates (g fish^{-1} day^{-1})			%BW
PAF (cm)	TL (mm)	Mean	Min.	Max.		Mean	Min.	Max.	
C. acrolepis									
2–5		0.17	0.06	0.38	4.94 ± 0.42	0.03	0.01	0.08	0.31%
6–10		0.53	0.17	1.39	4.86 ± 0.91	0.11	0.03	0.35	0.16%
11–15		1.09	0.29	3.34	5.23 ± 1.32	0.21	0.04	0.85	0.08%
16–20		3.17	1.74	7.52	5.21 ± 1.87	0.61	0.25	2.25	0.10%
21–25		5.07	2.92	12.09	5.55 ± 1.82	0.91	0.40	3.23	0.08%
26+		6.89	4.29	16.51	5.52 ± 2.00	1.25	0.57	4.70	0.07%
C. armatus									
4–12	100–299	0.34	0.04	1.12	4.94 ± 0.36	0.07	0.01	0.24	0.12%
13–16	300–399	1.19	0.15	4.44	4.56 ± 1.06	0.26	0.03	1.27	0.07%
17–21	400–499	1.84	0.22	7.26	4.72 ± 1.71	0.39	0.03	2.41	0.05%
22–25	500–599	2.68	0.27	11.47	4.71 ± 2.34	0.57	0.04	4.85	0.04%
26+	>600	3.52	0.23	16.99	5.76 ± 1.99	0.61	0.03	4.51	0.02%

similar to the *C. acrolepis* and *C. armatus* budgets with one exception – reproduction. Metabolism generally accounts for 30–50% of the budget in 2- to 3-year-old cod and increases to approximately 50% of the budget in mature fish (Jobling 1982). These values are very similar to those of *C. acrolepis*. Reproduction costs increase from 43% to 66% of the total in *C. acrolepis* with fish length (Fig. 2). Jobling (1982), estimating reproductive costs in the same manner as this study, found that reproduction was at most 30% of the energy budget of cod. The reasons for the different reproductive costs will be discussed in detail below.

Seasonal variation in feeding activity, mobilisation of energy stores and reproductive status should not have a major effect on the models presented. The data used for reproduction and growth are long-time averages. Furthermore, a detailed examination of temporal variation in the nutritional condition of *C. acrolepis* and *C. armatus* yielded no significant changes in growth, reproductive or metabolic parameters (Drazen 2002).

I believe that the energy budgets in this study are reasonable approximations, but they should be viewed as minimum estimates of energy requirements. Macrourids slowly cruise over the sea floor (Priede and Bagley 2000). However, the in situ respirometry was conducted on fish enclosed in benthic chambers. The fish did not look excessively stressed (Smith 1978), but because they were not able to continue their normal swimming the metabolic rates are likely underestimates. Furthermore, the effects of specific dynamic action were not included, which will also lead to underestimation of metabolism. Therefore, the feeding rates calculated from the model should be considered conservative estimates.

Energetic adaptations/strategies

The way in which an organism uses its food energy can be viewed as an energetic strategy or adaptation. The macrourids are active compared to other demersal deep-

sea fishes, which may be a trade-off between metabolism and feeding rate. *C. acrolepis* and *C. armatus* swim continuously but very slowly (Priede et al. 1994; Priede and Bagley 2000). They invest a considerable proportion of their energy budgets in metabolism even at juvenile sizes, reflecting the costs of this type of locomotion. It is possible that their active foraging strategy results in feeding rates higher than those of more sedentary species. Koslow (1996) found a similar trade-off between activity and feeding rate in seamount-associated fishes such as orange roughy, *Hoplostethus atlanticus*. When compared to benthopelagic fishes, seamount-associated fishes live in a more physically dynamic environment, requiring greater locomotory capacity, but these habitats are also comparatively rich in food, resulting in higher feeding rates.

With regard to energetic strategy, the most interesting aspect of the energy budgets was the costs of reproduction in *C. acrolepis* and *C. armatus*. The energy budgets were constructed on the assumption that reproductive strategies are different for *C. acrolepis* and *C. armatus*. The results provide a test of the energetic advantages of each strategy.

The reproductive costs for *C. acrolepis* are relatively great (Fig. 2). Integrated over the life-span of the fish, they total ~108,000 kJ, more than half the lifetime energy expenditure (Fig. 2). They are also nearly double the daily energy expenditure of this species. As stated above, this investment in reproduction is much greater than the cod's on a proportional basis (Jobling 1982). On an absolute basis reproductive cost is similar to Atlantic and Pacific cod, the mean GSIs of which are higher (12–22%: Jobling 1982; Smith et al. 1990) and the mean egg energy density of which is lower (2 kJ g^{-1}: Craik and Harvey 1987) than the macrourid's.

Two explanations exist for such a high cost of reproduction in *C. acrolepis*. First, it is possible that reproductive output must be maintained regardless of lower food availability on the continental slope. Macrourid eggs are buoyant, and once released they rise

Table 4 *Coryphaenoides* spp. Estimated population feeding rates of *C. acrolepis* and *C. armatus*. See "Model results – Feeding rates" for references used to calculate population densities. Ranges in population feeding rates take into account the range in individual feeding rates and the range in population density values. Feeding rates on the various prey groups/taxa are calculated from the gravimetric composition of the diet in Table 2

PAF (cm)	Popul. density (ind. km^{-2})			Popul. feeding rates (g km^{-2} day^{-1})			Prey group/Taxon								
	Mean	Min.	Max.	Mean	Min.	Max.									
C. acrolepis							Infauna	Small epifauna	Large epifauna	Micro-nek.	Macro-nek.	Squid	Fish	Scav.	Unident.
6–10	1,742	1,350	2,588	189	40	909	36	8	16	36	25	1	3	0	64
11–15	1,971	1,528	2,927	410	68	2,500	64	16	41	22	13	9	102	53	89
16–20	1,009	782	1499	615	192	3,379	17	21	55	7	44	167	177	46	82
21–25	1,323	1,026	1,966	1,207	406	6,358	4	2	103	2	192	59	446	244	153
26+	276	214	410	345	122	1,928	0	0	17	0	22	80	141	65	19
All fish	6,321	4,900	9,390	2,766	829	15,074	121	48	233	68	296	316	868	408	408
C. armatus							Holo-thur.	Poly chaetes	Benthic crust.	Pelagic crust.	Crust. rem.	Squid	Fish	Misc.	Unident.
4–12	371	105	828	25	1	203	0	0	3	1	3	0	0	1	17
13–16	247	70	552	65	2	700	6	0	1	5	4	19	2	5	23
17–21	177	50	394	69	2	949	5	0	1	2	3	34	11	2	12
22–25	71	20	158	40	1	766	0	0	0	0	0	36	1	0	2
26+	18	5	39	11	0	176	0	0	0	1	0	0	10	0	1
All fish	884	250	1,971	156	5	2,795	11	0.4	5	8	9	89	24	9	54

towards the surface (Merrett and Barnes 1996). It has been hypothesised that as they develop their buoyancy decreases and the eggs begin to sink, hatching near the seafloor (Merrett and Barnes 1996). While the eggs are in the water column they could be advected off the continental slope, where the hatching larvae would die. Some macrourid eggs are ornamented, which may inhibit their ascent rate and reduce advection of eggs (Merrett and Barnes 1996). However, if egg mortality remains high, *C. acrolepis* may require high fecundity, GSI and reproductive costs (Stein and Pearcy 1982).

The second explanation is that reproductive periodicity has not been assessed correctly. There is evidence that spawning is continuous in *C. acrolepis* (Drazen 2002; D. Stein and R. Albright, unpublished data). Indeed, it might be a serial batch spawner, releasing gametes at intervals throughout the year. If this were the case then, the entire gonad mass might not be spawned every year and reproductive costs could be considerably less. This has been demonstrated in some midwater fishes (Gartner et al. 1997). It is also possible that not all members of the population spawn every year. In the deep-sea, where food is scarce relative to shallow-water habitats, *C. acrolepis* might have to invest energy into gonads over periods of time exceeding a year, so they may only be ready to reproduce every few years. Some shallow-living fishes are known to reproduce only every few years, including haddock, phylogenetically related to the macrourids, and arctic char (Dutil 1987; Jobling 1994). In the deep sea, 45% of mature orange roughy were not in spawning condition despite the presence of spawning aggregations at the time, suggesting that these fish may not breed every year (Bell et al. 1992). If *C. acrolepis* reproduces every other year then the reproductive costs determined by the model would be one-half of the estimates given. Lifetime reproductive costs would only be ~54,000 kJ, which is similar to metabolism values. Further investigations into the reproductive biology of the macrourids are required to determine whether the energy budgets are accurate.

C. armatus may save energy in its oligotrophic abyssal habitat by having a semelparous reproductive strategy. This type of reproduction might be favoured where food supplies are low but the environment is relatively stable. Energy would be saved by spawning only once (compare *C. acrolepis* with *C. armatus* in Fig. 2), but the fish only have one chance to contribute their offspring to the population. However, in a stable environment, if juvenile survivorship remains relatively constant, semelparity could be both successful and energetically adaptive. Adult survivorship must also be consistent, so that sufficient numbers of fish survive to reproductive age. Several bathypelagic fishes are assumed to have semelparous reproduction for these reasons (Childress et al. 1980). A study of anadromous American shad lends support to this hypothesis (Leggett and Carscadden 1978). Reproductive frequency changed with the latitude of their home river. In the north, there was considerable variability in environmental conditions where they spawned, and most fish were iteroparous. In the south, where the environment was more stable and egg and juvenile survivorship were more constant, almost all individuals had very high fecundity and were semelparous.

Individual feeding rates and meal frequency

To put the feeding rates of *C. acrolepis* and *C. armatus* into perspective they can be compared with those

of shallow-water fish and other studies of deep-sea fishes. The estimated daily ration of cod ranges from 0.5% to 5.0% BW day^{-1} (Daan 1973; Jones 1978; Majkowski and Waiwood 1981; Du Buit 1995). The feeding rates of the macrourids, even at the smallest sizes examined, are much lower (Table 3), as expected from low metabolic rates. Only two other studies have estimated the feeding rates of deep-sea demersal fishes. Koslow (1996), using a bioenergetics model, gave similar results to this study, although he did not attempt to scale the energy budgets to fish length. He estimated a daily ration for *C. acrolepis* of 0.10% BW day^{-1} and for *C. rupestris* 0.05% BW day^{-1}. Macpherson (1985) estimated the food consumption of the macrourid *Coelorhyncus fasciatus* at 0.55–2.15% BW day^{-1}. The estimates from the present study (Table 3) and by Koslow (1996) suggest much lower rates for macrourids. Macpherson used a gastric evacuation model but had to infer rate information from cod; the use of these data probably inflated his estimates of feeding rates. Even at very low temperatures cod exhibit higher metabolic rates and probably feeding rates than macrourids (Smith 1978).

Feeding rates or average daily ration do not indicate meal frequency. It has been hypothesised that some macrourids feed infrequently based on the presence of large energy reserves (Smith and Hessler 1974; Smith 1978). Stomachs are often full, but it has not been possible to determine what period of time it took the fish to fill its stomach. The daily feeding rates and prey-item sizes of *C. acrolepis* can be used to determine meal frequency. The average stomach content of *C. acrolepis* ranges from 0.65% to 1.0% BW, with the lowest stomach content in the largest fish (Drazen et al. 2001). For 2–5 cm PAF fish, their stomach contents could sustain them for approximately 3 days. For the largest fish, stomach contents could sustain them for approximately 10 days. Average prey-item mass increases dramatically from 0.1% to 0.38% BW with predator length (relatively undigested prey items only; Drazen, unpublished data). At 0.1% BW a 2–5 cm fish must eat approximately three prey items per day. A prey item equivalent to 0.38% BW could sustain a 26 + cm PAF fish for 5.6 days. This analysis suggests that meal frequency for large *C. acrolepis* is high and similar to large piscivores, such as pike (Diana 1979), and some bathypelagic stomiid fishes (Sutton and Hopkins 1996).

Although meal frequency is high, gorging is not the normal foraging strategy for *C. acrolepis*. I calculated the proportion of large (21 + cm PAF) fish examined that had eaten a prey item big enough to sustain it for at least 20 days. Of the examined fish, 10% had such large prey items in their stomach. In an extreme example, one fish ate a large squid approximately 10% BW (fish PAF = 19 cm). The feeding rate from Table 3 for a fish of this size is 0.1% BW, thus this prey item could sustain the individual for 100 days.

Population feeding rates and the role of macrourids in the deep-sea food web

The population feeding rates on various prey groups or taxa give quantitative estimates of predation pressures (Table 4). Although tempting to perform, a comprehensive analysis of cropping rates, the proportion of biomass removed by a predator, on various prey groups is not possible at this time for several reasons. First, the prey biomasses available in the literature are sparse and are often for groups such as "fish" or "epifauna", whereas neither *C. acrolepis* nor *C. armatus* prey on all species in such categories. Second, diet data and available data on prey biomasses have not been collected concurrently, either spatially or temporally. This could be important because regional differences in the diet of *C. acrolepis* and *C. armatus* have been noted (Martin and Christiansen 1997; Drazen et al. 2001). Also, regional changes in the population density or structure, such as the "bigger–deeper" trend in *C. armatus* (Stein and Pearcy 1982; Merrett and Haedrich 1997), will change population feeding rates from region to region.

The influx of particulate matter to the deep-sea benthos often does not meet their energy requirements (Smith 1987; Smith and Kaufmann 1999; Smith et al. 2001). It has been suggested that large organic particles (such as dead fish, squid and whales) not captured in sediment traps provide for the remainder of the energetic needs of the benthic community (Smith 1985; Smith 1992). Large organic particles are quickly consumed by deep-sea scavengers, which include the macrourids examined in the present study (reviewed in Gage and Tyler 1991). Because consumption occurs rapidly, the frequency and quantity of carrion cannot be measured directly. An alternative approach is to quantify the amount of carrion eaten by the scavengers over time.

Scavenging has been documented as an important foraging behaviour in *C. acrolepis*, and carrion is important to its diet (Drazen et al. 2001). Using the dietary information listed in Table 2 and the feeding rates given in Table 4, we can determine the rate at which the *C. acrolepis* population eats carrion and estimate the contribution of large organic particles to the deep sea as an energy source. From this information, *C. acrolepis* consumes ~408 g km^{-2} day^{-1} of scavenged food. If we assume that 10% of this material is organic carbon, then this is equivalent to a flux rate of 0.04 mg C m^{-2} day^{-1}. Particle flux rates near the seafloor in the bathyal eastern North Pacific are approximately 10–20 mg C m^{-2} day^{-1} (Smith 1987; Reimers et al. 1992; Pilskaln et al. 1996). Therefore, the carrion eaten by *C. acrolepis* is only 0.2–0.4% of the average small particulate flux. Using the upper end of the feeding rates from the model, a maximum contribution of 1.1–2.2% is derived. These estimates are for consumption by *C. acrolepis* only. Other scavengers on the continental slope include hagfish, sablefish and amphipods (Dayton and Hessler 1972; Smith and Baldwin 1982; Smith 1985). Even if these

other scavengers consumed 75% of the carrion arriving on the seafloor, flux rates would only increase to a mean of 0.8–1.6% of the average small particulate flux. Given the nature of these calculations, I do not intend the numbers to be taken as definitive quantitative estimates of carrion flux. However, they strongly suggest that carrion is not an important component of the carbon flux into the deep-sea benthic environment.

In conclusion, energy expenditure and feeding rates of *C. acrolepis* and *C. armatus* were considerably lower than those of shallow-living fishes. Energy partitioning in the macrourids was similar to budgets constructed for cod, with the exception of reproductive costs. The high costs in *C. acrolepis* may be necessary to retain adequate numbers of eggs and larvae on the continental slopes. Alternatively, if this fish does not reproduce on an annual basis, the calculated costs are an overestimate. *C. armatus* may be semelparous, which would be of great energetic savings in its oligotrophic but stable environment. Finally, although scavenging is important to *C. acrolepis*, the flux of carrion into the deep-sea environment probably is a small fraction of the small particle flux and is not an important food supply to the community.

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