

Energetics of Grenadier Fishes

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Abstract.—Energetic parameters such as metabolism, growth, and reproduction represent investments by an animal in maintenance and production. The available literature was reviewed to examine trends in these parameters for grenadiers to better understand their biology in relationship to shallow living species. Grenadiers are adapted to deep-sea habitats that have fundamentally different environmental conditions than the continental shelves where most exploited fishes live. Grenadiers have very low metabolic rates, similar to other deep-sea demersal and pelagic fishes. This appears to be the result of a relaxation in the selective pressure for locomotory capacity in dim or totally dark waters. Longevities are variable and dependant, in part, on body size. Regardless of longevity, low rates of mass-specific growth are typical and may be limited by its relationship to metabolism. Finally, reproductive outputs may be much lower than originally anticipated from gross measures of fecundity, and at least some species may reproduce less often than annually. Energetic data are sparse but until more are available for diverse species, we must assume that with a similar body form, phylogeny, and habitat, that all grenadiers have low rates of metabolism, growth, and reproduction. Grenadiers are exceptionally diverse and certainly variation exists, some of which can be explained by individual ecologies. Nevertheless it is clear that models based on the energetics of shallow living fishes cannot be used for grenadiers. Their energetic characteristics are different and make them extremely vulnerable to overexploitation. Grenadiers have become targets or major components of the bycatch in slope fisheries, so it is especially important that this basic fact be understood.

Introduction

Over the last several decades fisheries for deep-sea species have developed on continental slopes and seamounts around the world (Clark 2001; Devine et al. 2006; Garibaldi and Limongelli 2003; Koslow et al. 2000; Merrett and Haedrich 1997; Moore 1999; Roberts 2002). This expansion is partly in response to collapses in shallow waters and the need to find new stocks. Fisherman will likely continue to explore deep waters

for resources. Grenadiers, fishes in the family Macrouridae, are very abundant and often are the dominant fishes at bathyal depths (Cailliet et al. 1999; Lauth 2000; Marshall and Iwamoto 1973; Merrett 1992; Merrett and Haedrich 1997; Percy et al. 1982; Stefanescu et al. 1994; Williams et al. 2001). There are ~400 species worldwide (Iwamoto 2008, this volume). Several fisheries have developed for them (Devine et al. 2006; Gordon 2001a; Gordon 2001b; Lorance et al. 2001; Matsui et al. 1990) and in some cases they have become a major constituent of discards in slope

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fisheries directed at other species (Allain et al. 2003; Laptikhovsky 2005; Novikov 1970; Zenger and Sigler 1992). Some grenadier fisheries have only recently been developed (Andrews et al. 1999; Tuponogov et al. 2008, this volume) whereas some that began decades ago have already been exhausted (Devine et al. 2006; Haedrich et al. 2001). Many ecological and physiological studies have focused on grenadiers because of these fisheries and a desire to understand their role in ecosystems (see Gage and Tyler 1991; Merrett and Haedrich 1997 and references therein).

Of great importance is an understanding of energetics, the rates at which these animals consume and transform energy and ultimately, produce new biomass. Metabolism is a process of energy assimilation, transformation, and allocation. Growth represents the fraction of energy stored by the individual as new mass. Reproduction can be defined as the energy allocated to gametes and reproductive behaviors. These processes are linked and metabolism influences, perhaps even controls, the others (Brown et al. 2004; McNab 2002). Information on metabolism, growth and reproductive expenditures can be brought together to form an animal's energy budget. An energy budget assumes that the energy consumed in food must be spent by the fish in growth, reproduction, metabolism, or lost as wastes (Brett and Groves 1979; Jobling 1993), such that

consumption (C) = metabolism (M) + growth (G) + reproduction (R) + excretion (E) (1)

The budgets can be used to compare data from each parameter converted to units of energy and to assess the validity of parameters that were assumed or estimated rather than measured, not an unusual situation in deep-sea studies. Energy budget approaches can compare energetic strategies provide estimates of consumption, potential for growth and reproductive output of individuals (Childress

et al. 1980; Drazen 2002a; Koslow 1996). Through the integration of individuals the resource requirements, productivity, and dynamics of populations can be derived (Brown et al. 2004). Potential population sizes could be estimated from resource requirements and habitat productivity. Understanding population dynamics leads to an understanding of the response to fishing mortality. Therefore, energetics is fundamentally important to fisheries science.

Here I review the information available on each energetic component and whole energy budgets for grenadiers. Comparisons are made between grenadier species to assess whether any commonalities exist. Gadiform fishes are diverse and the shallow-living cods and hakes are well studied because of the considerable fisheries for them (Cohen et al. 1990). Studies for grenadiers are fewer, thus it is tempting to extrapolate our more familiar knowledge of shallow species to the deep-sea grenadiers. The energetics of grenadiers are compared to those of cods, in particular, throughout this review because the cods are a familiar benchmark, are phylogenetically related to grenadiers, and to show that such extrapolations are not justified. I summarize with comparisons to other groups of deep-sea fishes to place grenadier energetics into a broader context.

Metabolism

Many factors are known to have important effects on animal metabolic rates. Among the best described are temperature and body mass. Temperature affects metabolism, presumably through kinetic effects on reaction rates although the precise link is poorly understood. Broadly speaking, higher temperatures lead to higher metabolic rates within a species (Clarke 2004; Clarke and Johnston 1999). Body size also has dramatic effects on metabolism. The classic "mouse to elephant" curve relates the variation in meta-

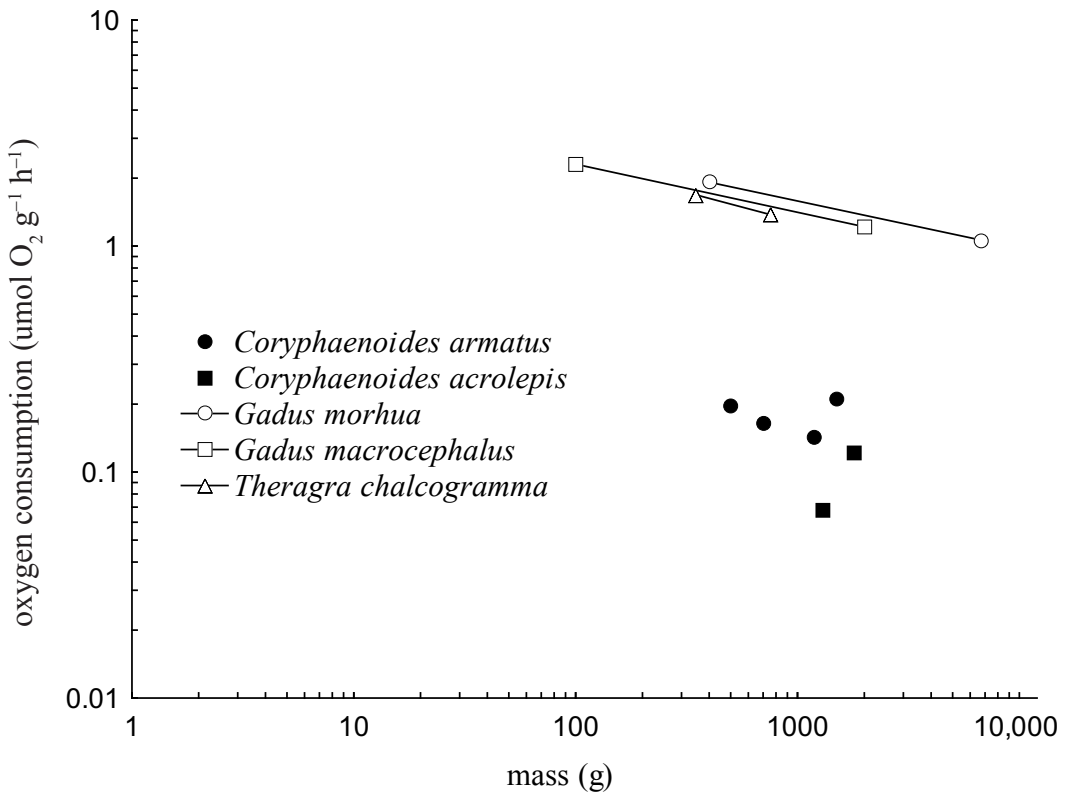


Figure 1. Oxygen consumption as a function of fish mass for grenadiers and shallow living gadids. All measurements are adjusted to 5°C. All individual measurement for grenadiers are shown. Data for the grenadiers were taken from the sources listed in the text. Data for gadids are represented by many measurements and the published mass scaling relationships are shown. Data are from the following sources: *Gadus morhua* (Saunders 1963), *Gadus macrocephalus* (Paul et al. 1988), *Theragra chalcogramma* (Smith et al. 1988).

bolic rates to body sizes with a power law. Although the exact slope of the relationship is actively debated (Bokma 2004; Clarke and Johnston 1999; Glazier 2005; Suarez et al. 2004), smaller animals generally have higher mass-specific metabolic rates (Clarke and Johnston 1999; Darveau et al. 2002; Suarez et al. 2004). Even after taking into account the important effects of body size and temperature, grenadiers have an order of magnitude lower metabolic rates than shallow living species. Grenadiers do not survive recovery to the surface without the aid of pressure retaining vessels (Phleger et al. 1979; Wilson and Smith 1985) so routine metabolic rates

of grenadiers have been measured directly using in situ respirometers (Bailey et al. 2002; Smith 1978; Smith and Hessler 1974) and high pressure systems which retrieve the animals from depth under in situ conditions (Drazen et al. 2005). Due to the difficulty and expense, there are relatively few measurements. Comparisons to shallow living but phylogenetically related gadids (Drazen and Seibel, in revision) clearly indicate that grenadiers have routine metabolic rates an order of magnitude lower (Figure 1).

Due to the difficulties associated with direct measurements, several biochemical proxies for metabolism have been used (Dal-

hoff 2004; Graham et al. 1985). The most commonly employed are measurements of key enzymes of intermediary metabolism. Several studies have found that they correlate well with oxygen consumption rates (Childress and Somero 1979; Dalhoff 2004; Moyes and LeMoine 2005). Several enzyme activities have been measured in grenadiers. Both lactate dehydrogenase (LDH) and pyruvate kinase (PK) are active in glycolysis and are indicative of anaerobic metabolism. LDH activity is thought to be closely linked with burst swimming performance (Dalhoff 2004; Somero and Childress 1980; Sullivan and Somero 1980). Citrate synthetase (CS), active in the Krebs cycles, is an indicator of aerobic metabolism (Dalhoff 2004). MDH, also active in the Krebs cycle, is much more variable than CS and may also play a role in redox balance (Siebenaller et al. 1982; Sullivan and Somero 1980).

Grenadier enzyme activities are much lower than those of shallow living fish species and corroborate the generality of the respirometry results. Siebenaller et al. (1982) first compared enzyme activities among five species of grenadiers. Table 1 presents data from additional sources bringing the total to 9 species. The CS and LDH activities are much lower than shallow-living benthopelagic fishes that have CS activities ranging 0.75–1.0 units g^{-1} and LDH ranging 150–650 units g^{-1} (Drazen and Seibel in revision). The MDH and PK activities of grenadiers are also much lower than those for shallow living species (Siebenaller et al. 1982).

There is considerable variation among grenadier species which reflects both size and the metabolic effects of individual ecologies. Enzyme activities scale with body size; anaerobic activities generally increasing with body size and aerobic activities decreasing with body size (Somero and Childress 1980; 1985). Increases in anaerobic enzyme activities in white muscle are correlated with similar increases in burst locomotory power

requirements while activities of aerobic enzymes scale to body size in a very similar fashion to mass specific aerobic metabolism (Childress and Somero 1990; Somero and Childress 1980; 1985). These effects do not explain the majority of variation in the rates seen in Table 1. For instance, if we assumed that the LDH activity of carapine grenadier *Coryphaenoides carapinus* (4.70 units g^{-1} wet weight at an average mass of 80 g) scaled with an exponent of 0.4, an average for many species (Childress and Somero 1990), then at 500 g its LDH activity would be ~9.8 units g^{-1} wet weight, still dramatically different than Pacific grenadier *C. acrolepis* for instance (Table 1). Furthermore, not all species exhibit scaling relationships for anaerobic enzymes. Data for ghostly grenadier *C. leptolepis* ranging in size from 90 to 960 g gave no evidence of mass scaling which may indicate that this species does not maintain a high burst swimming capacity with increased size (Siebenaller et al. 1982). The influence of the scaling relationships will be more important for the other enzyme activities such as CS which show less variation overall (Table 1) and more predictably scale with body size.

Despite these complications clear differences are evident with direct bearing on metabolism. First of all, LDH and PK activities for abyssal grenadier *C. armatus*, *C. acrolepis* and *C. yaquinae* are much higher than for most other species and are indicative of a relatively high burst locomotory capacity which may be tied to their active roles as predators and scavengers (Drazen et al. 2001; King et al. 2006; Martin and Christiansen 1997; Percy and Ambler 1974; Wilson and Smith 1984). The data for CS and MDH are relatively similar across the species considering potential size influences, with the lowest rates found in giant grenadier *Coryphaenoides pectoralis* which has watery, gelatinous flesh (Table 1). This species is unusual in its high water content (Drazen 2007), poorly ossified skeleton and regressed gas bladder

Table 1. Metabolic enzyme activities in grenadier fishes. Activities were measured in white muscle and are expressed at units g⁻¹ wet weight at 10 °C, under substrate-saturating conditions. The average size of the fish for which the measurements were made is given as well as the water content of the white muscle. Values for *C. armatus* and *C. acrolepis* come from published scaling relationships. Where more than one study presented data values were averaged. Lactate dehydrogenase (LDH), citrate synthetase (CS), malate dehydrogenase (MDH), and pyruvate kinase (PK).

species	mass (g)	LDH	PK	CS	MDH	%water	refs
<i>Coryphaenoides pectoralis</i> *	1158	46.4		0.09		91.9	1
<i>Coryphaenoides acrolepis</i>	500	167.8	10	0.22	9	83.4	2, 3
<i>Coryphaenoides armatus</i>	500	83.0	8.13	0.68	18.5	82.9	2, 4
<i>Coryphaenoides carapinus</i>	80	4.70	5.9	0.50	6.8	85.3	4
<i>Coryphaenoides cinereus</i>	148	12.1				83.0	1
<i>Coryphaenoides leptolepis</i>	456	4.30	2.6	0.41	6.9	82.3	4
<i>Coryphaenoides rupestris</i>	84	16.0	5.4	0.58	9.7	84.6	4
<i>Coryphaenoides yaquinae</i>	475	111.2		0.53		83.5	2
<i>Nezumia bairdii</i>	56	8.67	4.6	0.78	17.5	81.2	4, 5

1. Drazen and Seibel (in revision), 2. Drazen (2002b), 3. Sullivan and Somero (1980), 4. Siebenaller et al. (1982), 5. Somero and Childress (1980)
 * The generic assignment of this species is disputed and it has been placed in its own genus, *Albatrossia*, (Iwamoto and Sazonov 1988) but most recently moved to *Coryphaenoides* (Neighbors and Wilson 2006; Wilson and Attia 2003) as used here.

(Iwamoto and Stein 1974). It feeds predominantly on midwater animals and its ecological niche may be distinct from the other species in Table 1 which are benthic scavengers, predators or browsers (Crabtree et al. 1991; Drazen et al. 2001; Mauchline and Gordon 1984; Neighbors and Wilson 2006). *Coryphaenoides armatus* and *C. acrolepis* have relatively high enzyme activities compared to the rest of the species in Table 1 but direct measurements of metabolic rate are low suggesting that the other species have similar or even lower metabolic rates (Siebenaller et al. 1982).

Specific ecologies may explain intraspecific variations but other deep-sea animals have significantly lower metabolic rates than their shallow living counterparts indicating that habitat differences contribute in some fundamental way to the observed disparity between deep and shallow living animals. Studies have shown that other demersal fishes (Drazen and Seibel in revision), pelagic fishes (Smith and Laver 1981; Torres et al. 1979), crustaceans (Childress 1975; Childress et al. 1990a), and cephalopods (Seibel et al. 1997) exhibit rapid declines in metabolic rates with depth and the trend cannot be explained by correcting for temperature or animal mass. It has been shown that the observed declines are related to the demand for energy for predator-prey interactions and that such interactions are dependent, primarily, on vision and light (Childress 1995; Childress et al. 1990a; Childress and Thuesen 1995; Seibel and Drazen, in press). This hypothesis, dubbed the “visual-interactions hypothesis” (Childress et al. 1990a) suggests that in the absence of light and with low animal densities, the distances and frequencies with which predators and prey interact are reduced, relaxing the selective pressure for rapid locomotory capacity either to chase prey or evade predators. Reductions in metabolic rate follow. This argument has been supported by a lack of depth related declines

in the metabolism of taxa which do not rely heavily on vision such as copepods (Thuesen et al. 1998), medusae (Thuesen and Childress 1994), and chaetognaths (Thuesen and Childress 1993). In addition the declines are most prominent in the first 500 m and cease below ~1000 m where visible light is absent (Warrant and Locket 2004). For both pelagic (Torres et al. 1979) and demersal (Drazen 2007) fishes the water content of muscle increases significantly with depth further suggesting that locomotory ability drives the metabolic differences.

Growth

Data on the growth of deep-sea fishes can vary tremendously based on the techniques used, size range of fish studied, and other factors (Swan and Gordon 2001). It is not the purpose of this paper to evaluate the variation in rates and methodologies. Several recent reviews on this subject have already been published (Morales-Nin and Panfili 2005; Swan and Gordon 2001). Typically parameters for the von Bertalanffy growth equation (L_{inf} , the asymptotic size of the species, k , the growth coefficient, and t_0 , the theoretical size at age 0) are used to describe the growth characteristics over the life history of the animal. From the energetic perspective it is important that energy is used as the growth metric rather than length, particularly for comparisons between species with different morphologies. Estimates of the energy density of grenadiers in the eastern Pacific suggest muscle values of ~3–4 kJ g^{-1} (Drazen 2007). Values between 3.8 and 5.1 kJ g^{-1} were calculated for several *Coryphaenoides* spp. and *Nezumia bairdii* (Koslow 1996). The variation in energetic density is much smaller than the variation in the published growth parameters, so mass can be used as a proxy to examine broad trends.

For this paper a subset of the available data for macrourids was used (Table 2). For all of these species, annual periodicity of

Table 2. Von Bertalanffy growth parameters and length-mass relationships for select macrourid fishes in comparison to shallow living gadids. All lengths for gadids are total length and for macrourids are pre-anal fin length except where noted. Length-mass parameters are from the general equation $W(g) = a \times L(\text{cm})^b$. L_∞ —asymptotic length, K —coefficient of growth, and t_0 —theoretical age when length is zero.

species	K	L_∞	t_0	refs	a	b	refs
<i>Coelorinchus coelorinchus</i>	0.132	10.7	-1.535	1	0.0011	2.4200	1
<i>Coryphaenoides acrolepis</i>	0.041	27.2	0.25	2	0.2555	2.6970	3
<i>Coryphaenoides armatus</i>	0.021	34.0	0.25	3	0.1290	2.9440	3
<i>Coryphaenoides rupestris</i> ^a	0.126	1248	1.185	4			
<i>Gadus macrocephalus</i>	0.200	105	-0.21	5	0.0079	3.0968	5
<i>Gadus morhua</i>	0.200	105	0.00	5	0.0104	3.0000	5
<i>Nezumia aequalis</i> ^b	0.175	6.76	5.6×10^{-9}	6	-0.22	3.1500	6
<i>Nezumia schlerorhynchus</i>	0.125	7.35	0.238	1	0.0024	2.5200	1
<i>Theragra chalcogramma</i>	0.300	62.6	0.00	5	0.0104	2.9120	5
<i>Trisopterus esmarkii</i>	0.600	20.5	0.00	5	0.0068	3.0000	5
<i>Trisopterus minutus</i>	0.300	23.3	0.00	5	0.0059	3.2170	5

^a Growth parameters were fit directly to mass (g) in original reference.
^b Lengths are head length and length to mass conversion takes the form of $\log W(g) = a + b \times \log HL(\text{cm})$.
1. Labropoulou and Papaconstantinou (2000), 2. Andrews et al (1999),
3. Drazen (2002a), 4. Kelly et al (1997), 5. Froese and Pauly (2006),
6. Coggan et al (1999).

the bands counted in otoliths was validated through either radiometric techniques (Andrews et al. 1999) or via marginal increment analysis (Coggan et al. 1999; Kelly et al. 1997; Labropoulou and Papaconstantinou 2000; Morales-Nin 2001). Growth coefficients were typically published as a function of fish length and these values were converted to fish mass using published length-mass regressions (Table 2). Growth rates of macrourids are known to be very slow (Bergstad 1990; Koslow et al. 2000; Swan and Gordon 2001) as for other deep-sea fishes (Cailliet et al. 2001; Smith et al. 1995). This is clearly demonstrated by comparing fish mass as a function of age in several *Coryphaenoides* spp. to that of shallow water gadids (Figure 2a). Grenadiers with relatively short longevi-

ties (~10 years), such as *Caelorinchus* sp. and *Nezumia* sp., are small species (Figure 2b). Their growth rates (Figure 2b) are lower than those of similarly sized shallow living gadids but the distinction between these groups is not as great as for the larger fishes. Regardless of longevity, grenadiers appear to have slow growth in comparison to similarly sized shallow living fishes.

The reasons for slow growth in grenadiers are not entirely clear but several possibilities can be explored. Deep-sea fishes live in environments which can be much colder than those on the neighboring continental shelves and low temperatures could slow growth rates. However, this explanation seems unlikely because saddled grenadier *C. caelorrhynchus* and bluntnout grenadier *N. schlerorhynchus* live

on the upper to middle slopes of the Mediterranean where bottom temperatures average 12.8°C (Locarnini et al. 2006; NOAA, National Oceanographic Data Center) yet they have slower growth rates than shallow living species from the colder North Atlantic (Figure 2b). Phylogenetic effects are another possibility but all grenadiers inhabit the slopes and abyssal plains so it will not be possible to constrain these impacts much more than has been done by comparing grenadiers to shallow living gadiforms. Even when phylogenetic effects can be constrained as in the case of work on scorpaenid fishes, the deeper dwelling species are much longer lived (Cailliet et al. 2001). Other potential factors are likely habitat related. Low food availability is a characteristic of some deep-sea habitats although it varies regionally and seasonally (Gage and Tyler 1991; Tyler 1988). Low ration levels certainly affect growth intraspecifically (Brett and Groves 1979; Sullivan and Smith 1982). For low food availability to result in lower growth rates interspecifically, slower growth would have to be selected for. It is unclear why slower growth would be favored per se in the deep sea.

As Cailliet et al. (2001) point out, great longevities are not solely the domain of deep-sea fishes but also occur in a variety of shallow living fishes such as elasmobranchs and sturgeons. Greater longevity has a variety of life history advantages such as longer reproductive lifespan and a more stable population structure (Musick 1999), but, as shown here, grenadiers with a variety of longevities all have slow growth rates. Rather the generally slow rates of growth may be the result of metabolic limitation. Metabolism is a measure of the rate at which animals transform materials and it is the sum of catabolism and maintenance functions and anabolism which results in growth. Therefore, it has been argued that metabolism may constrain the rate of growth and empirical fits of growth data suggest that a relatively constant proportion of metabolic

expenditures is allocated to growth (Brown et al. 2004). However, seamount associated fishes, such as orange roughy, have higher metabolic rates than grenadiers but lower growth rates (Koslow 1996). They expend a large fraction of their energy on metabolism and associated locomotory capabilities so that they can actively forage in the dynamic and physically energetic seamount environment. Future studies should focus on the relationship between metabolism and growth.

Reproduction

With regard to energetic investment, reproduction can be viewed as the energy used in the generation of gametes over a given time increment. Parameters of interest are fecundity, the ripe gonad mass (or a gonadosomatic index; GSI) and energy density so that an estimate of the energetic investment can be made. Eggs are larger than sperm and the costs associated with gamete production will be more for females. Certainly reproductive mating behaviors and potential migrations will add to reproductive costs but at this time there are no data upon which to evaluate these expenditures in grenadiers. The time increment is usually thought of as a year because many shallow living animals have distinct annual spawning seasons. Whether deep-sea animals reproduce seasonally or not has been the subject of much debate for several decades (D'Onghia et al. 1999; Gage and Tyler 1991; Rokop 1974; Tyler 1988). Some grenadiers have protracted reproductive periods with one or two month peaks in activity (Coggan et al. 1999; Geistdoerfer 1979; Murua and Motos 2000) while others appear to reproduce year-round, asynchronously (D'Onghia et al. 1999; Drazen 2002b; Stein and Percy 1982). Regardless of timing, these fishes are thought to reproduce at least once per year.

Estimates of the GSI of ripe females are usually lacking in the literature but there are

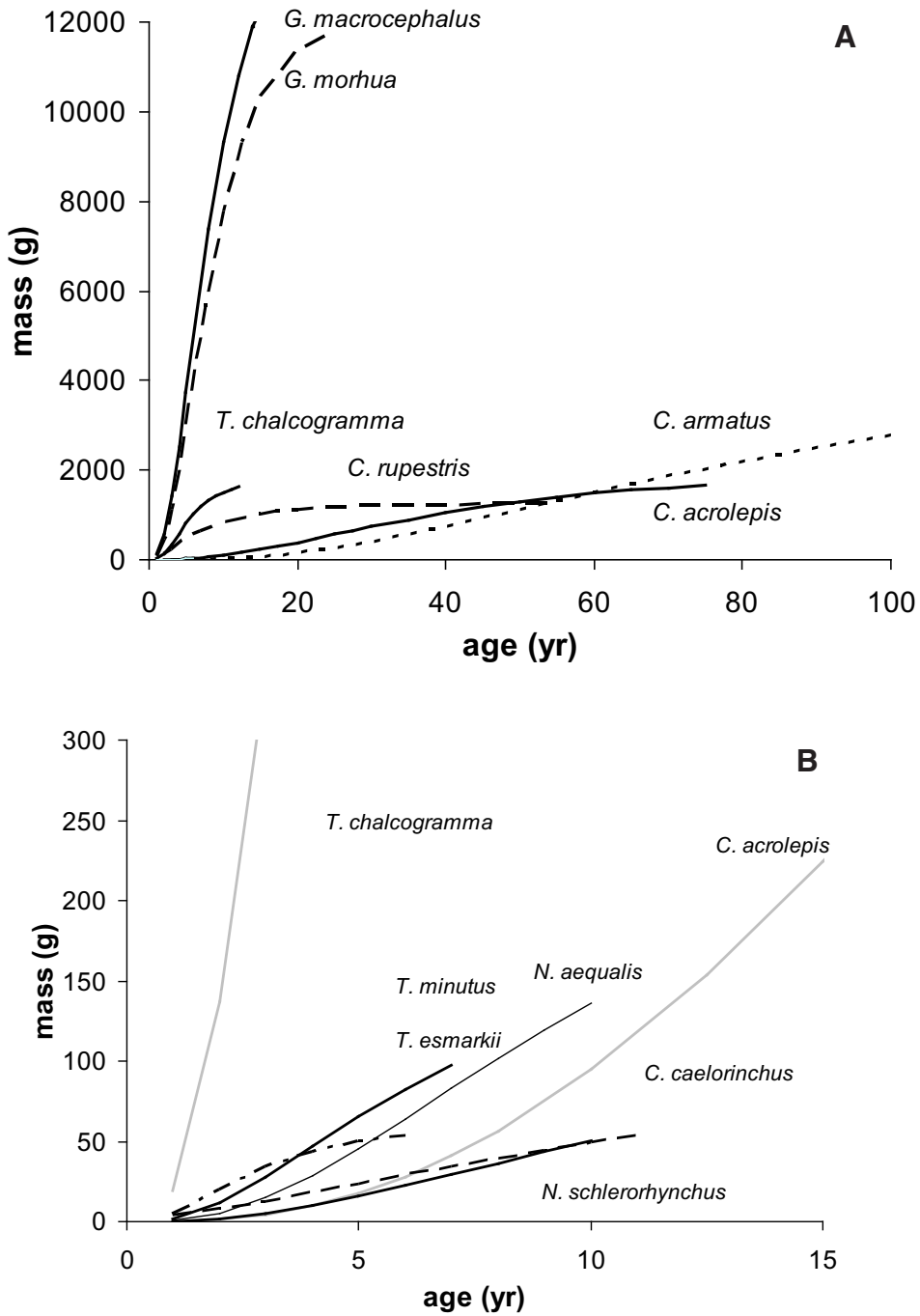


Figure 2. Fish mass versus age in macrourid fishes. Data for gadiforms is shown for comparison. Curves represent average mass at age derived from published von Bertalanffy growth functions and length-mass relationships as shown in Table 2. A) Data for larger sized macrourids and B) smaller size animals with the lower portions of the growth curves for several larger species shown for comparison.

estimates of egg energy density and quite a few estimates of fecundity. Grenadiers appear to have similar sized eggs (1.1–2.4 mm) with a large oil droplet (Grigor'ev and Serebryakov 1983; Marshall 1965; Marshall and Iwamoto 1973; Stein and Percy 1982). The proximate composition of ripe roundnose grenadier *Coryphaenoides rupestris* eggs (Craig and Harvey 1987) eggs has been measured and by using conversion factors (Childress et al. 1990b), the energy density can be estimated as 5.23 kJ g^{-1} . Due to the intraspecific similarity in grenadier eggs, fecundity has been used as a relative proxy for energetic investment for females (Merrett 1994). Large slope-dwelling species such as *C. acrolepis*, *C. rupestris*, and roughhead grenadier *Macrourus berglax* have fecundities of 10,000–100,000 eggs depending on female body size (Allain 2001; Murua and Motos 2000; Stein and Percy 1982). Smaller species of macrourids such as common Atlantic grenadier *Nezumia aequalis* have from 10,000–25,000 eggs (Coggan et al. 1999). The abyssal grenadier *C. armatus* has a very high fecundity of several million eggs (Stein and Percy 1982). Despite extensive collections, only one ripe and no post spawning *C. armatus* have been captured, suggesting that this species is semelparous (Stein 1985). Estimates of grenadier fecundity are slightly less than those for similarly sized gadids. For instance, small species such as *Trisopterus* spp. Or polar cod *Boreogadus saida* produce 10,000–100,000 eggs (Cohen et al. 1990). Species reaching very large size such as Atlantic cod *Gadus morhua* and Pacific cod *G. macrocephalus* are among the most fecund fishes in the world, producing up to 9 million eggs (Bleil and Oeberst 2005; Cohen et al. 1990; Skjaeraasen et al. 2006). Other deep-sea species such as orange roughy also have relatively low fecundities compared to shallow living groups (Pankhurst and Conroy 1987).

Although grenadiers have lower fecundities than shallow-living gadiforms batch spawning and reproductive frequency must be considered. If eggs are developed and spawned in multiple batches then static estimates of fecundity will underestimate annual reproductive output. For instance *C. rupestris* is a batch spawner and batch fecundity can be up to 70,000 eggs while annual fecundity is indeterminate because there is no information on the number of batches that are spawned each year (Allain 2001). The frequency with which individuals spawn or the average spawning periodicity in the population is very important and may range from several batches in smaller fishes (Merrett 1994) to less than one spawning per year (Drazen 2002a; Rideout et al. 2005). This has huge implications for population dynamics and will be discussed further under “energy budgets.”

Excretion

Food energy is lost during the digestive process through faecal losses of undigested and/or undigestible material and through the deamination of proteins which result in nitrogenous waste products. Reviews of these processes have suggested that carnivorous fishes excrete ~20% of the food energy consumed (Brett and Groves 1979; Jobling 1993; Pandian and Vivekanandan 1985). Collection of data for deep-sea species is extremely difficult because specimens must be held for collection of excretory products. The excretory rates of several *C. armatus* were measured in situ (Smith 1978) but these numbers could not be used to calculate assimilation efficiency because the amount of food eaten by these wild caught animals was unknown. Two species of deep-sea zoarcids can be successfully maintained in refrigerated, darkened aquaria and data on their excretion rates in a controlled experiment are available (Drazen et al. 2007). This study compared the absorp-

tion and assimilation of food in the two deeper living species to two shallow-living species. The rate of digestion was much slower in the deeper-living species but no significant differences were found between their assimilation efficiencies with total excretion at ~15% of energy ingested. Certainly, the selective pressure to maximize absorption and assimilation is universal and is not affected by the productivity of the habitat occupied. Thus it is unlikely that deep-sea fishes will function differently with regard to the efficiency of digestive processes even if the rate at which digestion proceeds is different.

It seems reasonable that values for excretion of grenadiers can be estimated from shallow living gadiform fishes or from ecologically similar carnivorous fishes from the continental shelves. However, care should be taken to evaluate similarity in feeding habits which can result in variation in digestion (Cleveland and Montgomery 2003; German and Horn 2006; Pandian and Vivekanandan 1985).

Energy Budgets

By combining data on the energetic parameters for a species, the energy budget can be constructed. This can allow for explorations of energetic strategies and for the evaluation of terms in relation to each other. Grenadier energy budgets have been examined in only two studies because of the scarcity of data. Koslow (1996) constructed budgets for a variety of deep-sea fishes including four grenadiers. Metabolism and growth were considered and some of the data are the same as that presented in this paper (i.e., enzyme activities, oxygen consumption). Estimates of these components for the group as a whole were compared to other groups which will be discussed in the next section.

The other study analyzed the energy budgets of *C. acrolepis* and *C. armatus* in detail and with respect to animal size (Dra-

zen 2002a; Figure 3). The partitioning of the energy budgets is fairly similar to generalized budgets for shallow-living carnivorous fishes (Brett and Groves 1979). 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, accounting for between 50 and 60% of the budget, but dropping to 35% once reproduction begins. Metabolism generally accounts for 30–50% of the budget in 2–3 year old cod and increases to approximately 50% of the budget in mature fish (Jobling 1982). For *C. armatus* growth is always less than metabolism even at the smallest sizes. Metabolism ranges from 65 to 94% of the energy expenditure. Growth declines with fish length as is typical in almost all fish (Brett and Groves 1979). Koslow (1996), presenting data on average sized adults for four species, found that growth was approximately 35% of the total of growth and metabolism.

Seasonal variation in feeding activity, mobilization of energy stores, and reproductive status did not have a major effect on the models presented for *C. acrolepis* and *C. armatus* because a detailed examination of temporal variation in the nutritional condition yielded no significant changes in growth, reproductive, or metabolic parameters (Drazen 2002b). This may not be the case for other species.

Energy budgets for North Atlantic cod, shallow-living and well-studied relatives of the macrourids, are also similar to the *C. acrolepis* and *C. armatus* budgets with one exception—reproduction. Reproductive costs increase from 43 to 66% of the total in *C. acrolepis* with fish length (Figure 3). 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. As stated above, *C. armatus* may be semelparous so reproductive costs can be viewed as part of growth. Integrated over the

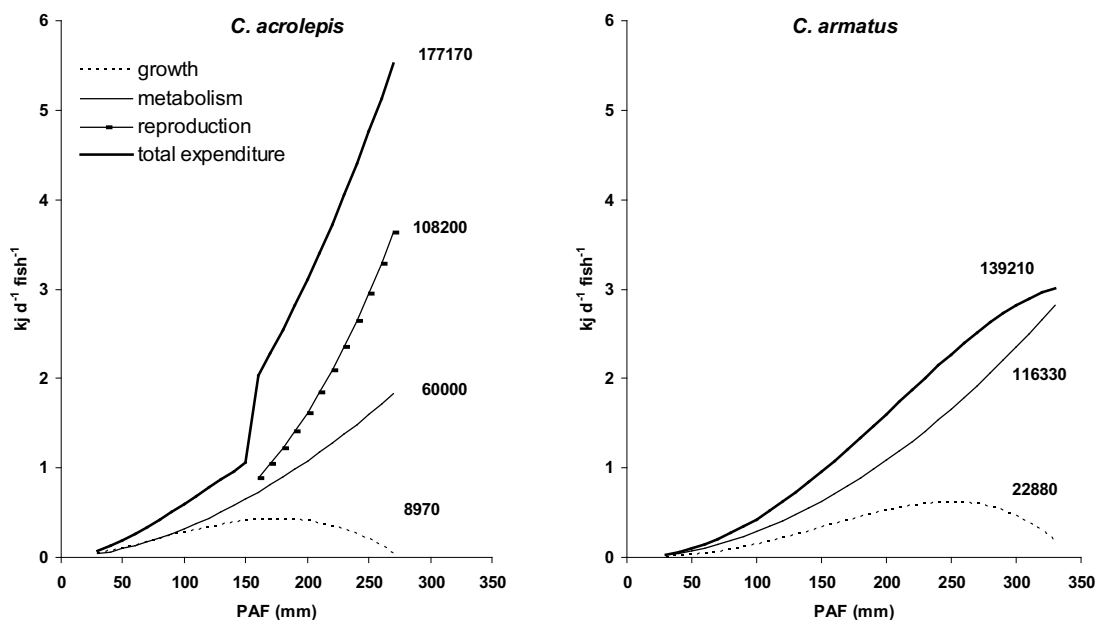


Figure 3. Daily energy budgets are presented as a function of size. Total daily expenditure is the sum of metabolism, growth, and reproduction and it is 80% of the feeding rate (see text). The lifetime expenditures derived from each function are given at the right and are in kJ . PAF is preanal fin length. Reproduced from Drazen (2002a) with permission.

life-span of the fish reproductive costs total $\sim 108,000 \text{ kJ}$ for *C. acrolepis*, more than half the lifetime energy expenditure (Figure 2). They are also nearly double the daily total 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 whose mean GSIs are higher (12–22%; Jobling 1982; Smith et al. 1990) and egg energy density 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 high on the continental slope. Macrourid eggs are buoyant and once released they rise towards the surface. 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 Percy 1982).

The second explanation is that reproductive periodicity has not been assessed correctly. There is evidence that spawning is continuous in *C. acrolepis* (Drazen 2002b). Most shallow living species spawn annually (even if aseasonally) and this is often the assumption for macrourids and other deep-sea fishes. However, we must ask the question, does every individual spawn every year? As described above, either serial batch spawning or skipping reproduction in some years could dramatically reduce the annual costs of reproduction. In the deep-sea where food

is scarce relative to shallow water, *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 and atlantic cod, phylogenetically related to the macrourids (Dutil 1987; Jobling 1994; Rideout et al. 2005). This is usually the result of poor nutrition resulting from scarce food resources. 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* reproduced every other year, then the reproductive costs from the model would be one half of the estimates given. Lifetime reproductive costs would only be ~54,000 *kJ* which is similar to metabolism.

Coryphaenoides armatus may take this strategy to the extreme and save energy in its oligotrophic abyssal habitat by having a semelparous reproductive strategy (Drazen 2002a; Stein 1985). This type of reproduction might be favored where food supplies are low but the environment is relatively stable. Energy would be saved by spawning only once, 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 (Stearns 1992). 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). American shad *Alosa sapidissima* in environmentally variable northern rivers are iteroparous whereas southern stocks living in stable rivers are semelparous (Leggett and Carscadden 1978). Certainly investigations into the annual reproductive output of the macrourids

are needed. Clearly energy budgets are a useful tool to evaluate the accuracy of estimates for energetic processes and may shed light on adaptations of the animals to their habitats.

Energy budgets are also a useful tool to estimate the feeding rates of fishes.

Drazen (2002a) estimated the feeding rates of *C. acrolepis* at 0.31–0.07% of body weight (BW), decreasing with increasing fish size. Estimates for *C. armatus* ranged from 0.12 to 0.02% BW. Koslow (1996) derived similar results 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 d⁻¹ and for *C. rupestris* 0.05% BW d⁻¹. The estimated daily rations of cod are much higher and range from 0.5 to 5.0% BW d⁻¹ (Daan 1973; Du Buit 1995; Jones 1978; Majkowski and Waiwood 1981). Two other studies have estimated feeding rates in macrourids but they used gastric evacuation models. Macpherson (1985) estimated the food consumption of the macrourid, banded whiptail *Coelorinchus fasciatus*, at 0.55–2.15% BW d⁻¹. Madurell and Cartes (2006) suggested a rate of 2.1–2.9% BW for saddled grenadier *Coelorhynchus coelorhynchus*, 1.5% BW for *Hymenocephalus italicus*, and 0.4–0.7% BW for bluntnout grenadier *Nezumia schlerorhynchus*. These are all small macrourids from the Mediterranean. There is a large discrepancy between the two methods for estimating feeding rates but this can be explained in large part by energetic rate processes. Gastric evacuation models require an estimate of a rate process, namely the rate of gastric emptying in the fish (Bromley 1994). In the above studies, the models employed rates estimated from shallow living fishes (either cod or flatfishes) at low temperatures. As can be clearly seen from the discussion of energetic parameters above, this is not a justified extrapolation and probably led to overestimation of feeding rates.

Comparisons to other deep-sea fishes

Not all demersal deep-sea fishes are alike which is not surprising since they come from different branches of the ichthyological tree but the differences also reflect the importance of habitat variables driving locomotory requirements and metabolic rates. Many grenadiers live on the continental slopes and have been termed benthopelagic because they swim above the bottom but remain in association with it (Drazen and Seibel, in revision; Koslow 1996; Neighbors and Wilson 2006). Benthic fishes rest on the seafloor for much of the time and include flatfishes and some scorpaenids. Benthic and benthopelagic species are very similar in their muscle water and protein content (Drazen 2007) however, benthic fish oxygen consumption and CS activity are generally less than for grenadiers which corresponds to their low levels of activity (Drazen and Seibel in revision). So called seamount-associated species, such as orange roughy and oreos, are benthopelagic species which aggregate at elevated topographic features. They stand out from the other demersal groups energetically. Energy budget calculations estimate comparatively higher total energy expenditure as a result of greater metabolic rates. Fishes living on seamounts encounter high and variable currents and an active locomotory capacity is probably required to maintain their position in the water column. Corroborating this suggestion, they have more robust morphologies and lower muscle water content than either grenadiers or benthic species suggesting a much greater swimming capabilities (Koslow 1996; Koslow et al. 2000). Despite their high energy use, these fishes had slow growth, even slower than that of other demersal species with a very small proportion of their annual energy budget allocated to growth (Koslow 1996).

Comparisons between the grenadiers and meso- and bathypelagic fishes are more diffi-

cult to make because of dramatic differences in body size but pelagic fishes exhibit some of the same depth related trends in energetics as demersal species. Metabolism and enzyme activities scale with body size but so do longevity and other life history parameters (Stearns 1992). The metabolism and enzyme activities of grenadiers are not too dissimilar to those of nonmigratory meso- and bathypelagic species (Drazen and Seibel, in revision; Seibel and Drazen, in press). However, estimates of longevity in these animals ranges from 4 to 8 years (Childress et al. 1980) and differ greatly from all but the smallest grenadiers. Perhaps what is more illuminating is to examine relative trends for pelagic species. Epipelagic species have much higher metabolic rates, the highest growth rates, and early onset of sexual maturity. Metabolic rates decline with depth such that the bathypelagic species have the lowest (Childress 1995; Childress et al. 1980). With respect to growth the bathypelagic species had much lower growth rates compared to epipelagic ones but they were still higher than those of the mesopelagic species. Bathypelagic species may not require good locomotory capacities in their dark environment, so instead invest energy in growth to increase the size range of potential prey they could eat and to reduce predation risk. Mesopelagic species appear to mature at about 3 years of age and the bathypelagic species were semelparous (Childress et al. 1980). These trends of lower metabolism and growth and a reduced reproductive output in deep-sea versus shallow-water species, are not too dissimilar to those found in gadiforms and other deep-sea demersal fishes.

Summary

Grenadiers are certainly unlike many shallow-living gadiformes in that their rates of energetic processes are much lower. They are adapted to deep-sea habitats with fundamentally different environmental conditions

than the continental shelves where most exploited fishes live. Grenadiers have metabolic rates, determined directly using *in situ* and high pressure respirometers, an order of magnitude lower than shallow living gadiforms. Metabolic enzyme activities, indirect estimates of metabolic capacity, are low for all of the grenadiers examined and suggest low metabolic rates where direct estimates are not available. Intraspecific differences are important and are probably related to different locomotory capacities and foraging modes (Siebenaller et al. 1982). In addition to intraspecific variation, deep-sea demersal and pelagic fishes show depth-related declines in metabolism (Drazen and Seibel, *in revision*). This trend appears to be the result of a relaxation in the selective pressure for locomotory capacity in dim or totally dark waters.

Low rates of growth are not as easily explained. Longevities range from ~10 years for relatively small species to ~75 years for larger animals, yet many of these animals have similarly slow mass-specific growth rates. It is not clear why slow growth would be adaptive for deep-sea species but it may be that growth, as a product of metabolism, is constrained by metabolic rate (Brown et al. 2004). Reproductive outputs may be low. Relative fecundity of grenadiers is moderate but as an analysis of energy budgets has shown, current measurements of fecundity may overestimate annual reproductive output (Drazen 2002a). Grenadiers may require more than one year to build sufficient energy reserves to support gamete development.

Energetically grenadiers are similar to other benthopelagic and benthic deep-sea fishes. Seamount-associated species represent a group adapted to a particularly dynamic deep-sea environment and appear to differ dramatically, having higher metabolic rates and lower growth rates (Koslow 1996). Comparisons have been made between the energetics of shallow and deep-living pelag-

ic species and reduced rate processes of the deeper living species (Childress et al. 1980) generally mimic those found within demersal species and strengthen the conclusions of this paper.

New studies and new tools to measure energetic parameters have added to our knowledge in recent years but their development and application are outpaced by the exploitation of the world's continental slopes (Haedrich et al. 2001). Unfortunately this trend may continue. Until more data are available for more species, we must assume that with a similar body form, phylogeny, and habitat that grenadier species all have low rates of metabolism, growth and reproduction. At the same time, general trends, such as that found for metabolic rates, must be developed more fully so that we may better effectively model the energetics and ultimately population dynamics of slope dwelling fishes. Grenadiers are exceptionally diverse and certainly variation exists. Only additional studies will elucidate the nature of the specific variation.

Nevertheless it is clear that models based on the energetics of shallow living species cannot be used for grenadiers. Their energetic characteristics make them extremely vulnerable to overexploitation. Whether targets of fisheries or bycatch, their role as top predators and dominant fishes of many areas of the deep sea necessitates additional study that will lead to management for sustainability and conservation.

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