REVIEWS

Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes

Jeffrey C. Drazen[1]
Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, Hawaii 96822

Brad A. Seibel
Biological Sciences, University of Rhode Island, 100 Flagg Road, Kingston, Rhode Island 02881

Abstract

 The metabolism of several animal groups declines with depth even after adjustments for size and temperature. The "visual-interactions hypothesis" explains this trend as the result of declining light levels that reduce the distances over which predators and prey interact. This reduction relaxes the selective pressure for locomotory capacity, and reductions in metabolic rate follow. The decline in visual interactions and metabolism is most pronounced among pelagic species, as this environment affords no refuge from predators. The visual-interactions hypothesis thus predicts less depth-related variation among benthic species. However, it has been tested primarily with pelagic animal data. Summarizing many scattered studies and data sets to further test the hypothesis, here we analyze the data for benthic and benthopelagic fishes. Oxygen consumption rates declined significantly with depth in benthopelagic and, to a lesser extent, benthic species. Trends in muscle metabolic enzyme activities generally corroborated these patterns. The anaerobic capacity of the white muscle indicated the greatest decline in pelagic and the smallest reduction in benthic species, as expected. Similar trends were not found in aerobic capacity, but this result may reflect a paucity of enzyme data for benthic species. Most of the studied fishes live off of California, where the presence of an oxygen-minimum zone may influence some of the patterns observed. This preliminary analysis of data clearly illustrates that temperature and body mass cannot explain the variability evident in metabolism. Rather, some covariate of habitat depth acts to influence metabolism in benthic and benthopelagic fishes. The general trends are explained by the visual-interactions hypothesis, but considerably more data are required to account for the variation in metabolism and lifestyle that is apparent. In particular, regional comparisons are needed to separate the influences of environmental factors, such as oxygen, which covary with depth.

Rate of metabolism is of fundamental importance to ecology because it is the process of energy assimilation, transformation, and allocation, and as such, it can be used to construct models of the flow of energy and materials in an ecosystem (Smith 1992; Smith et al. 2001). Therefore, there have been many efforts to describe patterns of metabolism and their mechanistic underpinnings (Childress 1995; Gillooly et al. 2001; Clarke 2004). 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 and Johnston 1999; Clarke 2004). Body size also has

dramatic effects on metabolism. The classic "mouse-to-elephant" curve relates the variation in mammalian metabolic rates to body sizes with a power law. Although cause and generality of the relationship is actively debated (Childress and Somero 1990; Suarez et al. 2004; Glazier 2005), smaller animals generally have higher mass-specific metabolic rates than larger ones. While some have argued that the metabolic rates of everything from microbes to blue whales can be predicted based solely on size and temperature (Gillooly et al. 2001; Brown et al. 2004), more recent analyses demonstrate a wide variation in both the slopes and elevations of the scaling relationships after temperature adjustment (Glazier 2005; Seibel 2007; Seibel and Drazen in press).

 Metabolic rates within some groups of deep-sea organisms are much lower than in their shallow-water counterparts even after mass and temperature effects have been taken into account. Studies have shown that pelagic fishes (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.

The "visual-interaction hypothesis" (Childress et al. 1990a) suggests 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; Seibel and Drazen in press). This hypothesis suggests that in the absence of light, the distances over 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 rates follow. This argument has been supported by a lack of depth-related declines in the metabolism of taxa that 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 ~1,000 m, where visible light is absent (Warrant and Locket 2004). The visual-interactions hypothesis should not be confused with a general interaction hypothesis, due to decreasing animal abundance with depth. The latter predicts metabolic declines to continue below 1,000 m and across all animal groups, but this is not supported by the data.

Several alternative hypotheses to explain depth-related patterns in metabolism have been explored. Pressure could limit metabolic rate because some enzymes adapted to high pressures are inefficient (Somero and Siebenaller 1979). However, capacity adaptations allow an organism to maintain a level of performance regardless of pressure (Hochachka and Somero 2002); this has been confirmed by constant levels of enzymatic activity in the brains and hearts of fishes regardless of depth (Childress and Somero 1979; Sullivan and Somero 1980; Siebenaller et al. 1982). Studies of metabolic rates under varying pressure show no effect in fishes or crustaceans (Meek and Childress 1973; Childress 1977; Belman and Gordon 1979). Other studies explain the slow rates of deep-sea animals as an adaptation to lower food availability at depth (Childress 1971; Smith and Hessler 1974; Dalhoff 2004). Animal biomass declines exponentially with an order of magnitude difference between the surface and 1,000 m (Haedrich and Rowe 1977; Angel and Baker 1982; Thurston et al. 1994). However, metabolic rates of animals in oligotrophic surface waters are higher than those of deep-sea animals in eutrophic regions, suggesting that food supply does not constrain metabolism interspecifically (Cowles et al. 1991; Seibel and Drazen in press).

Most of the work on deep-sea metabolism has been conducted in the pelagic environment. There has been much less work on the metabolism of deep-sea benthic animals. Working with them is certainly more difficult because collection of specimens in good health is more complicated. Benthic trawling usually crushes or suffocates the animals in the cod end with rock and sediment. For fishes, the situation is exacerbated by the presence of gas bladders in many groups, which expand upon recovery to the surface, killing the fish. As a result, many of the data have been acquired using in situ manipulations from submersibles and remotely operated vehicles (ROVs; Smith and Baldwin 1997).

With regard to the visual-interactions hypothesis, the most important difference between the pelagic and benthic realms is the opportunity for crypsis. In the open pelagic environment, animals may hide by being transparent, but this possibility is limited to small zooplankton and gelatinous animals due to the refraction and absorption of light through large, robust bodies of the micronekton and nekton (Johnsen 2001). As a result, when large pelagic animals encounter predator or prey, they must swim. In the benthic realm, the substrate affords many hiding places and the opportunity for camouflage of even large organisms. In addition, the presence of a substrate changes buoyancy requirements, possibly allowing normally sedentary animals to retain large muscle masses for burst swimming. Indeed benthic crustaceans, octopods, and echinoderms generally do not show declines in metabolic rate with depth (Seibel and Childress 2000; Seibel and Drazen in press). Curiously, however, more mobile groups that spend at least some of their time swimming in the water column, such as caridean shrimps, do show declines (Childress et al. 1990a; Company and Sarda 1998).

Deep-sea fishes represent a variety of locomotory modes and lifestyles in the benthic environment and are an ideal group with which to explore the visual-interactions hypothesis. Fishes can be classified as either pelagic, benthic, or benthopelagic. Although the terms "benthic" and "pelagic" are rather straightforward, the term "benthopelagic" is not. It is used to describe those species that spend their lives near, but rarely on, the bottom. Data do not exist that allow quantification of the relative amount of time spent on or above the bottom for deep-sea species. Thus, the somewhat arbitrary classification of benthic and benthopelagic will be employed cautiously here. Recent instruments developed for measuring oxygen consumption in these animals in situ (Bailey et al. 2002) and under in situ conditions aboard ship (Drazen et al. 2005) have added to our data set. In addition, key enzymes of intermediary metabolism have been measured for a much greater diversity of deep-sea fishes and can be good proxies for metabolic rates (Childress and Somero 1979; Dalhoff 2004). These data have not yet been synthesized and presented as a function of habitat depth. Here, we present a synthesis of our data and those from the literature on the metabolism of deep-sea benthic and benthopelagic fishes in order to test the visual-interactions hypothesis.

Methods

Data from 66 studies and our own measurements were assimilated into a database for analysis of depth-related influences on metabolism. Studies of oxygen consumption were included only if several basic criteria were met, but given the general paucity of deep-sea data, we were unable to be highly selective. In all studies, measurements were made over at least 4 h, and most experiments lasted 12–48 h. In laboratory studies, a 12-h period of food deprivation prior to measurement was employed. Microbial respiration was controlled, and animal incubation chambers were kept in the dark. Where activity was monitored, a rate corresponding to a minimum activity was used. These measurements were of "routine" metabolism that

made some allowance for spontaneous activity in the absence of obvious external stimuli.

To examine the relationship between metabolic variables and depth, we used the minimum depth of occurrence (MDO). Most studies to date define MDO as the depth below which 90% of the individuals of a given species are captured (Childress 1995; Seibel and Drazen in press). Organisms typically do not occupy a single depth that can easily be plotted as a potential predictor of metabolism. Many pelagic fishes migrate on a diel basis, and many benthic and benthopelagic species are known to exhibit ontogenetic, downslope migration (Jacobson et al. 2001; Collins et al. 2005), sometimes ranging vertically over thousands of meters in their lifetime, from epipelagic larvae to adults at bathyal or even abyssal depths. MDO as used here is not quite the same as that from pelagic studies. Here, we used the MDO of the adults, omitting the distributions of pelagic larval phases and shallow-living juveniles, to accurately represent the habitat of the individuals upon which estimates of metabolic rate have been measured. In most cases, there is no information with which to assess the depth below which 90% of the adult population is found. There is information, however, on the depth below which adult specimens are regularly captured, from a variety of ecological studies (*see* Web Appendix 1). Global databases, such as fishbase.org (Froese and Pauly 2006), and reviews were used with care because they often do not present enough detail to determine the influence of ontogeny or vagrants on the depth ranges. For instance, fishbase.org gives a minimum depth for the abyssal rattail *Coryphaenoides armatus* as 282 m. Most sampling efforts do not normally capture this species shallower than ~2,000 m (Pearcy et al. 1982).

Oxygen-consumption data were analyzed allometrically and by depth. In both analyses, metabolic rates were corrected to 5°C using measured temperature coefficients where available or assuming a Q_{10} of 2.3, a value found to be representative for diverse fishes (Clarke and Johnston 1999). Oxygen consumption was analyzed as a function of body mass to determine relationships between individual species, closely related groups, and different locomotory habits (i.e., benthic vs. benthopelagic). For comparisons by depth, differences in mass must be considered as well. Mass-specific metabolic rate (*Y*, temperature corrected) typically decreases with body mass (M) according to the allometric equation $Y = aM^b$, where *a* and *b* are the taxon-specific intercept and slope, respectively. Previous studies on pelagic fishes and crustaceans have used mean values for regression to MDO because their size range is generally narrow and similar for each species (Childress 1975; Childress and Somero 1979; Torres et al. 1979). The size range of benthic and benthopelagic fishes is large. Therefore, rates plotted as a function of MDO were adjusted to a mean size of 500 g. Size-scaling information was available in many cases, so we used the published regressions to determine the oxygen consumption for a 500-g individual. If no scaling was provided, we adjusted to the mean size using a mass-specific scaling exponent of −0.20, as has been done in previous studies for fish (Childress et al. 1990*a*; Clarke and Johnston 1999). Almost all of the species in the analysis normally reach 500 g, but a few (five shallow-living fishes) do not, and they were not included in the MDO analysis.

Difficulties of laboratory-based and in situ studies of deep-sea fishes have resulted in a small data set of oxygen-consumption measurements. To augment these data, measurements of key enzymes of intermediary metabolism can be used as proxies for metabolic rate. Several studies have found that they correlate well with oxygen consumption rates (Dalhoff 2004; Moyes and Lemoine 2005; Seibel 2007). The most widely measured anaerobic and aerobic enzymes were chosen. Data for a few other enzymes' activities are available, but for fewer species, which limits their use for a broad, depth-related comparison. Citrate synthetase (CS), active in the Krebs cycles, is an indicator of aerobic metabolism, whereas lactate dehydrogenase (LDH) is a glycolytic enzyme, indicative of anaerobic metabolism and burst swimming capacity (Dalhoff 2004). Enzymatic activities were measured at, or normalized to 10°C, under substrate-saturating conditions. A measurement temperature of 10°C has become a standard because it is a temperature high enough to prevent the difficulties of condensation in spectrophotometers, but it is safely below the temperatures known to denature the enzymes (Somero 1992; Dalhoff 2004). Enzyme activities scale with body size, where anaerobic activities generally increase and aerobic activities decrease with body size (Somero and Childress 1980; Somero and Childress 1985). Thus, enzyme activities were scaled to a body mass of 500 g using published coefficients for each species before examining the relationship to MDO. For a few species, coefficients were unavailable, so we used only data for fishes that were close to the standard size, 300–700 g. In a few cases, more than one study provided data for a species. In these cases, the values were averaged.

The relationship between oxygen concentration and metabolism was examined. For each species an oxygen concentration was assigned that corresponded to its MDO. Data for oxygen concentration were taken from profiles to a depth of 3,500 m off central California (Monterey Bay Aquarium Research Institute's [MBARI] expedition database). Regressions were performed between metabolic rate and oxygen concentration.

All of the data used in this study, the information used for determining MDO, and associated references are presented in Web Appendix 1 (http://www.aslo.org/lo/toc/vol_52/issue_5/2306.pdf).

Results

Respirometry—An allometric analysis of temperature-adjusted (5°C) oxygen-consumption rates was performed on various groups of benthic and benthopelagic species (Fig. 1). For this analysis, deep-sea groups are species living on the continental slopes or abyssal plains, whereas shallow-living species inhabit the continental shelves, most above 100 m. Amongst gadiforms, it is clear that shallow-living species such as cod have metabolic rates an order of magnitude higher than deep-living *C. armatus* and *Coryphaenoides acrolepis* of the same size. For scorpaenids, the two deep-living species have metabolic rates that are on the lower end of the rather large spectrum for both shallow- and deep-
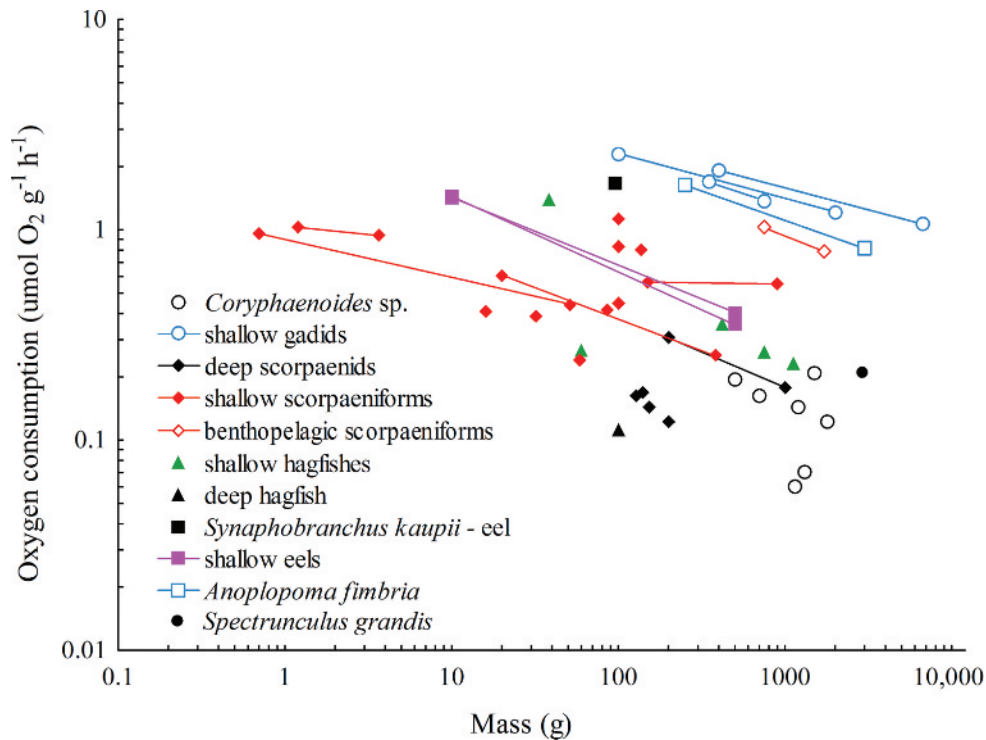
Fig. 1. Oxygen consumption rate (5°C) as a function of body mass for various groups of benthic and benthopelagic fishes. Points connected by lines indicate the mass scaling relationship for many data points. Data for deep-sea species are few and are plotted as individual data points except for the case of one scorpaenid that was studied in the laboratory (Yang et al. 1992).

living species. A striking difference is not apparent. Scorpaeniforms are the only group in this analysis that includes both benthic and benthopelagic species. The oxygen consumption of a benthopelagic scorpaenid is much higher than the others. There is only a single measurement of a deep-sea eel's metabolism, and this value is much higher than for shallow-living eels. Data are also available for hagfishes. The deep-sea species has very low rates compared to species of similar size inhabiting the continental shelves. Finally, data are available for *Anoplopoma fimbria*, the sablefish, which lives at depths ranging from close to the surface off the coast of Alaska to as deep as 1,500 m off of southern California (Jacobson et al. 2001; Neighbors and Wilson 2006). This species has a metabolic rate similar to shallow-living gadids. Lastly, the abyssal ophidiid *Spectrunculus grandis*, which is a large, relatively mobile benthopelagic species, has a metabolic rate similar to *Coryphaenoides* spp. of similar size.

In addition to the allometric approach, a data point for each species was generated at a common size of 500 g (*see* Methods) and compared to its MDO (Fig. 2). Oxygen consumption of benthopelagic species declined significantly with depth ($p < 0.01$) with relatively little change below 600 m. Metabolic rates of benthic species also declined ($p = 0.02$), but data for only three deep-sea species were available (*Sebastolobus alascanus*, *Sebastolobus altivelis*, and *Eptratretus deani*), all of which had MDOs of 400–500 m.

Enzyme activities—Enzyme activity measurements were available for more species across a greater range of depths.
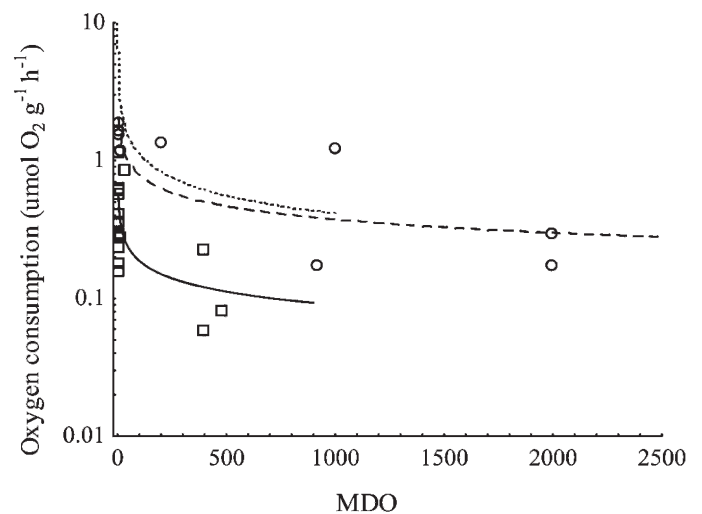

Fig. 2. Metabolic rates (5°C, 500 g) of benthic (squares) and benthopelagic (circles) species as a function of MDO. Regressions are shown and are: benthic (solid line) $VO_2 = 0.82 \, MDO^{-0.32 \pm 0.12}$, $r = -0.57$, $p = 0.02$; benthopelagic (dashed line) $VO_2 = 3.42 \, MDO^{-0.32 \pm 0.09}$, $r = -0.78$, $p < 0.01$. For comparison, the regression for data on pelagic species from Torres et al. (1979) is shown as a dotted line: $VO_2 = 8.08 \, MDO^{-0.43 \pm 0.05}$, $r = -0.89$, $p < 0.001$. All slopes are given with standard errors.
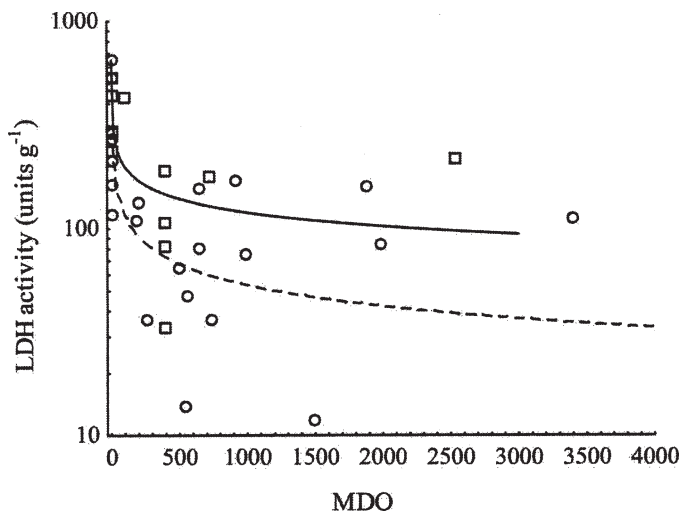
Fig. 3. Lactate dehydrogenase (LDH) activity versus MDO for benthic (squares) and benthopelagic (circles) fishes. Regressions are shown and are: benthic (solid line) LDH = 545 $MDO^{-0.22\pm0.10}$, $r = -0.59$, $p = 0.04$; benthopelagic (dashed line) LDH = 564 $MDO^{-0.34\pm0.10}$, $r = -0.60$, $p < 0.01$. All slopes are given with standard errors. The data point for the benthopelagic fish *Coryphaenoides leptolepis* (4.3 units g^{-1}; MDO – 1998 m; *see* Web Appendix 1) is not shown due to the scale of the figure.
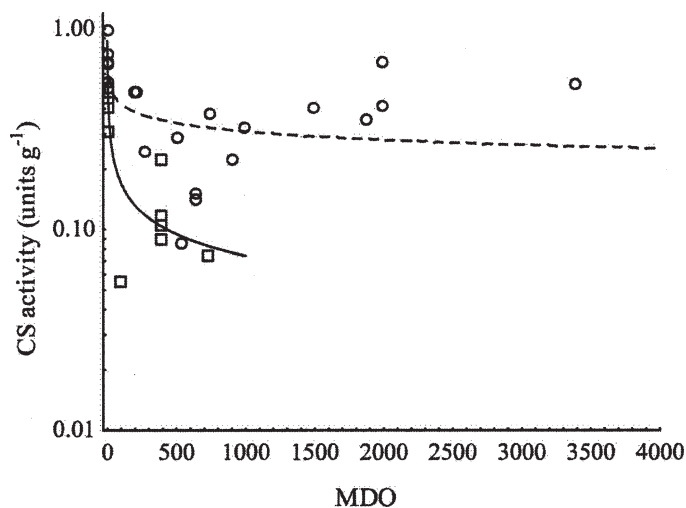
For benthopelagic fishes, LDH activities across a range of species with MDOs from 10 m to 3,400 m exhibited a significant decline (Fig. 3). CS activities also showed a significant decline, where a cluster of species with MDOs of ~600 m had the lowest activities (Fig. 4). Benthic species exhibited a significant decline in LDH activity (Fig. 3) and in CS activities (Fig. 4) in contrast to results for direct respirometry. There is a single rather high LDH activity for the hydrothermal vent zoarcid (Hand and Somero 1983; probably *Thermarces cerberus*, but the species is not given in the original reference) with an MDO of 2,550 m (Fig. 3). If the data point for this animal is removed, the slope of the regression (LDH = $712MDO^{-0.30\pm0.10}$, $r = -0.70$, $p = 0.02$) is closer to that for the benthopelagic fishes. As for measurements of oxygen consumption, data for benthic species were the sparsest ($n = 11$).

Table 1. Exponents for the relationship between enzyme activity and MDO with the form of activity = $a \times MDO^b$. Data for benthic and benthopelagic fishes are from the present analysis. Data for pelagic fishes are shown for comparison. Data for pelagic fishes lactate dehydrogenase (LDH) are from Childress and Somero (1979), and citrate synthetase (CS) data are from Childress and Thuesen (1995). All regressions are statistically significant ($p < 0.05$). Slopes are given with standard errors.

|	LDH		CS	
	Intercept (a)	Slope (b)	Intercept (a)	Slope (b)
Pelagic	734	-0.69 ± 0.22	10.4	-0.56 ± 0.23
Benthopelagic	560	-0.34 ± 0.10	0.81	-0.14 ± 0.06
Benthic	546	-0.22 ± 0.10	0.89	-0.36 ± 0.08

Fig. 4. Citrate synthetase (CS) activity versus MDO for benthic (squares) and benthopelagic (circles) fishes. Regressions are shown and are: benthic (solid line) CS = 0.89 $MDO^{-0.36\pm0.08}$, $r = -0.84$, $p = 0.001$; benthopelagic (dashed line) CS = 0.81 $MDO^{-0.14\pm0.06}$, $r = -0.49$, $p = 0.03$. All slopes are given with standard errors.

A comparison of the regression equations for benthopelagic, benthic, and pelagic fishes was performed to examine the relative rates of declines in metabolic enzyme activities (Table 1). The regression equation for pelagic fishes was taken directly from Childress and Somero (1979) and Childress and Thuesen (1995). For LDH activities, it is clear that the highest intercept (activity of species in surface waters) is for pelagic species followed by the benthopelagic and benthic species. Rates of decline (slopes) are highest for pelagic and lowest for benthic species. For CS activities, the intercept is 10 times higher for pelagic than benthic and benthopelagic fishes. The rate of decline in these activities is highest in the pelagic animals and much lower for benthopelagic species. Curiously, the slope for benthic species is intermediate between the pelagic and benthopelagic groups of fishes.

The influence of oxygen—The majority of the data on metabolic rates and metabolic enzyme activities come from species that inhabit the northeast Pacific. These waters are characterized by an oxygen minimum zone (OMZ; Levin 2002) between ~600 m and 1,000 m. Data were inadequate to compare direct measurements of oxygen consumption to oxygen concentration statistically. However, *C. acrolepis* with an MDO at the heart of the OMZ has a metabolic rate similar to that for *C. armatus* and *S. grandis*, both of which live well below the OMZ. For the benthic species, all the deeper-living ones inhabit the OMZ.

Regressions were performed between LDH and CS activities and oxygen concentration at each species MDO. Oxygen concentrations in surface water can be 280 μmol L^{-1}, close to saturation, dropping to <10 μmol L^{-1} in the OMZ and rising back to ~100 μmol L^{-1} at a depth of several thousand meters (Levin 2002; Levin and Atkinson 2003; MBARI expedition database). Thus, species inhabiting surface waters with three times the oxygen concentration of deep-sea species living well below the OMZ will

drive any regression. As a result, it is informative to include only those species with MDOs greater than 100 m, so that the rates of animals inhabiting regions of higher oxygen both above and below the OMZ can be compared to those living within it. For the benthopelagic species, CS activity was significantly correlated with oxygen concentration below 100 m MDO (CS activity [units g^{-1}] = 0.213 + 0.148 × [O_2] [mL L^{-1}], r^2 = 0.52, $p < 0.05$), but LDH was not. The correlation is evident in Fig. 4 as a cluster of low enzyme activities at ~500 m MDO. For benthic species, LDH was significantly correlated with oxygen concentration (LDH activity [units g^{-1}] = 28.2 + 157 × [O_2] [mL L^{-1}], r^2 = 0.69, $p < 0.05$), but the regression is driven by a single species, the vent zoarcid *T. cerberus*, which had a high LDH activity at 2,550 m MDO (Fig 3).

Discussion

The limited respirometry data indicate that deep-sea benthic and benthopelagic fishes have lower metabolic rates than shallow-water species in the same groups. These patterns were first observed ~30 yr ago for rattails and deep-living rockfishes (Smith and Hessler 1974; Smith 1978; Smith and Brown 1983). Newer measurements (Bailey et al. 2002; Drazen et al. 2005) for these and other species confirm the original results (Fig. 1). In addition, as seen by plotting the data as a function of MDO, the declines in metabolic rates are most pronounced in the first several hundred meters of the water column. However, there are too few measurements to adequately assess variation in the deepest-living benthopelagic species, and there is no information for benthic species below 500 m (but see results for enzyme activities below). Previous studies have shown no depth-related differences in metabolic rates of benthic echinoderms, octopods (Seibel and Drazen in press), and meiofauna (Shirayama 1992). Within the crustaceans, only carideans, a group with arguably greater swimming capacity and sustained activity, show declines in metabolism with depth (Childress et al. 1990*a*; Company and Sarda 1998; Seibel and Drazen in press). It has been argued that the differences found for crustaceans are related to locomotory modes (sedentary vs. active swimming) and that the slopes of the declines vary with the exposure to predators on and off the bottom (Childress et al. 1990*a*). Our data clearly suggest that mobile benthopelagic species exhibit declines in metabolism, although these declines are not as steep as for pelagic species (Fig. 2). The more sedentary benthic species also exhibit a depth-related decline, but we consider this result much more tentative because it is really a comparison of a cluster of three benthic species at 400–500 m MDO to species with MDOs of 10–40 m. However, shallow-living benthic species probably require a greater locomotory activity than other benthic groups of animals. Unlike most echinoderms and crabs, they swim to relocate, to interact with other members of their population, and to forage. In the shallowest water, these habits undoubtedly expose them to a physically dynamic environment that would necessitate a higher level of locomotory capacity than in slope-dwelling species.

The visual-interactions hypothesis predicts strong declines in metabolism with depth for visual animals in general, and exceptions to the rule are expected for certain species. Two such cases were found. A comparison of shallow-water *Anguilla* spp. to the slope-dwelling *Synaphobranchus kaupii* suggests that the deeper-living species has a metabolic rate ~50% higher (Fig. 3). In situ respirometry, such as that used to measure *S. kaupii* oxygen consumption, is technically very challenging and arguably represents an advance over measurements made on deep-living species at atmospheric pressure (Bailey et al. 2005). However, the authors indicate that the eels were "active," and it is possible that they had just eaten the bait used to attract them. Certainly, the rates overestimate routine rates. The data presented for hagfish indicate that the single measurement on the deep-living species is nearly an order of magnitude lower than that for shallow-water animals. This result is surprising because hagfish lack true eyes (Martini 1998), and the visual-interactions hypothesis would predict no depth-related variation in this group. It is clear that the respirometry data are sparse, and while the analysis presents intriguing possibilities, it is difficult to come to many firm conclusions.

Trends in the activities of metabolic enzymes are derived from much more data and generally corroborate the respirometry results. Declines in both LDH and CS were significant in benthic and benthopelagic groups of fishes (Figs. 3, 4). However, the decline in benthopelagic CS, while statistically significant, is very small. The benthopelagic species with MDOs greater than 1,500 m, macrourids and a synaphobranchid eel, have relatively high values for deep-living fishes. All of these animals are scavengers (Sullivan and Somero 1980; Drazen 2002; King et al. 2006) and may rely on a higher level of activity to compete for sparsely distributed parcels of carrion. Other studies have come to similar conclusions that feeding and locomotory modes may lead to variation in the enzyme activities of fishes at a given depth (Sullivan and Somero 1980; Siebenaller et al. 1982). LDH activity correlates well with burst locomotory performance probably because it facilitates adenosine triphosphate (ATP) generation when tissue oxygen is rapidly depleted (Somero and Childress 1980; Dalhoff 2004). Implicit in the visual-interactions hypothesis is that burst locomotory performance used during predator–prey interactions would decline. However, it is clear that routine and maximum metabolism and burst locomotion are linked (Seibel and Drazen in press).

To examine the relationship between broad locomotory modes, we compared the exponents of the power regressions among benthic, benthopelagic, and pelagic species (Table 1), and it is clear that locomotory mode influences enzyme activities. The slopes of these relationships could be influenced by size because the pelagic fishes studied previously are typically much smaller than the benthic and benthopelagic species from the present analysis (~25 g vs. 500 g; Childress and Somero 1979; Childress and Thuesen 1995). However, metabolism and enzyme activities usually scale near quarter power with body mass, so our analysis is a reasonable approximation (Somero and Childress 1980; Childress and Somero 1990). Differences

in the size of normalization will affect a comparison of the intercepts. For LDH, the activities for larger, 500 g pelagic fish would be much higher than those in Table 1, and for CS, the intercept would be much lower. At the shallowest depths, pelagic animals have higher anaerobic and aerobic enzyme activities than benthopelagic and benthic species. Depth-related declines are much less pronounced in more sedentary species, so that the slopes of the declines are greatest for pelagic and lowest for benthic fishes. From the regressions, the LDH activities of benthic species are higher than benthopelagic ones but only at depth (Fig. 3). As noted above, LDH for the benthic vent zoarcid is quite high and contributes to the difference. It has been hypothesized that this fish has a higher LDH than other deep-sea benthic fishes because it ventures into hypoxic vent waters to forage (Childress and Thuesen 1995). The exception to the general trend with respect to locomotory mode is for benthic fish aerobic enzyme activity (CS), which exhibits a pronounced decline with depth, much greater than that for the benthopelagic group (Table 1). The CS results are difficult to interpret because there are no data for benthic species at depths below 500 m or from regions outside the oxygen minimum zone.

An OMZ is present off the coast of California (Levin 2002), where most of the fishes in the present data set live. These conditions could affect metabolic rate and the aerobic poise of metabolism as reflected in aerobic enzyme activities. Enzyme activity and O_2 at the MDO are correlated in benthopelagic species (CS) and in benthic species (LDH), but for the latter, the regression is strongly driven by a single species. We must note that with our approach, both light and oxygen decline together in the first ~800 m of the water column, making interpretation difficult (see below for regional comparisons).

Several studies have examined the influence of the OMZ on enzyme activities of benthic fishes and found varying results. Childress and Somero (1979) found no evidence of enhanced glycolytic power in pelagic fishes living in the OMZ relative to species living shallower and deeper. Similarly, neither benthic nor pelagic cephalopods appear to have enhanced glycolytic power in the oxygen minimum zone (Seibel and Childress 2000; Seibel et al. 2000). For some flatfishes, aerobic and, surprisingly, anaerobic enzyme activities (LDH) are reduced intraspecifically in the OMZ (Vetter et al. 1994). For the scorpaenid, *Sebastolobus altivelis,* activities decline strongly with depth with no apparent effect of the OMZ. Only CS activity in *S. alascanus* varied predictably with oxygen content at the habitat depth (Vetter and Lynn 1997). In *S. alascanus*, LDH in red muscle of animals living in the OMZ were much higher than those acclimated to normoxic conditions in the laboratory, suggesting a phenotypic response to the habitat oxygen conditions by shifting the muscle to a more anaerobic poise (Yang and Somero 1993). It is unclear whether this difference was due to acclimation to oxygen levels or food regimen. They found no evidence of greater anaerobic poise in brain or white muscle of the OMZ species relative to one living shallower. They did find high anaerobic capacity in red muscle relative to white muscle. This unusual finding suggests that this species may use anaerobic metabolic pathways for a greater proportion of its routine needs than is typical.

Permanent OMZ residents have a variety of circulatory and morphological adaptations, such as large gill surface areas, high ventilation volumes, and respiratory proteins with a high affinity for oxygen (Childress and Seibel 1998; Seibel et al. 1999). Comparisons of pelagic species living at comparable depths in regions with and without an OMZ have shown similarly low metabolic rates, but OMZ residents had a greater capacity for oxygen extraction and transport (Childress and Seibel 1998; Seibel et al. 1999). Furthermore, depth-related declines in pelagic animal metabolism occur in regions with and without OMZs, suggesting that low metabolic rates are not specific adaptations to low oxygen (Childress and Seibel 1998; Seibel and Drazen in press). Low metabolic rate may be advantageous, but it is not sufficient for aerobic survival in the oxygen minimum layer. Permanent residents do not seem to rely on metabolic suppression but rather adaptations to extract oxygen from water at very low concentrations (Childress and Seibel 1998). Regional studies of depth-related trends in benthic and benthopelagic fish metabolism are needed to tease apart the relative importance of oxygen and habitat depth.

Food availability is often cited as the reason for metabolic declines in some deep-sea groups (Smith and Hessler 1974; Vetter and Lynn 1997; Dalhoff 2004). This hypothesis is very intuitive and has been applied to cave-dwelling fishes (Poulson 2001) as well. An animal might adjust its rate of energy usage in response to food intake (Dalhoff 2004). A low metabolic demand could be functionally adaptive where meal frequency and overall energy intake are low (Smith 1978; Sullivan and Somero 1980). Laboratory studies on many fishes have shown that ration affects oxygen consumption and metabolic enzyme activities to some degree (Sullivan and Smith 1982). One species of deep-sea benthic fish, *S. alascanus*, held and fed in the laboratory, had a 68% higher respiratory rate compared to field-caught specimens, suggesting that food was indeed limiting in the environment (Yang and Somero 1993). However, these intraspecific differences have not been large enough to explain the large depth-related declines observed interspecifically.

Regional comparisons provide strong evidence against the food-limitation hypothesis. Zooplankton biomass declines nearly exponentially with an order-of-magnitude difference between the surface and 1,000 m (Angel and Baker 1982), but these trends are affected regionally by variations in the upper water-column productivity (Thurston et al. 1994, 1998). Biomass at the surface in an oligotrophic region can be comparable to that at 1,000 m in an eutrophic one. If food were the selective factor for metabolic rates, then animals living at 500 m in an oligotrophic area, for instance, should have lower rates than those living in a more eutrophic environment at the same depth, but the metabolic rates of crustaceans and other animals do not exhibit differences between regions as would be predicted (Cowles et al. 1991; Seibel et al. 1997). Also, whereas fishes inhabiting more productive regions have higher lipid contents, reflecting seasonal or pulsed

food supplies, they do not have significantly different protein contents, indicative of locomotory activity and metabolic rates (Bailey and Robison 1986; Childress et al. 1990*b*). There is a general lack of correlation between food supply and metabolic rates in the pelagic deep sea (Seibel and Drazen in press).

No such regional comparisons can be made for benthic or benthopelagic fishes. However, the measures of metabolism in this study changed strongly in the first several hundred meters and then varied little below ~1,000 m. Part of the visual-interactions hypothesis is that metabolic declines will be most evident in the first 1,000 m, where light levels decline. Megafaunal biomass, a proxy for food availability, will continue to decline below 1,000 m (Haedrich and Rowe 1977; Lampitt et al. 1986; Smith and Demopoulos 2003). If selection for reduced metabolic rates to conserve energy under food-poor conditions is important, then we would expect metabolic rates to decline below 1,000 m.

If food supply limited metabolism, then it could be hypothesized that animals in the deep sea would exhibit greater assimilation and absorption efficiencies to extract more energy from their meals. In contrast, a recent study has found similar assimilation and absorption efficiencies between two deep-sea and two shallow-living fishes (Drazen et al. 2007). It was suggested that fishes are adapted to maximize energetic efficiency in all environments regardless of productivity.

Studies of tissue composition provide some interesting comparisons to the findings presented here. For pelagic fishes, water contents increase and protein contents decline with depth, reflecting the loss of locomotory capabilities (Childress and Nygaard 1973; Stickney and Torres 1989; Donnelly et al. 1990). Protein and water contents do not vary between fishes living in eutrophic and oligotrophic regions, as they would if food supply were strongly affecting them (Bailey and Robison 1986; Childress et al. 1990*b*). Instead, higher and more variable energy and lipid storage in species from eutrophic regions were attributed to the seasonality in food availability. An initial study of the water and protein contents of benthic and benthopelagic fish, muscle showed that the deep-sea group had much lower protein, but attempts to correlate these parameters with depth of occurrence were not performed (Sullivan and Somero 1980). An examination of white muscle composition of 18 species of benthic and benthopelagic fishes off of California found a significant increase in water content with depth of occurrence (Drazen 2007). Four species were found with nearly gelatinous muscle (88–92% water), and all occurred at bathyal depths. There were no differences amongst species living below 1,000 m. These data suggest a decline in locomotory capacity as would be expected from the visual-interactions hypothesis. Another study of 48 benthic and benthopelagic fishes from the Atlantic used a carbon, hydrogen, nitrogen (CHN) analysis on whole fishes (Crabtree 1995). Water content and nitrogen (indicative of protein content) of benthopelagic fishes, but not benthic species, declined with depth, and these declines were significant even at abyssal and lower bathyal depths. Energy storage, in this case caloric content and carbon

concentration, declined with depth, but declines were predominantly in the first 1,000 m. There were also lower carbon and caloric content in fishes from an oligotrophic region compared to fishes living in a eutrophic region. Crabtree concluded that the trends in water content were the result of reduced food availability but that declines in energy were better explained by the visual-interactions hypothesis. In Drazen's study (2007), lipid concentration and caloric content increased with depth, driven primarily by the abyssal macrourid scavenger *C. armatus*. It was suggested that individual ecologies may play a larger role than food supply or depth in determining energy storage in a species. Clearly, the trends in benthic fish composition are not as straightforward as for pelagic species and probably reflect the release from morphological constraints imposed by locomotion and buoyancy in pelagic species.

Methods for directly measuring locomotory capacity in deep-sea fishes continue to develop (Priede and Bagley 2000). Slow routine swimming speeds in deep-living macrourid fishes are well documented (Priede et al. 1991; Priede and Bagley 2000) in accordance with low metabolic rates. In contrast to these data, routine and burst locomotory capacities for the morid *Antimora rostrata* and the eel *S. kaupii* are very similar to shallow-living species at similar temperatures (Bailey et al. 2003, 2005). However, routine swimming speeds, especially those measured remotely following attraction to bait, may be poor indicators of capacity. While *A. rostrata* and *S. kaupii* are clearly capable of greater swimming performance than rattails, we suspect the reported swimming performances of these species are elevated in response to the bait. Comparisons of the swimming performance of a scavenging morid fish inhabiting the continental slope (~2,500 m) and the deeper-living *C. armatus* (but with overlapping depth distribution) have shown that the morid's routine swimming rates were approximately two times higher (Collins et al. 1999). It was concluded that the differences between the species were due to adaptation to the food availability of the main part of their respective habitats. Priede et al. (2003) similarly invoked food availability to explain the fact that *Coryphaenoides* spp. living at abyssal depths under eutrophic regions of the north Pacific have higher swimming rates than individuals in oligotrophic regions. Metabolism and locomotion represent energetic expenses to the animal, and thus an elevation in these rates implies a requirement for elevated activity rather than a simple response to food availability. A possible alternative hypothesis is that faster swimming speeds are found in eutrophic environments where larger numbers of fishes increase competition for food falls (Collins et al. 1999). Locomotory studies continue to develop, and additional data on a greater diversity of species will provide a powerful tool for testing hypotheses about the capacities of deep-sea animals.

In conclusion, temperature and body mass, while extremely important determinants of organismal metabolism, do not fully explain the variability evident in benthic and benthopelagic fish metabolism. Significant depth-related trends are evident and generally support the visual-interactions hypothesis. Exceptions to its predictions were found, but these more subtle interspecific differences

cannot be readily predicted from any environmental data. Clearly, individual species ecologies affect their metabolisms and result in the variability observed. For instance, there are large differences in body form between cottids and flatfishes, both benthic groups, and their body forms and locomotory adaptations may lead to inherent differences in metabolism (Webb 1990). This analysis shows most prominently that there is much to be done, and a comprehensive study of these animals could be very fruitful because their range of habitats and locomotory styles may aid in delineating the factors that regulate metabolic rates. Describing the nature of these roles and determining depth-related influences on metabolism will greatly aid our understanding of the bioenergetics of slope-dwelling benthic and benthopelagic fishes, which are being exploited at an ever-increasing rate (Koslow et al. 2000; Haedrich et al. 2001; Roberts 2002). In order to construct energetic, productivity, and food-web models of these animals, we must generate a predictive capacity for their rate processes.

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