Are there physiological and biochemical adaptations of metabolism in deep-sea animals?

James J. Childress

The deep ocean is unlike terrestrial and shallow environments in many ways, but two of the most important are its vast scale as a habitat and the pervasiveness of conditions throughout it. For example, about 62% of the surface of the earth and 79% of the volume occupied by life on earth lie at depths greater than 1 km (Ref. 1) below sea level. Because of the properties of water, conditions throughout this region exhibit great temporal stability and considerable horizontal spatial homogeneity, lacking the tremendous microhabitat, seasonal and latitudinal variability found elsewhere. Major environmental parameters include hydrostatic pressures of 101.3 kPa for each 10 m of depth, very low ambient light, temperatures below 10°C, increasing distance from phytoplankton production, and decreasing biomass with increasing depth (Fig. 1). Two factors which do show considerable spatial variation within the deep sea are (1) biomass of organisms, which apparently reflects surface productivity, and (2) dissolved O₂, which can be less than 5% of air saturation over large areas at depths between 100 and 1200 m (Fig. 1). The physical and chemical conditions are believed to have been temporally stable for extended periods in the past. For example, it has been estimated that the deep sea has been cold for at least 50 million years andoxic for at least 90 million years (Ref. 1). However, in contrast, the recently discovered hydrothermal vents and related ecosystems differ in being very small, temporally unstable habitats with high primary productivity and often elevated temperatures, as well as possessing other unique characteristics (Ref. 1).

Comparative approaches to the adaptations of oceanic animals

Early studies of physiological and biochemical properties of deep-sea animals, limited to small groups of species within particular regions, revealed obvious depth-correlated changes in a variety of properties. Their adaptive significance could not be evaluated because of the confounding of changes in major environmental variables with depth within a region (Fig. 1). Biological changes were attributed variously to adaptation to elevated pressure, decreased light, decreased food or low environmental O₂ at greater depths. However, sufficient data are now available from different regions, deep-sea habitats and phyla, to enable the separation of depth-related environmental variables. I will consider first the patterns and adaptive basis of the metabolic rates of deeper living oceanic species and then the adaptations of such species to the oceanic O₂ minimum layer.

Harvey and Pagel (Ref. 2) emphasized that individual species often cannot be considered as independent data points, because phylogeny may have played a significant role in the evolution of their properties. In the studies described here, species are generally treated as independent. Since in many of these studies, most of the abundant species of a major taxon (e.g. fish, crustaceans or chaetognaths) in a particular region have been measured, this approach gives a valid description of the variation as a function of depth. The observed trends in properties with depth are probably not due to phylogeny for two reasons. First, single genera or families often occupy the entire depth range studied and the substantial variation within such a taxon, in characteristics such as proximate composition or metabolic rate, approaches the entire variation for such a parameter in a data set (Ref. 1). That is, there appears to be divergence of closely related species as a function of their habitat depths. Second, at any given depth, members of different families or even higher taxa have comparable properties. Thus, there is strong evidence of convergence of properties between genera, families and even phyla, whose origins lie outside the deep-sea and thus can hardly produce a phylogenetic bias.

It is possible to test the hypotheses put forward to explain variation with depth in biological properties by testing for correlation of a given biological property with the putative causal factor using data from different oceanic regions and habitats. This will be done with proposed causal factors for changes in metabolic rate with depth. In the oceanic realm, with respect to the pervasive physical, chemical and biological variables, it is also possible to compare evolved responses of different phyla to the same conditions to gain insight into the adaptive values of properties. In this case, environmental challenges are the same, but evolutionary starting points are quite different so convergence or its absence can provide robust evidence of the adaptive nature of particular properties. This
organisms at a given depth and location are exposed to the same environmental conditions. These two patterns.

Do metabolic rates decline with increasing depth of occurrence of species?

There is a common belief that biological processes proceed at slower rates in the deep-sea, and, in particular, that metabolic rates of deeper-living species are much lower than those of shallower-living relatives. That is, metabolic rates of deep-sea animals are thought to decline with increasing depth to a greater extent than expected from the decline in temperature (greater than a typical Q10 of about 2.5). Earlier studies of metabolic rates of deeper-living pelagic fishes and crustaceans showed such a large decline and suggested it might be an adaptation to lower food availability at greater depths12,13 (Table 1; Fig. 2). Others have suggested that it may be because of (1) enzymatic adaptations to elevated pressures at greater depths14 (2) adaptation to the O₂ minimum layer off California where the first studies were done18; or (3) to diminished light at greater depths relaxing selection for higher levels of locomotory muscle power17. In addition to metabolic rate measurements, the activities of key enzymes of intermediary metabolism have been used to estimate the metabolic potential of deeper-living and more-fragile species (Table 1; Fig. 2). Since these enzyme activity measurements have correlated well with metabolic rates, they can be compared as indicators of metabolic rates, serving as controls on the stress of capture and pressure effects, as well as allowing investigation of species that cannot be recovered alive.

The finding of a rapid decline in metabolic rates of pelagic fishes and crustaceans with increasing depth has been supported by many studies from different regions as reviewed by Childress19, and appears to hold true for pelagic cephalopods as well20 (B. Selbel, University of California, Santa Barbara, USA, unpublished) (Table 1). There is a difference of a factor of 15 in metabolic rates between species living at the surface and those which come no shallower than 800 m, with little or no decline below about 800 m. However, recent studies have clearly shown that such declines are not universal in mid-water animals, since pelagic chaetognaths, cnidarians, worms and pteropods do not show such declines with depth19–21 (Fig. 2; Table 1).

Thus, we have a pattern which is held in common by members of two phyla and not by three other phyla in the same habitat with the molluscs being split between these two patterns.

Among benthic crustaceans, burrowing and less active species show no significant decline in metabolic rate with depth beyond the effects of temperature, while those species which frequently swim off the bottom show a significant decline that is less than that of the pelagic species16 (Table 1). In addition, deep-sea ophiuroids, holothuroids and meiobenthic organisms do not show differences in metabolic rates between the surface and depths greater than 1000 m (Refs 22,23). The hydrothermal vent crab and other inhabitants of the deep-sea vent environments have metabolic rates comparable to similarly active shallow-living and deep-sea animals, after accounting for temperature, that is, they show no effect of depth on metabolic rates18,24,25.

The pattern can be summarized by saying that some groups, such as pelagic fishes, crustaceans and cephalopods, show large declines (beyond those resulting from decreasing temperature) in metabolic rates with increasing depth, benthic groups show lesser or no declines, and gelatinous pelagic groups appear to show no declines. This indicates that a lower metabolic rate is not in itself a necessary or even a usual characteristic or adaptation of deep-sea animals. This leaves unexplained the basis for the decline in fishes, crustaceans and cephalopods, and the data described above provide a rich source for examining this question.

Is there an adaptive basis for the declines in metabolic rates of fishes and crustaceans?

The basis of the declines in some groups can be examined by determining whether the various environmental parameters that covary with depth are correlated with metabolic rates when separated from depth. The failure to find a correlation allows the rejection of a particular variable as being involved in the causality of the observed declines. The first variable to consider is temperature. While
there is continuing controversy about the existence of temperature compensation in the metabolic rates of species living at cold temperatures, it now appears that in most cases comparable species living at lower temperatures have lower metabolic rates (Q10 of about 2.5) (Ref. 26) and this lower metabolic rates (Table 1). Another possibly important variable is hydrostatic pressure. It might be that pressure in some way acts to limit metabolic rates, perhaps by reducing the efficiency of enzymes as part of temperature compensation in the metabolic rates of species groups is a possible hypothesis. This notion can be readily tested because even in nearly isothermal Antarctic waters, deeper-living pelagic crustaceans and fishes have lower metabolic rates (Table 1). Another possibly important variable is hydrostatic pressure. It might be that pressure in some way acts to limit metabolic rates, perhaps by reducing the efficiency of enzymes as part of

Table 1. Relationships between minimum depth of occurrence and measures of metabolic power for a variety of oceanic marine groups from regions which differ in hydrography

<table>
<thead>
<tr>
<th>Group</th>
<th>Region/Organism</th>
<th>Habitat</th>
<th>Minimum depth</th>
<th>Parameter</th>
<th>n</th>
<th><em>C</em></th>
<th>±95% CI</th>
<th>P</th>
<th>Weight</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustaceans</td>
<td>California pelagic</td>
<td>0-1200</td>
<td>M12</td>
<td>27</td>
<td>depth</td>
<td>-0.57 ± 0.20</td>
<td>&lt;0.0001</td>
<td>29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>California benthiic</td>
<td>0-1500</td>
<td>M12</td>
<td>17</td>
<td>(10)</td>
<td>-0.33 ± 0.18</td>
<td>0.001</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>California benthopelagic</td>
<td>0-1250</td>
<td>M12</td>
<td>11</td>
<td>(10)</td>
<td>-0.23 ± 0.10</td>
<td>0.0006</td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hawaii shrimp pelagic</td>
<td>30-1000</td>
<td>M12</td>
<td>16</td>
<td>6</td>
<td>0.88 ± 0.30</td>
<td>0.0001</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gulf of Mexico shrimp pelagic</td>
<td>135-400</td>
<td>M12</td>
<td>10</td>
<td>14</td>
<td>&gt;0.05</td>
<td>&gt;0.05</td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fishes</td>
<td>California pelagic</td>
<td>0-1000</td>
<td>M12</td>
<td>12</td>
<td>0.2</td>
<td>-</td>
<td>&gt;0.05</td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Antarctic pelagic</td>
<td>0-1000</td>
<td>M12</td>
<td>16</td>
<td>0.5</td>
<td>-0.113</td>
<td>&lt;0.05</td>
<td>1</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>

*The habitat indicated is that occupied by adults of the species. Benthopelagic includes species that spend much time on the bottom but also swim off the bottom. Where two or more entries occur, the group of species is being considered again, either analysing data differently for the same parameter or presenting data on different parameters.

*Minimum depth of occurrence is the depth below which 90% of the population of a species is estimated to be found. Where two or more entries occur, the group of species is being considered again, either analysing data differently for the same parameter or presenting data on different parameters.

*The measured parameters can be used to estimate metabolic power. M12 is the wet weight specific O2 consumption rate. CS indicates citrate synthase, an indicator of aerobic power. LDH indicates lactate dehydrogenase, an indicator of anaerobic power. PK indicates pyruvate kinase, an indicator of glycolytic flux. N&K+ ATPase is involved in transp of ions. Enzymes were assayed in the white epaxial muscles of fishes except for the indicated analyses in brain tissues and Na+-K+ ATPase in the gills. In gelatinous animals, enzymes were analysed in whole body homogenates.

*Data points for these analyses are individual species; n represents the number of data points. Only data sets with substantial numbers of species are shown although the literature contains many studies of individual deep-living species that support the trends shown.

*Depth indicates that the metabolic rates at appropriate temperatures for each species were used: in the other studies, measurements were either all made at an intermediate temperature as indicated, measured at different temperatures and corrected to a common temperature indicated by parenthesis, or measured at different temperatures and their effect removed via inclusion as one variable in a multiple linear regression analysis using transformed data indicated by the absence of an entry.

*0.51 is the exponent in an equation of the form: In parameter = In a + Mn minimum depth. A minus sign by itself indicates that the comparison was not a regression but this typical effect of temperature on metabolism (Table 1), an exceptionally large response to temperature in some groups is a possible hypothesis. This notion can be readily rejected because even in nearly isothermal Antarctic waters, deeper-living pelagic crustaceans and fishes have lower metabolic rates (Table 1). Another possibly important variable is hydrostatic pressure. It might be that pressure in some way acts to limit metabolic rates, perhaps by reducing the efficiency of enzymes as part of
biological adaptation to elevated pressure. This suggestion can be rejected as well since gelatinous phyla do not show a metabolic decline with depth (Table 1; Fig. 2) and the benthic species, including hydrothermal vent species, of crustaceans or fishes, show no or lesser declines. A third variable possibly responsible for the decline is the decreased O₂ at intermediate depths. All else being equal, a given organism in an open system can regulate its O₂ uptake to lower O₂ partial pressures, and thus survive aerobically at lower O₂ partial pressures, if it has a lower metabolic rate. Thus, the lower metabolic rates of pelagic fishes and crustaceans found at depth off California are possibly adaptations to the very low O₂ in the mid-depth O₂ minimum layer. This possibility was contradicted by the comparison of the metabolic rates of species living in the minimum layer with those living below, which revealed that the latter have lower metabolic rates and less tolerance of low O₂ than do species living in the minimum layer. Another test was to measure the metabolic rates of mid-depth species from regions with less well-developed minima. In regions with more O₂, the mid-depth species, sometimes the same species as in lower O₂ regions, are less able to survive at low O₂ levels, but their metabolic rates are not significantly higher (Fig. 3). Thus, the lower metabolic rates of deeper-living pelagic fishes and crustaceans are adaptive for survival in the O₂ minimum layer, but not specific adaptations to it.

Yet another, and perhaps the most intuitively attractive, variable that is potentially responsible for the lower metabolic rates is lower availability of food at depth. This could act either through nutritional deprivation of individuals (i.e. starvation) or selection for lower metabolic rates in deep-sea species. It is clear for both pelagic and benthic deep-sea animals that biomasses tend to reflect the surface productivity suggesting food-limitation at the population level. Surface zooplankton biomass varies by more than an order of magnitude among oceanic regions due to variations in surface productivity. The biomass declines about an order of magnitude for each 1000 m of depth (Ref. 2) so that the biomass at 1000 m in a rich region can exceed that at the surface in a poor region (Fig. 1).

If low food availability itself is the primary variable responsible for the lower metabolic rates then one should find that the metabolic rates of deeper-living species vary from region to region correlated with surface primary production. Comparisons between tropical and temperate regions of different productivity have shown that among pelagic crustaceans living continuously below 400 m, there is no significant variation in metabolic rate once temperature differences are accounted for. In addition, the metabolic rates of the shallower-living species were higher in the lower productivity tropical region even after temperature was taken into account. Further, although deep-living fishes from more-productive regions do have significantly higher lipid contents suggesting access to more food, their protein contents are not significantly different, suggesting that food availability is not affecting locomotory abilities and metabolic rates in these species. Therefore, there appears to be no correlation of metabolic rate with surface productivity suggesting a lack of a correlation with food availability.

Fig. 2. Examples of typical metabolic rates and enzyme activities of pelagic animals plotted as functions of minimum depths of occurrence. Enzyme activities serve as a check that the metabolic rate patterns observed do not result from differential capture trauma or pressure effects on deeper-living species and also allow investigation of different kinds of metabolism, metabolic potentials of different tissues, and estimation of metabolic power for species that cannot be recovered in satisfactory condition. Both chaetognaths (crosses) and fish (filled circles) O₂ consumption data are measured at 5°C (Refs. 19, 46) on animals collected off the California coast. The fish enzyme data are for white muscle and were measured at 10°C (Ref. 40). The chaetognath enzyme data are for whole animals and were measured at 20°C (Ref. 19). Citrate synthase is a Krebs cycle enzyme that generally correlates well with aerobic metabolic rate. Pyruvate kinase is a glycolytic enzyme that reflects glycolytic flux for anaerobic metabolism as well as for supplying the Krebs cycle.

Fig. 3. The relationship between critical O₂ partial pressure and regulated O₂ consumption rates for individuals of the ichthyogastropod, Gnatolabrus ingens, from off California (filled circles) (minimum pO₂, about 6 torr) and from off the Hawaiian islands (crosses) (minimum pO₂, about 20 torr; Refs. 10, 44). This species is found at the lowest pO₂ values in the water column as it lives between 400 and 800 m for most of its life. The regression lines are not significantly different in slopes, but they are highly different in position (ANOVA; P < 0.000 5; Ref. 10). The metabolic rates of the two groups are not significantly different at pO₂ values above the pC's.
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This variable was also tested by comparing energy budgets of shallow- and deeper-living midwater fishes enabling metabolic rate to be examined relative to total energy usage. This showed that although deeper-living species had lower weight-specific metabolic rates, their total rates of energy usage per individual and total life-history energy usage were higher than for shallow-living midwater species because the deeper ones were larger. Thus, within midwater fishes, the decline in metabolic rates with depth contributes only to relative, not absolute energy conservation, and therefore can hardly be the result of reduced food supply at greater depths.

Another test of the importance of food availability for metabolic rates of deep-sea animals comes from the hydrothermal vent animals. These species, which live at much higher biomass concentrations than other deep-sea animals, do not have significantly elevated metabolic rates. Similarly, the metabolic rates of deep-sea benthopelagic shrimp, 2000 m depth, are not elevated above those of bathypelagic species although the benthopelagic live at higher concentrations of zooplankton biomass. Another compelling indicator that lower ambient food supply is not directly responsible for selecting lower rates in pelagic fishes and crustaceans is the finding that metabolic rates of pelagic gelatinous animals do not decline with increasing depth; although they live in the same environment as the fishes and crustaceans. These different lines of evidence all indicate that the metabolic rates of deep-sea animals are not correlated with ambient food levels or source productivity in comparisons that are free of the confounding of biomass and depth. These data show that, while lower metabolic rates may be adaptive for deep-sea animals, where found they are not adaptations to lower availability of food and apparently reflect some other factor(s) related to depth.

A fifth possible variable is the ambient light level. The exponential decline in metabolic rates of pelagic fishes and crustaceans initially follows the decline in downwelling light with depth. Although downwelling light continues to decline below the depth of about 800 m where metabolism ceases to decline, this depth approximately coincides with the limits for vision of these groups in the clearest oceanic waters. The mechanism by which light could affect metabolic rates is more obscure than in the other cases, because light itself has no direct effect on energy metabolism. Yet, there is abundant evidence that light influences the behavior of midwater animals, particularly as regards vertical migrations. This raises the notion that light could be involved in the evolution of differing locomotory and predatory capacities at different depths.

Several lines of research indicate that the metabolic decline is related to a reduction in locomotory abilities with increasing depth. The proximate compositions of midwater fishes and crustaceans show a decline in protein content with increasing depth which would be expected to limit locomotory capacities of these organisms. A bathypelagic mysid has reduced swimming capacity compared to shallow-living species. Enzyme activity measurements in fishes indicated that the metabolic decline is related to locomotory power because the activities of glycolytic and Krebs cycle enzymes declined in parallel with overall metabolic rate in the epaxial muscles (Fig. 2), but not in cardiac muscle or brain. Thus, the decline in metabolic rate with depth in pelagic fishes and crustaceans appears to be the result of a decline in locomotory capacity that is established in the muscle tissues.

One can imagine such a decline being the result either of selection against high activity levels or the relaxation of selection for high activity with the resulting reduction being the result of selection for conservation or other uses of food energy. The first case might result from increased exposure to predation of active animals at depth due to the bioluminescent "burglar alarm effect" in the darkness. Such a mechanism would be expected to involve the vision of the animals only insofar as the most active shallow-living species are visual predators with image-forming eyes. It would be predicted to produce reductions in activity and metabolism in sighted as well as unsighted groups - a hypothesis that is not consistent with the data. The second case might result from the reduction in reactive distances of predator-prey interactions because of the reduction in ambient light with depth. In this case, since selection is mediated directly by the vision of the organisms involved, only sighted predators or prey would be affected. A visual basis for the decline with depth of the metabolic rates of sighted groups (pelagic fishes, crustaceans and cephalopods, and, to some extent, benthic crustaceans and fishes) is further supported by the observations cited above that four major gelatinous groups that lack image-forming eyes fail to show a decline in metabolic rate with depth. Higher metabolic rates found for shallow-living tropical pelagic shrimps living in clearer waters with higher ambient light levels as compared with more-temperate species may also support such a visual basis.

Thus, this situation may resolve to the hypothesis that the higher metabolic rates at shallower depths in groups with image-forming eyes are the result of selection acting to favor the use of information on predators or prey at substantial distances from an organism when ambient light is sufficient for vision at a distance. This view holds that the lower metabolic rates found at depth in some deeper-living taxa result from the relaxation of this selection at greater depths and are not specific adaptations to the deep-sea, although they are adaptive there in the functional rather than the evolutionary sense.

Adaptations to the midwater $O_2$ minimum layer

The midwater $O_2$ minimum layers occupy vast regions at depths between 200 and 1000 m in the oceans (Fig. 1). They are best developed in the eastern tropical Pacific Ocean, the northern Arabian Sea, and the eastern tropical Atlantic Ocean with $O_2$ contents often less than 5% of air saturation and sometimes less than 2%. Although these $O_2$ contents are so low as to preclude the aerobic survival of most shallow-living marine species, there are abundant populations of zooplankton and micronekton throughout most of these regions. Except for the layers with the lowest $O_2$ concentrations, where abundance is restricted, midwater fishes and crustaceans appear to rely upon aerobic metabolism using highly developed mechanisms to remove $O_2$ from water. These abilities can be expressed as the $O_2$ partial pressure at the lower limit to which an organism can regulate its $O_2$ consumption rate, the critical $O_2$ partial pressure or PC. The PC, value of a given individual is dependent not only upon its inherent physiological and biochemical properties but also upon its activity level, since at lower activity (and therefore metabolic rates) the animal can regulate to a lower PC than at higher $O_2$ consumption rates. The existence of such a relationship has led to the suggestion that the lower metabolic rates of deeper-living species might be an adaptation to the $O_2$ minimum layer. However, although such lower rates are clearly adaptive, the data indicate that this is not a specific adaptation to the minimum layer since the same or similar species living at comparable depths and higher $O_2$ contents...
elsewhere have comparable metabolic rates, as was discussed earlier (Fig. 5). For pelagic crustaceans off California, the pC values at routine metabolic rates are comparable to the lowest O₂ concentrations to which the shrimp are exposed, that is about 5 torr (Ref. 29) (Fig. 4). Where O₂ at intermediate concentrations to which the shrimp are exposed, that is discussed earlier (Fig. 3).

Figure 4. The mean critical O₂ partial pressures of a wide variety of pelagic crustaceans (copepods, mysids, decapods, euphausiids, amphipods and ostracods) from different oceanic habitats (off California, off the Hawaiian Islands, the Antarctic and the Gulf of Mexico) plotted as a function of the lowest pO₂ to which they are normally exposed. The critical pO₂ is the partial pressure at which an individual fails to regulate its O₂ consumption rate and is taken here as an approximate indicator of the lowest pO₂ values, which fully support aerobic metabolism for a species. Since the lowest pO₂ in a region is the same for all species which pass through the O₂ minimum, there is a great deal of overlap of data points so that while 43 points are apparent, 62 are actually plotted.

Figure 5. Oxygen equilibrium curves for hemocyanins of midwater crustaceans from off California and Hawaii. (Curves from left to right: Gnathophausia ingens 5°C, G. ingens 15°C, Acanthephyra smithi 5°C, A. smithi 15°C, A. acutifrons 5°C.) The California Gnathophausia ingens have a hemocyanin with a very high affinity for O₂ (pO₂ = 1.34 torr at 5°C) which enables it to take up O₂ from the very low pO₂ in its environment. Like hemocyanins of other deep-living, non-migratory crustaceans, the hemocyanin O₂ affinity of G. ingens is only slightly reduced by higher temperatures. The Hawaiian oplophorid decapod crustacean Acanthephyra acutifrons, like G. ingens, lives continuously at greater depths. However, living at higher environmental pO₂ in its environment, it and other similar Hawaiian crustaceans have hemocyanins with lower affinities for O₂ (pO₂ = 1.34 torr at 5°C) which enable it to take up O₂ from the very low pO₂ in its environment. The critical pO₂ is the partial pressure at which an individual fails to regulate its O₂ consumption rate and is taken here as an approximate indicator of the lowest pO₂ values, which fully support aerobic metabolism for a species. Since the lowest pO₂ in a region is the same for all species which pass through the O₂ minimum, there is a great deal of overlap of data points so that while 43 points are apparent, 62 are actually plotted.

Similar adaptations have been found in a benthic fish, Sebastolobus alascanus, living off California. This species has the ability to regulate its O₂ consumption to very low pO₂ and has a high affinity hemoglobin. Elevated concentrations of glycolytic enzymes in heart muscle but not other muscle (indicating possible involvement of anaerobic metabolism in heart tissue) are also found in this species. Most striking of such adaptations is the finding that the cardiac lactate dehydrogenase of this species is of the anaerobically poised type, not the aerobically poised form, which is inhibited by high concentrations of pyruvate and is typical of cardiac muscle in other fishes. It is probable that even for O₂-minimum animals with highly developed aerobic adaptations, anaerobic metabolism may be necessary to support increases in activity above routine levels.

Thus, although there are clearly many physiological and biochemical adaptations of deep-sea animals to their habitats, their metabolic rates apparently have not evolved in response to biomass of possible food items, but rather reflect other overriding factors. The finding that the lower metabolic rates of deeper-living fishes, crustaceans and cephalopods are functionally adaptive for life in the deepsea and the O₂ minimum layer, and are not specifically evolved adaptations to the low food availability or low O₂ in these habitats is far from what one would intuitively.
expect. This result emphasizes the importance of vision as a factor that strongly affects the evolution of the metabolic rates of organisms.

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References

Phylogeny and stratigraphy
Empirical approaches examining patterns in the fossil record are necessary for evaluating temporal processes. In his recent TREE article1, Benton concluded that the palaeontological record is an adequate, and improving, data source for taxonomic groups (especially vertebrates) have been examined, and the correlation between stratigraphic ages and the fossil record is generally high. Subsequently, this relationship was purported to be ‘less convincing’. This disparity is the result of a misguided modification of Norell and Novacek’s method. My criticism focuses on the treatment of cladograms with secondary structure - so-called nonpectinate trees that do not conform to a strict cladogram, the first recognizes group A-E as a single taxon with a clade rank of 1 (Fig. 1d). Redundant correlation problems necessitate reduction of nonpectinate components by sequential passes through the cladogram; the first recognizes group A-E as a single taxon with a clade rank of 1. Our approach requires two passes through the cladogram; the first recognizes group A-E as a single taxon with a clade rank of 1. The second recognizes group F-I as a single element (Fig. 1c). Spearman rank coefficients (S) are 0.182 (Fig. 1b) and 0.939 for pass 1 (Fig. 1a) and 0.973 for pass 2 (Fig. 1c). Why the discrepancy? The result emphasizes the importance of vision as a factor that strongly affects the evolution of the metabolic rates of organisms.