# Biochemical ecology of deep-sea animals

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*Abstract.* Deep-sea ecosystems contain unique endemic species whose distributions show strong vertical patterning in the case of pelagic animals and sharp horizontal patterning in the case of benthic animals living in or near the deep-sea hydothermal vents. This review discusses the biochemical adaptations that enable deep-sea animals to exploit diverse deep-sea habitats and that help establish biogeographic patterning in the deep-sea. The abilities of deep-sea animals to tolerate the pressure and temperature conditions of deep-sea habitats are due to pervasive adaptations at the biochemical level: enzymes exhibit reduced perturbation of function by pressure, membranes have fluidities adapted to deep-sea pressures and temperatures, and proteins show enhanced structural stability relative to homologous proteins from cold-adapted shallow-living species. Animals from the warmest habitable regions of hydrothermal vent ecosystems have enzymes and mitochondria adapted to high pressure and relatively high temperatures. The low metabolic rates of bathypelagic fishes correlate with greatly reduced capacities for ATP turnover in locomotory muscle. Reduced light and food availability in bathypelagic regions select for low rates of energy expenditure in locomotory activity. Deep-sea animals thus reflect the importance of biochemical adaptations in establishing species distribution patterns and appropriate rates of metabolic turnover in different ecosystems.
*Key words.* Adaptation; deep sea; hydrostatic pressure; hydrothermal vents.

## *Introduction*

The physical and biological characteristics of deep-sea ecosystems confront animals with several major challenges that would seem to dictate pervasive adaptation at the biochemical level[34–37]. Hydrostatic pressure is perhaps the most familiar of these challenges. Pressure increases by approximately one atmosphere (1 atm = 0.101 megapascals (MPa) with each 10-m increase in depth. Abyssal pressures thus may reach approximately 1100 atm, and the average pressure in the marine realm is near 380 atm. Approximately 79% of the volume of the marine realm lies below 1000 m. Therefore, most of the biosphere, when viewed in terms of volume, is a high-pressure environment. Because most biochemical processes involve changes in system volume[28,35], the equilibrium positions and rates of biochemical reactions are generally perturbed by alterations in pressure[35,46]. Temperature and light, two other critical physical features of the deep-sea, likewise present challenges to biochemical systems. Deep-sea temperatures typically are low, in the range of 2–4 °C, and it is expected that deep-sea animals would possess cold-adapted, as well as pressure-adapted, biochemical systems. However, at deep-sea hydrothermal vents water temperatures near 400 °C have been recorded at 'black smoker' chimneys[42]. Even though it appears unlikely that life occurs in these hottest deep-sea waters[45], abundant life is found on and within the walls of smoker chimneys[16,17], i.e. within centimeters of the 400 °C waters. The change in species composition along thermal gradients in the vent ecosystems suggests that adaptation to different temperatures might play an important role in the biochemiccal ecology of vent animals[17,24].

The lack of sunlight in the deep sea also has an important selective influence on the biochemical characteristics of the resident fauna. Lack of sunlight precludes photosynthetic production below ~100 m; only at the hydrothermal vents and certain low-temperature sites, where reduced compounds can fuel chemoautotrophy, is primary production possible in the deep-sea[38]. The food supply of most deep-sea animals is dependent on parcels of nutrients that settle from the euphotic zone into deep water. The distributions of these food parcels in time and space and the difficulties in locating them in a dark environment may lead to selection for radically different metabolic capacities from those characteristic of shallow-living animals.

This brief overview of deep-sea ecosystems reveals that deep-living animals are likely to exhibit two general categories of biochemical adaptations for a deep-sea existence. First, modifications in many biochemical systems, notably protein and lipid-based systems, are likely to be necessary to permit life under conditions of high pressure and, in most deep-sea habitats, very low temperatures. At deep-sea hydrothermal vents adaptations to elevated temperatures also may be necessary to allow exploitation of some of the most food-rich habitats in the deep-sea. Adaptations that allow animals to tolerate the pressures and temperatures of the deep sea are termed *resistance adaptations*. Second, in view of the trophic ecology of the deep-sea, there is likely to be selection for biochemical adaptations that establish the appropriate rates of metabolic activity, *capacity adaptations*. This class of biochemical adjustment for life at depth may be especially important in the bathypelagic realm where darkness and stochastic food availability militate against the active lifestyles characteristic of most epipelagic animals.

*Resistance adaptations*

*Adaptations in membrane-based systems*

Membrane-based systems are a crucial site of perturbation by high pressure[10,26,27]. The packing of acyl chains in the lipid bilayer is strongly influenced by pressure[26]. Increases in pressure favor tighter packing of acyl chains, and this alteration in bilayer organization may affect membrane fluidity and, perhaps as a direct consequence, the activities of membrane-localized enzymes[18,19] and signal transduction systems[32,33]. Deep-sea animals living in typical cold deep-sea waters encounter a twofold challenge in maintaining membrane fluidity consistent with adequate function of membrane-localized processes. Low temperatures and high pressures act synergistically on membrane systems to reduce fluidity. An increase in pressure of 1000 atm is equivalent to a decrease in membrane temperature of approximately 13–21 °C[26]. For an organism inhabiting the Marianas Trough (depth 11 000 m; temperature 2 °C), the effective temperature of a membrane would be between −11 and −19 °C. It thus appears highly likely that adaptations that maintain appropriate membrane fluidity, homeoviscous adaptations, play a major role in adaptation to depth.

Cossins and Macdonald[8–10,27] have examined homeoviscous adaptation in marine fishes collected over a wide range of depths, but at approximately the same low temperatures. One of the major homeoviscous adaptations of membranes seen in studies of temperature adaptation is a shift in acyl chain saturation, such that membranes of low-body-temperature organisms contain a higher weight percentage of unsaturated fatty acids than the equivalent membranes of more warm-adapted species[6,7]. For marine fishes, the same type of shift was noted as a function of depth of capture[9]. For example, the saturation ratio for ethanolamine phosphoglycerides of a mitochondrial-rich fraction decreased approximately fourfold over a depth of capture range of 4000 m (fig. 1). These data, and similar results reported by other workers studying marine bacteria[14,15,47], support the hypothesis that adaptation to pressure includes biochemical adaptations that maintain the correct physical state of the bilayer. It also has been shown that acclimation to different pressures can elicit homeoviscous adaptation in marine bacteria[14]. It remains to be determined whether deep-sea animals are able to restructure their lipid bilayers during vertical movements, e.g. during ontogenetic migrations, through the water column.

The functional importance of biochemical adaptations in membrane systems for establishing resistance to high pressure is shown by studies of the $Na^+$-$K^+$-adenosine triphosphatase (Na-K-ATPase) of teleost gills (fig. 2-A)[18]. Na-K-ATPases isolated from fishes collected at different depths and temperatures displayed large differences in sensitivity to increased pressure. The Na-K-ATPases from fishes collected at depths greater than 2000 m were least inhibited by pressure; enzymes of shallow-living tropical fishes were most pressure-sensitive. The possibility that the differential responses of the

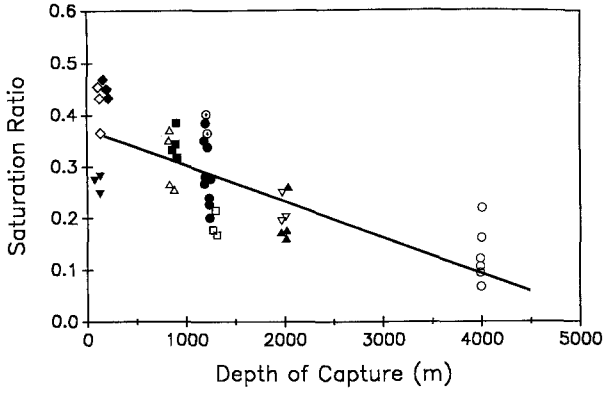


Figure 1. The change in saturation ratio (ratio of the weight percent of saturated fatty acids to unsaturated fatty acids) for the ethanolamine phosphoglyceride component of mitochondrial-enriched membrane fractions from fish captured at different depths. Each symbol represents a different species. (Figure modified after Cossins and Macdonald[9]).

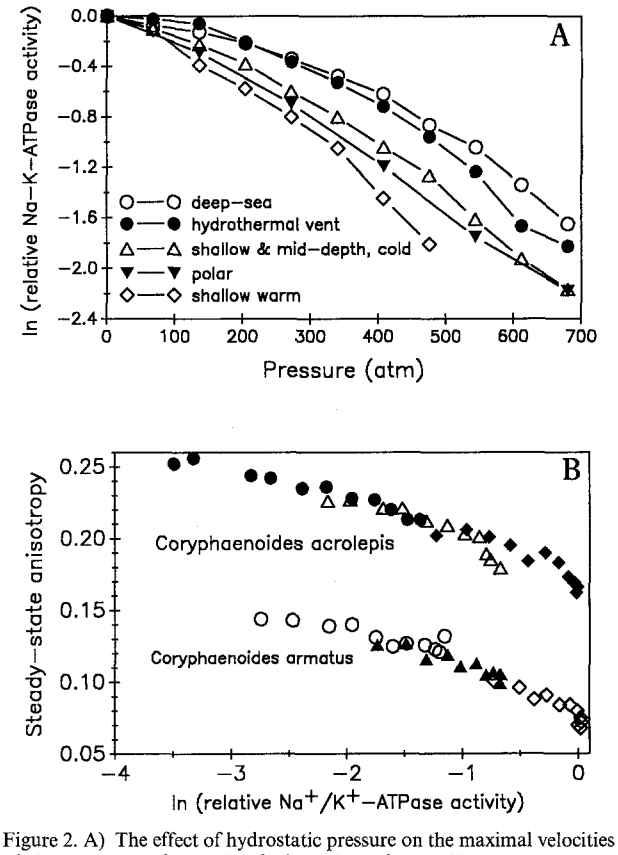


Figure 2. A) The effect of hydrostatic pressure on the maximal velocities of Na-K-ATPases from gills of teleost fishes from different marine environments. Rates, measured at 10 °C, are expressed relative to the rate determined at 1 atm. (Figure modified after Gibbs and Somero[18]). B) The relationship between steady-state fluorescence anisotropy of gill lipid preparations, measured using the fluorescent probe 1,6-diphenyl-1,3,5-hexatriene (DPH), and Na-K-ATPase activity from gills of *Coryphaenoides armatus* and *Coryphaenoides acrolepis*. Rates were determined at a series of pressures and at different temperatures. Symbols refer to different temperatures of measurement: diamonds = 25 °C; triangles = 17.5 °C, and circles = 10 °C. (Figure modified after Gibbs and Somero[19]).

Na-K-ATPases to pressure were due at least in part to interspecific differences in bilayer fluidity is suggested by the discovery that the activity of Na-K-ATPase was proportional to bilayer fluidity, as indexed by the steady-state fluorescence anisotropy of the probe 1,6-diphenyl-1,3,5-hexatriene (DPH)[5,19]. Figure 2-B shows the correlation between fluidity (inversely related to steady-state anisotropy) and Na-K-ATPase activity at different temperatures and pressures for the enzymes of two species of rattail fish, *Coryphaenoides acrolepis* (depth of occurrence: 700–1820 m) and *Coryphaenoides armatus* (depth of occurrence: 1885–4815 m). Each symbol represents a different temperature of measurement (see legend). The fluidity of the membrane lipids of the deeper-occurring species, *C. armatus*, is higher at all measurement temperatures. The regular variation in fluidity with temperature for each species is marked by a concomitant change in Na-K-ATPase activity.

The influence of bilayer fluidity on the activity of gill Na-K-ATPase was substantiated further by lipid replacement experiments[19]. When lipids extracted from *C. armatus* were added to delipidated Na-K-ATPase protein from a shallow species, the pressure sensitivity of the enzyme was reduced. However, lipid substitutions of this sort were not able to interconvert fully a pressure-sensitive Na-K-ATPase to a pressure-resistant enzyme. This finding suggests that alterations in the protein moiety of the enzyme, as well as changes in the lipid microenvironment of the Na-K-ATPase protein, are essential for adapting this enzyme to depth[19].

At hydrothermal vent sites in the eastern Pacific found at depths of 2500–2600 m, resistance to temperatures that are substantially higher than average deep-sea temperatures may be important in establishing species' distribution patterns. Within the vent ecosystem there is a characteristic distribution of species according to water temperature[17,24]. Some animals, e.g., polychaete worms of the genus *Alvinella*, are found almost exclusively at what appear for animals to be the warmest habitable regions of the vents, the walls of 'black smoker' chimneys. Other species, notably the symbiont-containing vestimentiferan tube worm *Riftia pachyptila* and the mussel *Bathymodiolus thermophilus*, occur primarily in warm (up to ~25 °C) waters that contain the mixture of hydrogen sulfide and oxygen that is needed to support the chemolithoautotrophic metabolism of their symbionts. Some species, e.g., the clam *Calyptogena magnifica*, are found primarily in waters with temperatures near 2 °C. Although this distribution pattern may be based in part on the different capacities of the endemic vent species to tolerate or exploit the high concentrations of hydrogen sulfide found in the warm vent waters[38], recent studies of enzymes[12,13] (see below) and mitochondria[11,29] of vent animals have shown strong correlations between the thermal microenvironment of species and the thermal resistance of their biochemical systems.

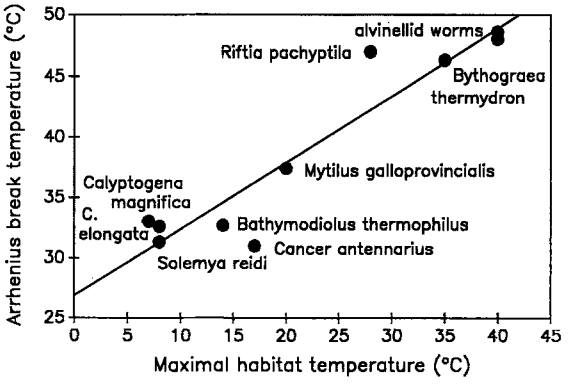


Figure 3. Arrhenius break temperatures (temperatures at which the slopes of Arrhenius plots of log respiration rate versus reciprocal of absolute temperature exhibited change in sign of slope) for mitochondrial respiration of marine invertebrates from different habitats. Arrhenius break temperatures are plotted against the maximal habitat temperatures recorded for the species (for temperature data see refs. 16, 17, 24). Hydrothermal vent species: alvinellid polychaete worms *(Alvinella pompejana* and *Alvinella caudata)*, vestimentiferan tube worm *(Riftia pachyptila)*, brachyuran crab *(Bythograea thermydron)*, mussel *Bathymodiolus thermophilus)*, and vesicomyid clam *(Calyptogena magnifica)*. Other species: clams *(Solemya reidi* and *Calyptogena elongata)*, crab *(Cancer antennarius)*, and mussel *(Mytilus galloprovincialis)*. (Data from Dahlhoff et al.[11]).

Mitochondrial respiration typically increases with rising temperature until a temperature is reached at which respiratory rate suddenly falls sharply[7]. When respiration data are displayed on an Arrhenius plot (logarithm of respiration rate versus reciprocal of absolute temperature), the fall-off in rate above a certain temperature, termed the 'Arrhenius break temperature', is shown by a change in the sign of the slope. The Arrhenius break temperatures of mitochondrial respiration and enzyme function have been shown to correlate with adaptation or acclimation temperature[7]. Thus, Arrhenius break temperatures can serve as biochemical indices of the adaptation temperatures of species.

We employed this principle to investigate whether invertebrates with different distribution patterns within the hydrothermal vent ecosystem were in fact adapted to different temperatures[11,29]. The data in figure 3 suggest that species found in the warmest zones, on the walls of 'smoker chimneys', were more warm-adapted than species found in areas peripheral to the warmest vent waters. These differences in the response of mitochondrial respiration to temperature show that even over very small distances, perhaps of the order of a few cm's, differences in resistance to temperature can play an important role in the species distribution patterns within an ecosystem.

*Enzymatic adaptations to pressure and temperature*

Enzymatic processes typically are perturbed by pressure, especially ligand (substrate, cofactor, and modulator) binding events[28,35]. As in the case of the lipoprotein enzyme Na-K-ATPase, the responses to pressure of soluble enzymes like lactate dehydrogenase (LDH) and malate (MDH) dehydrogenase differ adaptively among species found at different depths. Enzyme-substrate and

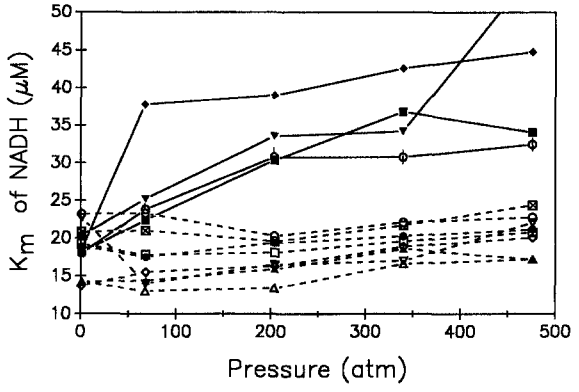


Figure 4. The effect of hydrostatic pressure on the Michaelis-Menten constant ($K_m$) of NADH for malate dehydrogenase of marine invertebrates from several shallow- and deep-sea environments. Measurement temperature was 5 °C. Shallow-living species (solid lines between symbols): *Mytilus galloprovincialis* (■), *Calyptogena elongata* (▼), *Cancer antennarius* (♦), *Chaetopterus variopedatus* (polychaete worm) (ϕ). Deep-living species (dashed lines between symbols): *Calyptogena magnifica* (●), *Alvinella pompejana* (△), *Alvinella caudata* (▲), *Bathymodiolus thermophilus* (□), unnamed mussel from the Florida escarpment (⊠), *Riftia pachyptila* (◇), *Calyptogena phaseoliformes* (○), and *Bythograea thermydron* (▽). (Data from Dahlhoff and Somero[13].)

enzyme-cofactor interactions, as indexed by apparent Michaelis-Menten constants ($K_m$), are largely, if not completely, insensitive to pressures between 1 atm and 476 atm for LDHs and MDHs of deep-living fishes[30, 31] and invertebrates[13] (fig. 4). In contrast, the homologous LDHs and MDHs of shallow-living animals are strongly perturbed by pressure, as indicated by large increases in $K_m$ of substrate or cofactor with rising measurement pressure (fig. 4).

What is especially striking are the low pressures at which perturbation, and adaptive differences in pressure sensitivity among species, are noted. Pressures of only 50–100 atm appear to be sufficient to favor selection for pressure-resistant variants of these two dehydrogenases. The similar responses of dehydrogenases of fishes and invertebrates to pressure suggest that animals of all taxa may face similar threats by elevated pressure and adapt to these through similar, i.e., evolutionary convergent, modifications of their enzymatic systems. Species zonation patterns in the marine water column are, then, correlated with changes in sensitivities to pressure of enzyme function, and the replacement of pressure-sensitive by pressure-resistant species may be necessitated at depths as shallow as 500–1000 m.

The distributions of deep-sea species in the hydrothermal vent ecosystem may be established in part by enzymatic adaptations to different temperatures, in agreement with observations on mitochondrial temperature sensitivities (fig. 3). Comparisons of the LDHs of deep-sea fishes occurring either exclusively in typical cold deep-sea waters or within the warm waters of the vent environment showed that the LDHs of cold-adapted fishes like *C. armatus* are not able to retain appropriate $K_m$ values under conditions of high pressure and elevated (10–20 °C) temperatures[12]. In contrast, the LDH of the vent zoarcid fish *Thermarces andersoni* exhibited a stable $K_m$ under pressure at temperatures up to 20 °C. Similar differences were observed among MDHs from vent invertebrates. MDHs of the most warm-adapted invertebrates, e.g., the Pompeii worm *(Alvinella pompejana)*, were substantially less perturbed by elevated temperatures under in situ presssures than were the MDHs of invertebrates from cold habitats, including cold microhabitats within the hydrothermal vent ecosystem[13].

*Protein structural adaptations to high pressure*

When members of a family of homologous proteins from species differing in adaptation temperature are compared, it is common to find that the temperature of heat denaturation is positively correlated with adaptation temperature[25]. Increased structural stability of proteins in high-body-temperature animals can be interpreted as facilitating retention of native structure at temperatures at which the homologous proteins of cold-adapted species might be partially unfolded and, thereby, less able to function well and more sensitive to degradative enzymes. Because abyssal temperatures are only a few degrees above the freezing point of seawater, it might be anticipated that proteins of deep-sea animals would have relatively low denaturation temperatures. However, for the proteins of deep-sea animals for which thermal stability data are available, high resistance to temperature has been found[34, 40]. Figure 5 shows how the resistance of monomeric (globular (G)) actin to heat denaturation varies among vertebrates adapted to different temperatures and pressures[40]. The most heat-stable G-actin is that of the thermophilic desert iguana, *Dipsosaurus dorsalis*, which experiences core temperatures near 47 °C. The most labile G-actins are those of the shallow-living antarctic teleosts, *Pagothenia borchgrevinki* and *Gymnodraco acuticeps*, whose body temperatures are −1.86 °C. Actins of three deep-sea fishes, *C. armatus*, *Coryphaenoides acrolepis*, and *Halosauropis macrochir*,

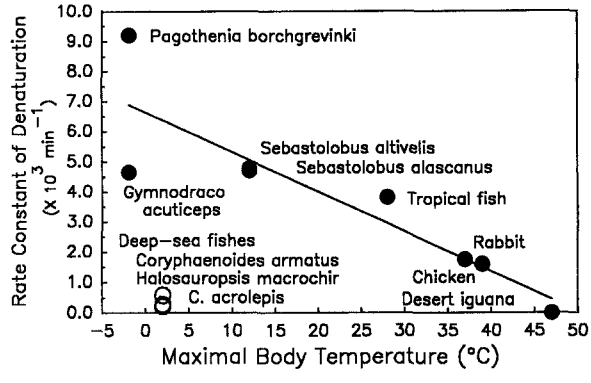


Figure 5. The relationship between adaptation temperature (maximal body temperature) and the thermal stability of globular (G) actins of several vertebrates. *Sebastolobus alascanus* and *Sebastolobus altivelis* are cold-water teleosts; *Pagothenia borchgrevinki* and *Gymnodraco acuticeps* are Antarctic teleosts. Deep-sea fishes: *Coryphaenoides armatus*, *Coryphaenoides acrolepis*, and *Halosauropsis macrochir*. (Data from Swezey and Somero[40]).

are very heat stable, more stable than the G-actins of a mammal and a bird, and almost as stable as the G-actin of the desert iguana. The stability of filamentous (F) actin is also enhanced in deep-sea fishes. F-actin of *C. armatus* is more resistant to pressure-induced depolymerization than F-actin of shallow-living and terrestrial species[41].

Differences in structural stability among LDHs from shallow- and deep-living fishes also have been demonstrated. Hennessey and Siebenaller[22,23] found that LDHs of deep-living fishes were substantially more stable during incubation under high pressure than the LDHs of shallow-living, cold-adapted species. A regular increase in resistance of LDH to pressure-induced loss of activity was observed in confamilial rattail species with different depths of maximal abundance.

The thermal and pressure stabilities of proteins from deep-sea species may reflect selection for especially rigid protein structures that resist disruption of tertiary and quaternary structure under high pressure. The differences noted in pressure sensitivity of proteins among confamilial and congeneric fishes and invertebrates offer additional evidence for the role of biochemical adaptations in establishing depth distribution patterns in the marine water column.

### *Capacity adaptations: depth-related changes in metabolic rate*

The biochemical adaptations of deep-sea animals that enable them to resist the effects of high pressure and tolerate different temperatures do not, in and of themselves, play a major role in establishing rates of metabolic activity. A distinct set of biochemical modifications, capacity adaptations, are instrumental in adjusting rates of metabolic function in accordance with the physical, biological, and nutritional characteristics of different pelagic and benthic deep-sea ecosystems[36].

*Metabolic rates of pelagic species fall sharply with depth*

The respiratory rates of pelagic fishes decreases rapidly with increasing minimal depth of occurrence (MDOC), especially over the first few hundred meters of the water column (fig. 6)[43,44]. In interpreting the selective factors underlying depth-related changes in metabolic capacities, minimal depth of occurrence, the depth below which 90% of a species is found, is the most appropriate characteristic of a species' depth distribution profile[3]. For many midwater species, nighttime depths are near the surface and daytime depths are at several hundred meters. It is access to the food-rich and predation-intense surface or epipelagic realm that plays the key role in selecting for metabolic properties of migrators. Non-migrators which share the same daytime depth as migrators do not require the high metabolic potentials possessed by their vertically-migrating daytime neighbors for function in food- and predator-laden surface waters.

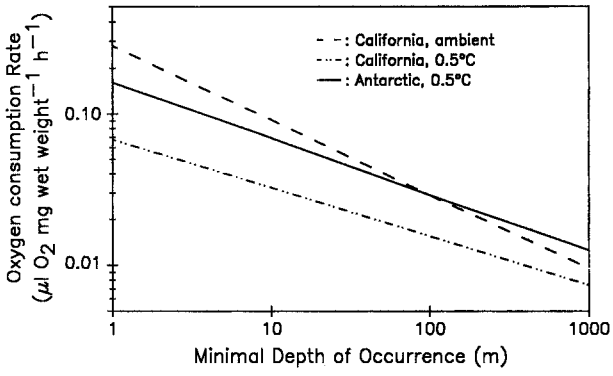


Figure 6. The relationship between minimal depth of occurrence (MDOC) and respiration rate for mesopelagic fishes captured along the coast of California and in Antarctic waters. California fishes were studied at either 10 °C (MDOC < 100 m) or 5 °C (MDOC > 100 m) (California ambient: dashed line). Antarctic fishes were studied at 0.5 °C (solid line). Rates for the California fishes were adjusted to 0.5 °C (dashed + dotted line) using a $Q_{10}$ of 2.0. (Figure modified after Torres and Somero[44]).

The factors that are of critical selective importance in establishing the depth-related changes in metabolism found for pelagic fishes (fig. 6) seem to be light and food availability[2,4,39,43,44]. Although temperature decreases with depth in most regions of the ocean, depth-related temperature change can explain only a small part of the decrease in respiration rate with depth. This conclusion is based in part on simple calculations of expected temperature coefficient ($Q_{10}$) effects on metabolism, and on empirical evidence, namely, comparisons of depth-related decreases in metabolic rate through thermally stratified and isothermal water columns (fig. 6). The patterns of depth-related changes in respiration rate found for midwater fishes from Californian (thermally stratified) and antarctic (isothermal) water columns show that temperature has the expected $Q_{10}$ effects on metabolic rate, but these $Q_{10}$ effects are not the major determinant of the observed patterns of respiration versus MDOC. Thus, a 10 °C decrease in temperature leads to about a 50% decrease in respiration, whereas an increase in MDOC of ~1000 m leads to an approximately 20-fold fall in respiration. When the respiration rates of the Californian fishes are corrected to the measurement temperature (0.5 °C) used in the studies of the Antarctic species, the extent of metabolic cold adaptation of the Antarctic fishes is clearly shown.

The extremely low metabolic rates of deep-living pelagic fishes have been attributed to selection for reduced locomotory activity[2,4,39,44]. In a realm where darkness prevails, except for bioluminescence, locating food and interacting with prey and predators may not necessitate the vigorous swimming capacities characteristic of epipelagic fishes. In support of this hypothesis, activities of ATP-generating enzymes in white locomotory muscle, the tissue of primary importance in driving high-speed swimming, decrease with MDOC in parallel with the decreases in respiratory rate (fig. 7)[2,39,44]. Because white locomotory muscle comprises approximately half of the mass of

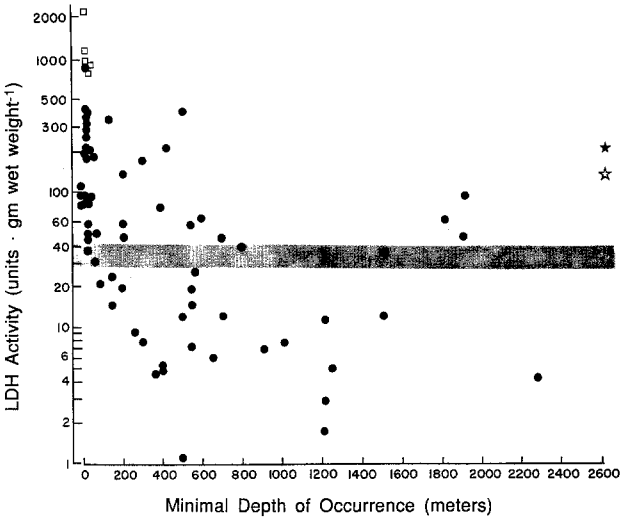


Figure 7. The relationship between minimal depth of occurrence and lactate dehydrogenase activity of white skeletal muscle for different marine fishes. Each symbol represents a different species of fish. Open squares: tunas, Stars: hydrothermal vent fishes. The shaded band running across the figure encloses all values of LDH measured in brain tissue of several of the species. (Figure based on data in refs. 4, 21, 38, 44).

a typical teleost and is responsible for a large share of ATP turnover, reducing the amount of metabolism in this tissue will greatly reduce overall respiratory rate. Decreases in gill Na-K-ATPase activity with MDOC also have been interpreted as reflecting reduced locomotory activity in deep-sea fishes[20]. In sluggish deep-living fishes, reduced locomotory activity is apt to be associated with reduced perfusion of the gills and reduced water flow over the gill surface, two conditions that minimize the exchange of water and ions with seawater. The finding that the activities of ATP-generating enzymes in brain tissue (fig. 7) do not decrease with increasing MDOC is further evidence that the depth-related reductions in respiration are largely a consequence of selection for reduced locomotory activity and not due to reductions in metabolism of all tissues.

Note that the LDH activities in muscle of two hydrothermal vent fishes, *Thermarces andersoni* and *Bythites hollisi*, are high relative to all other deep-sea fishes that have been studied (fig. 7). For hydrothermal vent fishes, there may exist the need for a vigorous locomotory capacity, e.g., to allow the fish to avoid lethally hot waters and attacks from active predators like brachyuran crabs that occur at the vents.

### *Depth-related metabolic changes are small for benthic animals*

The large decreases in metabolic rate with depth observed for pelagic fishes and invertebrates[1,2] are not characteristic of benthic invertebrates[2]. Childress and colleagues[1,2] have found that benthic invertebrates have only modest reductions in metabolic rate with increasing depth, reductions that appear to reflect only the influences of reduced temperature. Consistant with these metabolic data are the results of studies of enzymatic activities in tissues of benthic invertebrates from shallow water and hydrothermal vent environments[21]. Unlike the pattern shown for LDH of pelagic fishes with different MDOCs (fig. 7), no major depth-related differences among phylogenetically similar species were found in comparisons of benthic invertebrates.

The differences between pelagic and benthic species in the variation in metabolic rate with depth could be due to differing reliance on locomotory activity for obtaining nutrition in the two groups. The energy-saving benefits of greatly reducing swimming power in pelagic animals clearly do not apply for benthic species that do not need to move rapidly or over great distances.

### *Conclusions*

Although study of the biochemical ecology of deep-sea animals is a relatively new line of inquiry, it is already apparent that pervasive modifications in protein and membrane-based systems distinguish deep-living species from their shallow-living counterparts. The tolerance adaptations observed among congeneric species which occur at different depths, or in different temperature regimes within the deep-sea, offer an especially clear illustration of the importance of biochemical adaptations in helping to establish species zonation patterns within pelagic and benthic ecosystems. The capacity adaptations found in metabolic systems, e.g., the ATP-supplying systems of locomotory muscle of pelagic fishes, illustrate the extreme to which rates of metabolic activity can be adjusted to bring the metabolic properties of an organism into accord with the physical, biological, and nutritional characteristics of its habitat.

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