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LIFE AT STABLE LOW OXYGEN LEVELS: ADAPTATIONS OF ANIMALS TO OCEANIC OXYGEN MINIMUM LAYERS

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Summary

Zones of minimum oxygen level are found at intermediate depths in most of the world's oceans and, although the oxygen partial pressure in some of these 'oxygen minimum layers' is only a fraction of a kilopascal, populations of pelagic metazoans exist there. These oxygen minimum layers are areas of the water column and the associated benthos with stable conditions of continuously low oxygen level and low temperature at intermediate depths (400–1000 m depth) over vast areas. Off California, where P_{O_2} at the oxygen minimum is 0.8 kPa, there are abundant populations of animals both in the water column and on the bottom. Farther to the south in the eastern tropical Pacific, oxygen partial pressures of less than approximately 0.4 kPa result in very low biomasses and diversity of animals at minimum layer depths.

At the minimum oxygen levels found off California, most animals which inhabit the minimum zones appear to support their routine metabolic demands *via* aerobic metabolism. They do this by being very effective at removing oxygen from water. Among the adaptations of pelagic crustaceans to these conditions are: (1) enhanced ventilatory abilities, (2) enhanced percentage removal of O_2 from the ventilatory stream, (3) large gill surface areas, (4) short diffusion distances from the water to the blood, and

(5) hemocyanin respiratory proteins with a very high affinity for O_2 , high cooperativity and large Bohr effects. The lower O_2 consumption rates of many deeper-living species are also functionally adaptive in that they facilitate aerobic survival at low P_{O_2} . However, they are not adaptations to the minimum layer, since similarly low rates are found in the same and comparable species living at the same depths in regions without well-developed minima, and these animals are unable to survive at the low P_{O_2} values of the minima. While anaerobic metabolism may be important for metabolic rates above the routine level for most animals in the minimum layer, there is little evidence for the use of sustained anaerobiosis in the species studied. In summary, given the stable presence of very low O_2 levels in the minima, the primary adaptations of animals living within them are those that support aerobic metabolism by giving the animals remarkable abilities to extract O_2 from water. These abilities are notably better than those of animals adapted to unstable hypoxic environments, such as intertidal mudflats, while the latter animals rely to a much greater extent on anaerobiosis and perhaps on metabolic suppression to survive periods of anoxia.

Key words: oxygen minimum layer, metabolic rate, adaptation.

Introduction

Zones of minimum oxygen level are found at intermediate depths in most of the world's oceans and, although the oxygen partial pressures of these 'oxygen minimum layers' in some regions are only a fraction of a kilopascal, populations of pelagic metazoans exist there (Schmidt, 1925; Sewell and Fage, 1948; Banse, 1964). These oxygen minimum layers (OMLs) are pelagic habitats with stable conditions of continuously low oxygen level and low temperature at intermediate depths (400–1000 m depth) over vast areas. Where the OMLs intersect continental margins, stable low-oxygen conditions are also found in the benthic habitat. The oceanic oxygen minima differ from other hypoxic aquatic habitats in that very low oxygen levels are stable over long periods and large areas, while other aquatic hypoxic habitats

are typically short-lived, transient stages in the progression to anoxia where the region of hypoxia is quite small. One result of this is that OML inhabitants have dramatic adaptations for aerobic metabolism which often exceed those found in animals from other hypoxic habitats.

The oxygen minimum layers as oceanographic phenomena

The best-developed OMLs are found in the eastern tropical Pacific Ocean, the Northern Indian Ocean and the Eastern Atlantic off northwest Africa (Wyrki, 1962; Kamykowski and Zentara, 1990; Olson *et al.* 1993). In these regions, the minimum oxygen level is typically less than 0.1 ml l^{-1} at depths

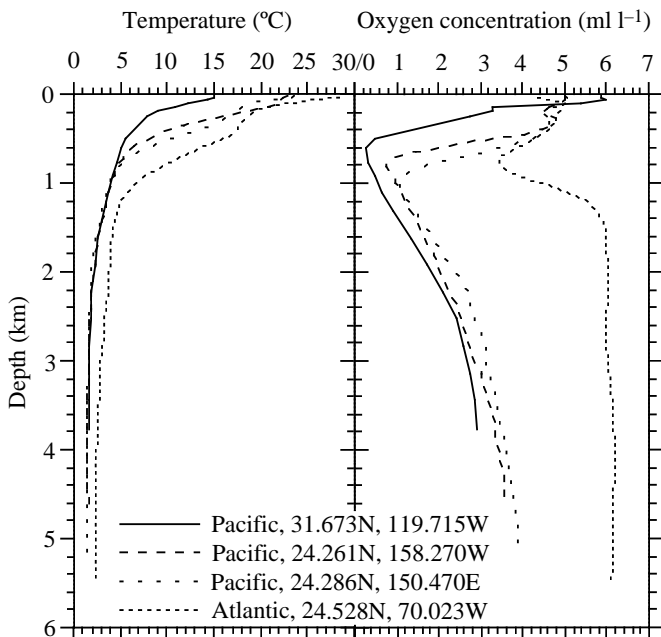


Fig. 1. Oxygen levels and temperature conditions as a function of depth at oceanic stations in the Pacific and Atlantic Oceans. Pacific temperature and O₂ data are taken from a March–June 1985 section along 24°N from the Trans-Pacific Sections expedition of the RV *Thompson*. Atlantic temperature and O₂ data are taken from an August–September 1981 cruise of RV *Atlantis II*. Both groups of data are taken from the data files accompanying the OceanAtlas program using OceanAtlas for access.

of 600–800 m and often over depths of 100–900 m. As one moves horizontally out from these ‘core’ regions, the minimum is reduced in thickness and the minimum oxygen level is higher (Fig. 1). These oxygen minima develop because the balance of consumption of oxygen relative to replenishment is greater than at shallower and greater depths. At shallower depths, the consumption is higher but the oxygen supply is even higher, while at greater depths the oxygen supply is lower but, owing to the greatly decreased biomass, the consumption is much lower. In areas where the OML is especially well developed, the ‘source’ waters are typically relatively low in oxygen and/or their circulation through the regions is slow (Wyrski, 1962, 1967; Olson *et al.* 1993), resulting in low replenishment of oxygen. High local primary production may also be a factor contributing to oxygen depletion.

As already noted, the oceanic oxygen minima persist for long periods, making this habitat different from other hypoxic marine habitats in that hypoxia is not a short-lived, transient condition between oxic and anoxic conditions. Furthermore, because of the great extent of the habitat, the quantity of oxygen is not a limiting factor as it may be in many of the limited-volume, transiently hypoxic marine habitats. To put the stability of deep-sea oxygen conditions in perspective, we will briefly consider our present knowledge about the past history of oxygenation in the deep sea. Present estimates from

palaeoceanography are that the deep sea has been oxic for the last 90 million years (Herbert and Sarmiento, 1991; Kaiho, 1991; Tyson and Pearson, 1991), although prior to that time there were periods of anoxia. A more recent event, 57.33 million years ago, apparently involved pronounced warming and reduction of oxygen concentrations in the deep sea but is unlikely to have produced anoxia, although it caused the extinction of many deep-sea benthic species (Kennett and Stott, 1991). More recently, studies of high-resolution palaeoclimatic and palaeoceanographic records from the Santa Barbara basin (which is at oxygen minimum depths) show relatively short-term oscillations between low-oxygen conditions (indicated by laminated sediments and correlated with warmer climate) and higher-oxygen conditions (indicated by the absence of laminations due to bioturbation and correlated with a cooler climate) during the last 20 000 years (Kennett and Ingram, 1995). These variations appear to be synchronous with ocean-climate variations at more distant points, suggesting widespread variations in the oxygen content of the oxygen minimum layers, with conditions being stable for only thousands of years at a time. In this context, we envision a world ocean in which the oxygen minima are always present, but the extent of the regions of lowest oxygen level varies considerably, with major oscillations having periods measured in thousands of years. In terms of the physiological adaptations of the midwater biota, this means that animals are faced either with having their vertical or horizontal ranges modified as ambient oxygen conditions change at intermediate depths or with being able to acclimate to the changed conditions. These possibilities warrant further study to discover which strategy is used by these organisms.

The impact of oceanic oxygen minimum layers on animal distributions

Perhaps the most striking observation is that, over a very wide range of oxygen contents and partial pressures (down to approximately 0.20 ml l⁻¹ or 0.63 kPa), there is apparently no effect of the low oxygen levels on the biomasses of midwater organisms and relatively little effect even on the distributions of major taxa and of many particular species (Banse, 1964). This is especially noteworthy because these oxygen contents are far below those normally considered hypoxic in shallower habitats (4–13 kPa) and are beyond the aerobic abilities of most shallower-living species. However, there is evidence that, even at these oxygen partial pressures, which do not reduce the animal biomass, particular species may be excluded while others may be limited to low-oxygen conditions (Pickford, 1946; Gibbs and Hurwitz, 1967; Roper, 1969; Brinton, 1979).

At oxygen concentrations below approximately 0.15 ml l⁻¹, there are pronounced effects on both species distributions and biomass. Typically, the zooplankton biomass is greatly reduced within these OMLs, and there is a secondary maximum of biomass at the lower edge of the OML where oxygen content is rising (Jespersen, 1935; Sewell and Fage, 1948; Vinogradov and Voronina, 1962; Childress, 1968;

Brinton, 1979; Judkins, 1980; Wishner *et al.* 1990; Böttger-Schnack, 1996; Saltzman and Wishner, 1997a,b). Those few species that do live in these very low oxygen concentrations are typically diurnal vertical migrators which enter shallower, more oxygenated waters at night (Vinogradov and Voronina, 1962; Longhurst, 1967; Childress, 1968; Brinton, 1979; Sameoto *et al.* 1987; Kinzer *et al.* 1993; Saltzman and Wishner, 1997a,b).

Adaptations of animals to the oxygen minimum layers

Within the vast oceanic realm, the problem of hypoxia is entirely one of a reduced gradient to drive diffusion of oxygen from the exterior of the animals eventually to their mitochondria. The quantity of oxygen in their environment is not limiting, just its availability. Thus, given the much higher energy yield of aerobic metabolism, one would expect that there would be strong selection for mechanisms to take up oxygen effectively from very low ambient partial pressures. However, at some point, one would expect that the available gradient would be too small to support aerobic metabolism fully, even with highly developed uptake mechanisms, and this could result either in a shift to anaerobic metabolism or to a reduction in metabolic rates. Thus, the three modes of adaptation to the oxygen minima which have been proposed are as follows. (1) The development of mechanisms for the highly effective removal of oxygen from water, allowing an animal to regulate its rate of oxygen consumption down to low partial pressures. (2) The reduction of metabolic rates so that the organism can live at lower oxygen partial pressures with a given set of uptake mechanisms. (3) The use of anaerobic metabolism to make up the difference between aerobic capacity and total metabolic demand. This could be on a sustained basis, during periods of increased demand due to higher activity or during transient periods spent in the oxygen minimum layer by diurnal vertical migrators. As we shall see below, there is evidence for all of these mechanisms depending upon the severity of the oxygen minimum, the complexity of the animals considered and the oceanic habitat involved.

The severity of the oxygen minimum is expected to be an especially critical factor below approximately 0.15 ml l^{-1} (0.48 kPa) since zooplankton biomasses are significantly reduced below this level. This suggests that there is a limit to the adaptations used throughout the less intensely developed minima at approximately 0.15 ml l^{-1} , with other strategies being required at lower oxygen levels. One of the goals of this paper is to consider the nature of this apparent limitation.

The structural complexity of the many taxa of animals found in the pelagic environment is another significant variable affecting the adaptations expected. Some groups, such as fishes, crustaceans, molluscs and polychaetes, have specialized respiratory surfaces, circulatory systems and respiratory systems which offer many possibilities for adaptive modifications. However, many other groups, such as the cnidarians, ctenophores, radiolarians and nemerteans, lack such organs and tissues yet are found in the oxygen minima.

They may well use different mechanisms to survive from those used by the more structurally complex taxa.

For pelagic species, higher oxygen partial pressures could potentially be accessed by swimming vertically for a few hundred meters; however, many of the species found in the minimum layer appear to spend extended periods there. In contrast, benthic species within an OML would typically need to go many kilometers along the bottom to change their depths sufficiently to find higher oxygen levels. This difference between the benthic and pelagic habitats may affect the kinds of adaptations found in these two habitats. As a result, we will primarily consider the pelagic species, for which there is a rich literature, and specifically discuss the much more limited literature on benthic species when appropriate.

The adaptive significance of the properties of species living in an oxygen minimum can be difficult to dissect because almost all the important variables such as oxygen level, temperature, downwelling light, pressure and zooplankton biomass covary with depth in the top 1000 m or so of the ocean. This means that, within a given geographic area, these variables are almost hopelessly confounded and it is difficult, if not impossible, to demonstrate an adaptive response to one of them when working within a single region (Childress, 1995). What is necessary for a definitive comparison is a horizontal comparison between species, or of the same species, living at the same depths but in regions with differing hydrographic properties. In the case of adaptation to the oxygen minimum, this means comparing animals from regions with different oxygen contents in the minimum layer. Comparisons among species living above the oxygen minimum and in it in a single region are exceedingly difficult to interpret because of the confounding of so many variables with depth (Childress, 1995). In some cases, survival at depth conditions, modeling or comparisons with deeper-living species can be useful approaches to testing whether a given parameter is an adaptation to low oxygen level.

Another possible problem in applying a comparative approach to the question of adaptation to the minimum layers is that phylogeny may have played a significant role in the evolution of the properties of individual species, and thus some workers contend that each species cannot be considered to provide an independent data point (Harvey and Pagel, 1991). We do not believe that this is a problem within the large data sets on pelagic species that we will be primarily considering, since these data sets show a great deal of convergence of properties across phyla, genera and families for species living within the minima (Childress, 1995). However, there is also much evidence of divergence of properties within genera and families as a function of whether they live within minima or not.

Aerobic adaptation to the oxygen minimum layer

It is clear that an enhanced ability to regulate oxygen uptake is fundamental to the survival of animals in the oxygen minimum layers. OML-dwelling midwater crustaceans, fishes and cephalopods from the oceans off California generally have

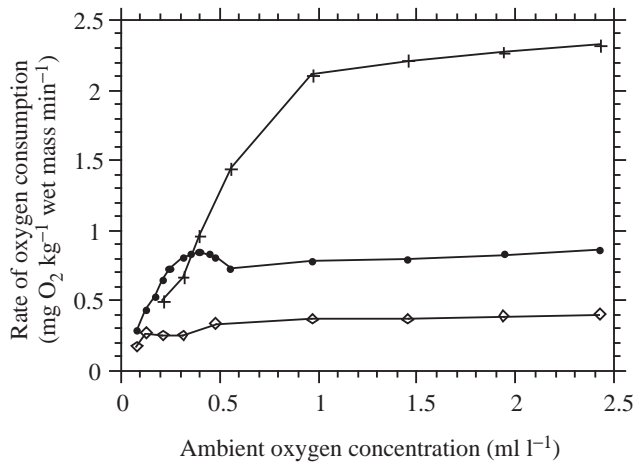


Fig. 2. Rates of oxygen consumption of *Gnathopausia ingens* from the seas off California measured at 5.5 °C (Childress, 1968). Crosses represent a single animal driven to maximal activity. Filled circles represent the means of 23 runs with eight individuals showing routine levels of swimming activity. Diamonds represent a single non-swimming animal.

the ability to regulate their routine oxygen consumption rates down to approximately the lowest oxygen level that they encounter in the ocean (Childress, 1968, 1969, 1971*a,b*, 1995; Meek and Childress, 1973; Torres *et al.* 1979; Seibel *et al.* 1997) (Fig. 2). In some cases, the critical partial pressures (P_c) where regulation of O_2 uptake failed were as low as 0.4 kPa. These enhanced regulatory abilities are clearly an adaptation to the minimum layer since (1) similar species or the same species from the same depths but from regions with higher oxygen levels have higher P_c values and cannot survive at lower P_{O_2} values for any time (Donnelly and Torres, 1988; Cowles *et al.* 1991; Torres *et al.* 1994*a,b*; Seibel *et al.* 1997), (2) species that live below the minimum layer have higher P_c values (Childress, 1975), and (3) OML species generally have very limited anaerobic abilities. In one case, a benthic fish living within the minimum off southern California has also been found to have a low P_c (Yang *et al.* 1992), indicating aerobic adaptations in benthic species as well.

Fig. 3 summarizes the available data on the regulation of oxygen consumption by OML-depth midwater crustaceans from the seas off southern California, Hawaii, the Gulf of Mexico and the Antarctic. This graph shows that the pelagic crustaceans have P_c values which generally enable them to maintain their aerobic metabolic rates even at the lowest O_2 concentrations in their environments. However, those species from regions with higher oxygen concentrations have much higher P_c values. The apparent flattening of the curve above a P_c of 4 kPa suggests that P_c values below 4 kPa are specific adaptations to reduced environmental oxygen levels in the minimum layer, while P_c values of approximately 4 kPa appear to be typical of midwater animals living at high environmental oxygen levels. Differences in the P_c in individuals from the same species caught in regions of differing minimum O_2 have also been documented, suggesting either an ability to acclimate

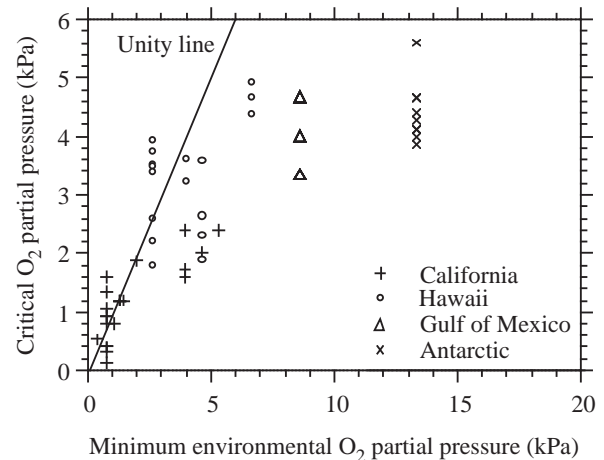


Fig. 3. The mean critical O_2 partial pressures of a wide variety of pelagic crustaceans living at oxygen minimum layer depths in different oceanic habitats plotted as a function of the lowest P_{O_2} to which they are normally exposed (Childress, 1975; Donnelly and Torres, 1988; Cowles *et al.* 1991; Torres *et al.* 1994). Since the lowest P_{O_2} in a given region is common to many species, there is a great deal of overlap of points so that, while 43 points are apparent, 62 are actually plotted.

their regulatory abilities or regional genetic differences in widespread OML-depth species (Sanders and Childress, 1990*a,b*; Cowles *et al.* 1991).

These enhanced regulatory abilities appear to be the result of a very high degree of development of the systems involved in uptake and transport of oxygen (Childress, 1995). In the most detailed studies of an animal from the oxygen minimum layer undertaken to date (Childress, 1968, 1971*a*; Belman and Childress, 1976; Sanders and Childress, 1990*a,b*), the mysid crustacean *Gnathopausia ingens* (which has a routine P_c of 0.8 kPa) has been shown to have the following properties which facilitate oxygen uptake at low partial pressures: (1) high ventilatory abilities (up to $81 \text{ kg}^{-1} \text{ min}^{-1}$); (2) high effectiveness of removal of O_2 from ventilatory stream (up to 90% removal from inhaled water); (3) high circulatory capacity (up to $225 \text{ ml kg}^{-1} \text{ min}^{-1}$); (4) high gill surface area ($9\text{--}14 \text{ cm}^2 \text{ g}^{-1}$ wet body mass); (5) thin blood-to-water diffusion distance across the gills ($1.5\text{--}2.5 \mu\text{m}$); and (6) hemocyanin with a high affinity for O_2 ($P_{50}=0.19 \text{ kPa}$), high cooperativity ($N_{50}=3.5$), large Bohr effect ($-0.80 \Delta \log P_{50} \Delta \text{pH}^{-1}$) and low concentration (24 mg ml^{-1} or $0.3 \text{ mmol O}_2 \text{ l}^{-1}$).

The first five of these properties are comparable to those of active fishes (Childress, 1971*a,b*; Belman and Childress, 1976). The high gill surface area and thin blood-to-water distance result in a high diffusing capacity for these gills, which means that *G. ingens* requires a lower oxygen gradient to take up a given amount of oxygen. The low hemocyanin concentration is in the range predicted to be necessary on the basis of other physiological properties (Belman and Childress, 1976; Sanders and Childress, 1990*a,b*) and is sufficient to account for approximately 75% of the oxygen in the blood at 0.8 kPa. The hemocyanin properties are clearly appropriate for

a hemocyanin functioning at very low partial pressures. It appears that individuals of *G. ingens* living at higher oxygen concentrations off Hawaii have a hemocyanin with a higher P_{50} (Sanders and Childress, 1990b), supporting the adaptive nature of the high affinity found in California animals. Other midwater crustaceans from Hawaii also have hemocyanins with lower affinities than found off California (Sanders and Childress, 1990a).

In addition to the crustaceans, some fragmentary observations have been made for other groups, suggesting that they use similar mechanisms. For example, larger gills have been observed in OML species of fishes (Parin, 1961; Ebeling and Weed, 1963; Gibbs and Hurwitz, 1967) and cephalopods (Roper, 1969; Young, 1972). High-affinity hemoglobins have been found in midwater OML fishes (A. J. Arp and J. J. Childress, unpublished observations) and a benthic OML fish (Yang *et al.* 1992). A single observation suggesting low-affinity hemoglobins in OML fishes (Douglas *et al.* 1976) was almost certainly an error due to the use of blood from trawl-captured specimens without measuring or adjusting the pH in the whole blood used in their studies. The blood of trawl-caught midwater fishes is typically very acidotic (pH values of 6–6.5 being common, A. J. Arp and J. J. Childress, unpublished observations). The same species of *Vinciguerria lucetia* measured under more physiological conditions gave P_{50} values below 1.3 kPa and had large Bohr and Root effects, explaining the results of Douglas *et al.* (1976) (A. J. Arp and J. J. Childress, unpublished observations).

Thus, it appears that the crustaceans, fishes and cephalopods all follow similar modes of adaptation to the OMLs; that is, the development of abilities to regulate their oxygen consumption rates very effectively so that they can remain primarily dependent upon aerobic metabolism down to P_{O_2} values of 0.5–0.8 kPa. This regulation is made possible by adaptations at the tissue and organ levels which increase the supply of medium to the respiratory surfaces, increase the diffusing capacity of the respiratory surfaces and manipulate the internal P_{O_2} to maintain suitable gradients for diffusion of oxygen at the gills and tissues. There are almost certainly also adaptations at the level of the oxygen-consuming tissues to allow aerobic functioning at these very low blood P_{O_2} values, but these have not been studied. One possibility is that the high lipid contents (greater than 10% of wet body mass in some cases) found in some midwater OML fishes and crustaceans (Childress and Nygaard, 1973, 1974; Neighbors and Nafpaktitis, 1982) could result in more rapid rates of diffusion of oxygen through tissues to the mitochondria (Desaulniers *et al.* 1996). However, since such high lipid contents are also found in animals from comparable depths without pronounced oxygen minima (Donnelly *et al.* 1990, 1994; Torres *et al.* 1994a,b), it is unlikely that this is a specific adaptation to the oxygen minimum layer.

We would expect that polychaetes would have a pattern of adaptations similar to those of fishes, cephalopods and crustaceans, but other major groups lack the organ and tissue specializations to adapt to the OMLs in this manner. The study

of these groups is made especially difficult by the fact that they are often fragile organisms with low metabolic rates. In preliminary studies, we have found excellent regulation in midwater ctenophores, chaetognaths and the aberrant polychaete *Poebius meseres* (J. J. Childress and E. V. Thuesen, unpublished observations). In the case of the ctenophores, this regulation may be possible because the major oxygen demand is peripheral to the body in the ctene rows, resulting in short diffusion distances to the mitochondria. For the chaetognaths, the animals are so thin that diffusion distances are always relatively modest. In *Poebius meseres*, the organ and tissue specializations, including the properties of their circulating chlorocruorin, may be critical (Robbins, 1965). For the remaining groups, such as nemerteans and cnidarians, no data are available. Although one can conceive of specializations to reduce diffusion distances by peripheral location of mitochondria, it is difficult to envision how such large organisms could be fully aerobic at low oxygen partial pressures.

It is clear that a variety of midwater fishes, crustaceans and cephalopods from the seas off California can regulate their routine oxygen consumption rates down to 0.8 kPa, with others going as low as 0.4 kPa, and most OML species can continue to consume O_2 all the way to anoxia (Childress, 1969, 1971a,b, 1975; Torres *et al.* 1979). The very limited anaerobic capacity of many of these species (<0.5 h anoxic) suggests that these regulated rates represent the bulk of the metabolic demands (Childress, 1969, 1971a,b, 1975; Torres *et al.* 1979). There is, however, no evidence that midwater animals are able to regulate their routine oxygen consumption rates down to the level of 0.3 kPa or less found in large areas of the most highly developed OMLs. Thus, we suggest that the notable reduction in biomass found in OMLs with oxygen contents below approximately 0.15 ml l^{-1} is due to an inability of midwater species to adapt to regulating their O_2 consumption rates below this level, forcing them to rely on anaerobic metabolism for extended periods for survival in these OMLs.

Another important aspect of the regulation of O_2 uptake by these species is that the oxygen consumption rates of midwater fishes, crustaceans and cephalopods which are resident at OML depths are typically almost an order of magnitude lower than the rates of comparable animals which live at the surface or migrate to the surface (Childress, 1995). The rates of fishes, in fact, approach those of benthic species (Childress *et al.* 1990), while those of some cephalopods are lower than those of benthic species and approach those of cnidarians (Thuesen and Childress, 1994; Seibel *et al.* 1997). Without such low rates, these species could not regulate down to the low O_2 levels of the OMLs off California. An example of the importance of this can be found in the diurnally vertically migratory oplophorid decapod crustaceans of the genera *Oplophorus*, *Acantheephyra* and *Systemaspis*. These vertically migrating species have much higher metabolic rates than do their congeners and confamilials which live at comparable daytime OML depths (Donnelly and Torres, 1988) and are found throughout the temperate and tropical oceans of the world except where OMLs are well-

developed (Omori, 1974). Thus, the lower metabolic rates of midwater fishes, crustaceans and cephalopods are clearly adaptive in a functional sense for survival in the OMLs, but whether they are adaptations to the OMLs in an evolutionary sense is another story, as we shall see below.

Increased reliance on anaerobic metabolism as an adaptation to the oxygen minimum layer

Given the substantial abilities of midwater animals to extract O_2 from water and the much greater energy yield of aerobic metabolism, we would expect anaerobic metabolism to be used at most as a supplement to aerobic metabolism and not as the sole form of oxidative metabolism. In this context, we will distinguish between the use of anaerobic metabolism to support activity levels and metabolic rates above routine rates and its use to support part of the routine rates.

Several cases where midwater crustaceans must rely on anaerobic metabolism to satisfy part of their routine metabolic needs have been documented. The large copepod *Gaussia princeps* has a P_c of approximately 1.6 kPa but lives part of the time at P_{O_2} values as low as 0.8 kPa off California. It has a substantial anaerobic capacity, being able to survive anoxia for between 10 and 14 h. It has been proposed that when it is in the core of the OML as much as 50% of its metabolic requirements may need to be provided by anaerobic metabolism, but as it moves up or down from the lowest O_2 concentrations this percentage drops rapidly (Childress, 1977). The large isopod *Anuropus bathypelagicus* is parasitic on the very large medusa *Deepstaria enigmata* (Barham and Pickwell, 1969). *Anuropus bathypelagicus* can only regulate its O_2 consumption down to 1.9 kPa, although it lives down to at least 1.3 kPa, but it has a substantial capacity for anaerobic survival (Childress, 1975). Another cnidarian parasite, *Hyperia* sp., can survive without O_2 for 30 h (Childress, 1975). It has been suggested that these parasitic species can more readily use anaerobic metabolism because of the abundant substrate supply represented by their hosts. The benthopelagic galatheid *Pleuroncodes planipes* is able to regulate its O_2 consumption rate down to 0.26 kPa when resting on the bottom; however, in the eastern tropical Pacific where this species lives, O_2 concentration is often at or below this level at depths where the crabs are found (Boyd, 1967; Quetin and Childress, 1976). The substantial anaerobic capacity of this species, greater than 12 h of anoxia, is probably necessary for its forays into low- O_2 water (Childress, 1975). Thus, it is apparent that part of the routine metabolic energy needs of some midwater crustaceans when in OMLs may be supplied by anaerobic metabolism, although the majority of species do not appear to rely on this mechanism. Our general impression is that vertically migrating midwater cephalopods may have greater anaerobic capacities than comparable crustaceans and may rely more on anaerobic metabolism for part of their routine metabolism in the OMLs, but this point has not been well documented.

In the very highly developed OMLs, where O_2 content is less than approximately 0.15 ml l^{-1} , most species migrate out

on a daily basis (Vinogradov and Voronina, 1962; Childress, 1968; Brinton, 1979; Sameoto *et al.* 1987; Kinzer *et al.* 1993; Saltzman and Wishner, 1997a,b). Given the observed limitations on aerobic adaptations, we propose that these species rely to a great extent on anaerobic metabolism while at depth and then burn off their oxygen debts when they migrate to higher oxygen concentrations at night. As shown by Teal and Carey (1967), however, these species still have the ability to obtain some O_2 from the water even at these very low concentrations. Thus, the limitation of biomass below $0.15 \text{ ml O}_2 \text{ l}^{-1}$ may be the result of relatively few species being able to live largely anaerobically for half of each day and then undertake an extensive migration to shallower depths.

The support of activity levels above routine almost certainly requires anaerobic metabolism for most fishes, crustaceans and cephalopods which live at P_{O_2} values as low as 0.8 kPa or so, since the data generally show that these animals are only able to regulate their routine rates to the lowest P_{O_2} that they encounter (Childress, 1968, 1971a,b; Torres *et al.* 1979; Cowles and Childress, 1988; Seibel *et al.* 1997). Higher activity levels must require anaerobic metabolism for most of their support. This should have the effect of restricting higher levels of activity depending upon the anaerobic capacity of any given species.

Analyses of enzyme activities have also been used as an approach to looking for greater reliance on anaerobic metabolism in OML species. In a series of midwater fishes, there was no evidence of enhanced glycolytic capacity in those species living at $0.25 \text{ ml O}_2 \text{ l}^{-1}$ compared with those living shallower and deeper (Childress and Somero, 1979). In a series of flatfishes living off the California coast, there was also no apparent increase in glycolytic capacity (pyruvate kinase and lactate dehydrogenase) relative to aerobic capacity (citrate synthase and malate dehydrogenase) (Vetter *et al.* 1994). In a comparison of a shallow-living benthic scorpaenid species, *Scorpaena guttata*, with an OML-inhabiting species, *Sebastolobus alascanus*, there was little indication of a greater glycolytic poise in brain or white muscle of the OML species (Yang and Somero, 1993). However, in the OML species, the red muscle lactate dehydrogenase (LDH) activities were greater than the white muscle activities, a very unusual finding suggesting that this species may use glycolysis for a greater fraction of its routine metabolic needs than is usually the case. In addition, the heart of *S. alascanus* has only a single LDH, which appears to be an anaerobically poised one unlike the usual finding of aerobically poised LDH in heart tissues (Yang *et al.* 1992). This finding suggests that the heart may use anaerobic metabolism to a greater extent than is usual for fishes.

The sum of these lines of evidence is that, in OMLs with O_2 contents above 0.20 ml l^{-1} , most of the more complex animals rely on aerobic metabolism for their routine rates of metabolism but quickly begin to use anaerobic metabolism at higher activity levels. This shift to anaerobic metabolism is expected to happen at much lower relative activity levels than is typical of more oxic environments.

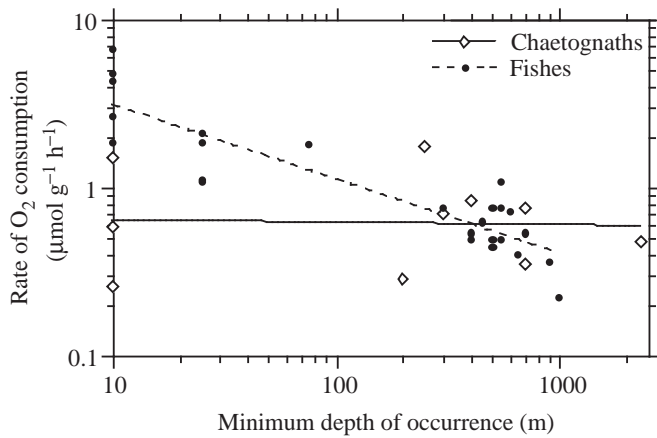


Fig. 4. Routine rates of oxygen consumption, measured at 5 °C, of midwater fishes and chaetognaths from the seas off California (Torres *et al.* 1979; Thuesen and Childress, 1993).

Reduced metabolic rates as an adaptation to the oxygen minimum layer

The metabolic rates of deeper-living pelagic fishes, crustaceans and cephalopods are much lower than those of surface-living species even when temperature is taken into account (Fig. 4) (Childress, 1971*a,b*, 1975, 1995; Torres *et al.* 1979; Childress *et al.* 1990). Since this phenomenon has recently been reviewed in depth, we will only concern ourselves here with the relationship between these reduced rates and the OMLs (Childress, 1995). Although, as noted earlier, these lower metabolic rates in pelagic OML fishes, crustaceans and cephalopods are functionally adaptive for their aerobic survival in the OMLs, they do not appear to have evolved as adaptations to the low oxygen levels in the OMLs. This statement is based on several lines of evidence.

(1) Midwater crustaceans and fishes living at OML depths (400–800 m) in regions with higher oxygen concentrations have metabolic rates comparable with those of the same or similar species living at oxygen concentrations as low as 0.20 ml l⁻¹, while having much poorer regulatory abilities (Figs 3, 5) (Donnelly and Torres, 1988; Torres and Somero, 1988*a,b*; Cowles *et al.* 1991; Torres *et al.* 1994*a,b*; Seibel *et al.* 1997).

(2) Midwater crustaceans, fishes and cephalopods living below the oxygen minimum layer have lower metabolic rates and higher P_c values than those living in the minimum layer (Childress, 1975; Cowles *et al.* 1991; Seibel *et al.* 1997).

(3) Non-visual deep-sea groups, such as cnidarians and chaetognaths, do not show any decrease in metabolic rate with depth off the California coast, a region with a minimum O₂ content of approximately 0.20 ml l⁻¹ (Fig. 4) (Thuesen and Childress, 1993, 1994).

Thus, in those pelagic groups that do show reduced metabolic rates at OML depths, the rates are reduced whether O₂ content is low or not, which refutes the suggestion that the lower metabolic rates are an adaptation to the OMLs.

In a group of benthic crustaceans from the seas off California, there is a small decline in metabolic rate with depth

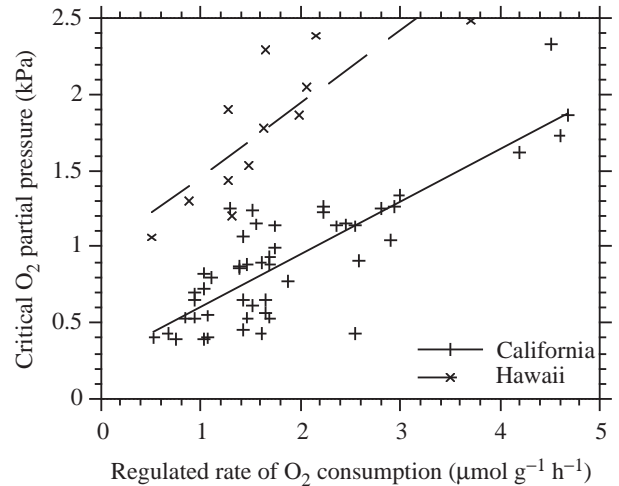


Fig. 5. The relationship between critical O₂ partial pressure (P_c) and regulated rates of O₂ consumption for individuals of the lophogastrid mysid *Gnathophausia ingens* from the seas off California (+) (minimum P_{O_2} approximately 0.8 kPa) and from the seas off the Hawaiian Islands (×) (minimum P_{O_2} approximately 2.7 kPa) (Childress, 1971*a,b*; Cowles *et al.* 1991). The slopes of the regression lines are not significantly different, but the lines are different in elevation (ANCOVA, $P < 0.0001$). The metabolic rates of the two groups are not significantly different at P_{O_2} values above the P_c values (Childress, 1971*a*; Cowles *et al.* 1991).

for the caridian and peneid decapods, but not for the other groups (Childress *et al.* 1990). However, there was no sign of a relationship between metabolic rate and the OML because deeper-living species had comparable or lower metabolic rates. The suggestion has been made that the low metabolic rates (measured or inferred from enzyme activities) of two OML-dwelling benthic species, the Dover sole and *Sebastes alascanus*, are partially adaptations to the OML (Yang and Somero, 1993; Vetter *et al.* 1994). In the case of the Dover sole, this contention rests upon the description of the results of unpublished experiments showing lower metabolic rates and feeding rates in fish acclimated to hypoxia (Vetter *et al.* 1994). In the case of *S. alascanus*, this contention rests on the comparison with a shallower-living scorpaenid species (Yang and Somero, 1993). However, it has been found that a deeper-living congener, *S. altivelis*, has lower levels of glycolytic and Krebs cycle enzymes and therefore presumably a lower metabolic rate while living at higher P_{O_2} values (Siebenaller and Somero, 1982). It may be, as these authors suggest, that benthic fishes are different from pelagic ones and that their reduced metabolic rates are adaptations to the OML, but the definitive test of measuring the metabolic rates of the same or similar species living in regions with higher minimum O₂ content has yet to be carried out.

A case where it is likely that the metabolic rates are reduced in OML inhabitants is where resting stages are in the minimum layer. High concentrations of apparently overwintering stage V *Calanus helgolandicus* copepods have been found in the OML off California and Baja California (Longhurst, 1967;

Allredge *et al.* 1984). It has also been suggested, on the basis of observations from submersibles, that some species of diurnally vertically migrating fishes have reduced levels of activity, 'lethargy' and presumably lower metabolic rates at their daytime depths in the OML (Barham, 1971). Such reduced rates could also play a role in allowing aerobic adaptation to the OMLs without reducing the overall metabolic potential of vertically migrating species. The species for which this is suggested are close to neutrally buoyant and so little metabolic energy would need to go into maintaining their vertical position in the water column. Whether this is an adaptation to the OML or simply an energy conservation mechanism of vertical migrators, it would be expected to be adaptive for aerobic life in the OMLs.

In summary, there are many data indicating that lower metabolic rates in OML species are adaptive, but not adaptations, to the OMLs. There are some other situations where OML animals may have further reduced metabolic rates, but it has not been resolved whether these are evolved adaptations to OML conditions or adaptations to the deep-sea at OML depths which are also adaptive for life in the OML. Anaerobic metabolism appears to be essential to support activity levels above routine levels for many OML species and to support a large part of the metabolic needs of diurnal vertical migrators from regions with O₂ concentrations below 0.20 ml l⁻¹ during their daytime residence in the OML. However, the primary adaptation for life in OMLs with more than 0.20 ml O₂ l⁻¹, as well as an important one for even lower concentrations, is the ability to regulate rates of oxygen consumption to very low O₂ partial pressures.

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