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The role of the oceanic oxygen minima in generating biodiversity in the deep sea

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Abstract

Many studies on the deep-sea benthic biota have shown that the most species-rich areas lie on the continental margins between 500 and 2500 m, which coincides with the present oxygen-minimum in the world's oceans. Some species have adapted to hypoxic conditions in oxygen-minimum zones, and some can even fulfil all their energy requirements through anaerobic metabolism for at least short periods of time. It is, however, apparent that the geographic and vertical distribution of many species is restricted by the presence of oxygen-minimum zones. Historically, cycles of global warming and cooling have led to periods of expansion and contraction of oxygen-minimum layers throughout the world's oceans. Such shifts in the global distribution of oxygen-minimum zones have presented many opportunities for allopatric speciation in organisms inhabiting slope habitats associated with continental margins, oceanic islands and seamounts. On a smaller scale, oxygen-minimum zones can be seen today as providing a barrier to gene-flow between allopatric populations. Recent studies of the Arabian Sea and in other regions of upwelling also have shown that the presence of an oxygen-minimum layer creates a strong vertical gradient in physical and biological parameters. The reduced utilisation of the downward flux of organic material in the oxygen-minimum zone results in an abundant supply of food for organisms immediately below it. The occupation of this area by species exploiting abundant food supplies may lead to strong vertical gradients in selective pressures for optimal rates of growth, modes of reproduction and development and in other aspects of species biology. The presence of such strong selective gradients may have led to an increase in habitat specialisation in the lower reaches of oxygen-minimum zones and an increased rate of speciation. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

High species diversity in the deep sea was first recorded by Sanders et al. (1965) and Hessler and Sanders (1967). This discovery was made possible by advances in

sampling technology that allowed collection of semi-quantitative and quantitative samples of smaller animals (the macrofauna and meiofauna) living in deep-sea sediments (Gage and Tyler, 1991; Gooday et al., 1998). Subsequent observations have confirmed that high species diversity in the deep sea, particularly the benthic macrofauna and meiofauna, is a global feature (e.g., Jumars, 1976; Hecker and Paul, 1979; Rowe et al., 1982; Gage, 1996; Gooday et al., 1998; Paterson et al., 1998). In deep-sea samples, there may be as many as 250 species of macro- and meio-benthic invertebrates in a single square meter of sediment (Smith et al., 1998). Estimates of total species diversity, within the deep sea, have suggested that there may be up to 10 million macrobenthic species (Grassle and Maciolek, 1992; Poore and Wilson, 1993).

Observations have indicated several patterns in the distribution of diversity of deep-sea species. Firstly, the density of all size categories of organisms gradually decreases with increasing distance from the continental shelf (e.g., Hessler and Sanders, 1967; Rex, 1981; Rex et al., 1990). Secondly, the diversity within the deep sea is not evenly distributed amongst phyla, but polychaetes, crustaceans (Peracarida) and molluscs (Bivalvia) form the highest proportions of species in the macrofauna (e.g., Hessler and Sanders, 1967; Grassle and Maciolek, 1992). Finally, species diversity shows a parabolic distribution with depth, reaching a peak in the bathyal zone, before decreasing to the abyssal plain (e.g., Sibuet, 1977; Rex, 1981; Paterson et al., 1985).

The first theories explaining high diversity of deep-sea communities were based on long-term evolutionary processes, particularly extreme niche specialisation in a constant physical environment (the Stability-Time hypothesis; Sanders, 1968). Subsequent hypotheses have concerned the maintenance of high species diversity in the deep sea and have concentrated on processes generating patches over a variety of spatial scales (Thistle, 1998). These have included the generation of patch mosaics by disturbance (e.g., Grassle and Maciolek, 1992; Lamshead, 1993; Snelgrove et al., 1994) or by the activities of deep-sea organisms that modify the benthic environment (e.g., Jumars, 1976; Thistle, 1979; Levin, 1991; Gage, 1996). In the latter case, patches may be extremely small, even down to the ambit of an individual organism (e.g., Levin and Edesa, 1997). Such levels of disturbance lead to a spatially and temporally random mosaic of patches on the deep-sea bed, at differing stages of recovery from disturbance (Gage, 1996). Random, low-intensity recruitment of individuals, from a diverse pool of larvae, to such a patchy community, also characterised by slow growth and low turn over of populations, further enhances local species diversity.

Discussions of the causes of the parabolic pattern of species richness, with depth, have centred on gradients of biological and physical parameters (Pineda and Caswell, 1998). Biological factors that change with depth may include productivity, competitive displacement, predation and disturbance (e.g., Rex, 1981; Gage and Tyler, 1991). Physical factors have included changes in levels of physical disturbance or in features of the physical environment such as sediment particle size (e.g., Paterson and Lambhead, 1995; Etter and Grassle, 1992). Recently, the possibility that a random distribution of species between two boundaries (shallow water/abyss) has given rise to the parabolic pattern of diversity has been discounted (Pineda and Caswell, 1998). This study also revealed significant differences in distribution patterns between different faunal groups (e.g., gastropods and polychaetes). Some studies of diversity have not

revealed parabolic patterns with depth (e.g., Hessler and Jumars, 1974; Jumars and Hessler, 1976). Observations of decreasing diversity, moving from bathyal to abyssal depths, may have arisen from limited sampling of very low-density communities (Gage and Tyler, 1991).

Much of the work recently carried out on the diversity of the deep-sea benthos has examined mechanisms maintaining diversity. The present paper is intended to provide an evolutionary perspective on the role of oxygen and oxygen-minimum zones in the generation of high species diversity and patterns of diversity distribution in the deep sea. It is intended to take into account the role of oxygen minima in the evolution of species, in the deep sea, over long periods of time (macroevolutionary processes). It is also intended to elucidate the role of oxygen minima in maintaining species diversity in the present day and also in influencing microevolutionary processes such as selection and/or the promotion or restriction of gene-flow between populations.

2. Temporal and spatial occurrence of oxygen-minimum zones and effects on the deep sea fauna

2.1. The present

In the present day, oxygen-minimum zones (oxygen concentration below 0.5 ml l^{-1}) are confined to a number of regions (see Fig. 1). These include the Arabian Sea, the Bay of Bengal, the Philippine region, the northwest Pacific margin, the eastern Pacific and off southwestern Africa beneath the Benguela current (Kamykowski and Zentara, 1990). Hypoxic (oxygen concentrations below 0.2 ml l^{-1}) or anoxic conditions also are found in some shallow-sill basins and trenches such as the Black Sea, the Red Sea, the basins of the California Continental Borderlands and the Cariaco Trench (Wishner et al., 1995; Gorsline et al., 1996). Hypoxic conditions also are found near the outflows of large rivers, in fjords, sea lochs and shelf seas (Diaz and Rosenberg, 1995; Wishner et al., 1995). The scope of this paper is mainly limited to oceanic oxygen-minimum zones, including the shallow sill basins of the Californian Continental Borderland.

Oxygen-minimum layers are formed because of high productivity and poor water circulation. Wyrki (1962) first suggested that the biological degradation of organic matter sinking from the surface consumed oxygen, causing an oxygen-minimum at the depth where horizontal water circulation is poorest. He put forward the hypothesis that oxygen concentrations subsequently increased below this depth because of decreasing biological oxygen demand. His theory has been modified through placing differing emphases on the relative contributions of productivity, circulation and initial oxygen concentration (oxygen solubility) of source water, but it remains substantially unchanged (Sarimento et al., 1988; Kamykowski and Zentara, 1990). In these regions, reduced oxygen conditions generally occur between the near surface, down to 1500 m and occasionally deeper (Kamykowski and Zentara, 1990). Where they impinge on the continental margins, the oxygen-minimum zones occur with or above regions where peak species diversity is expected along the depth gradient (see above).

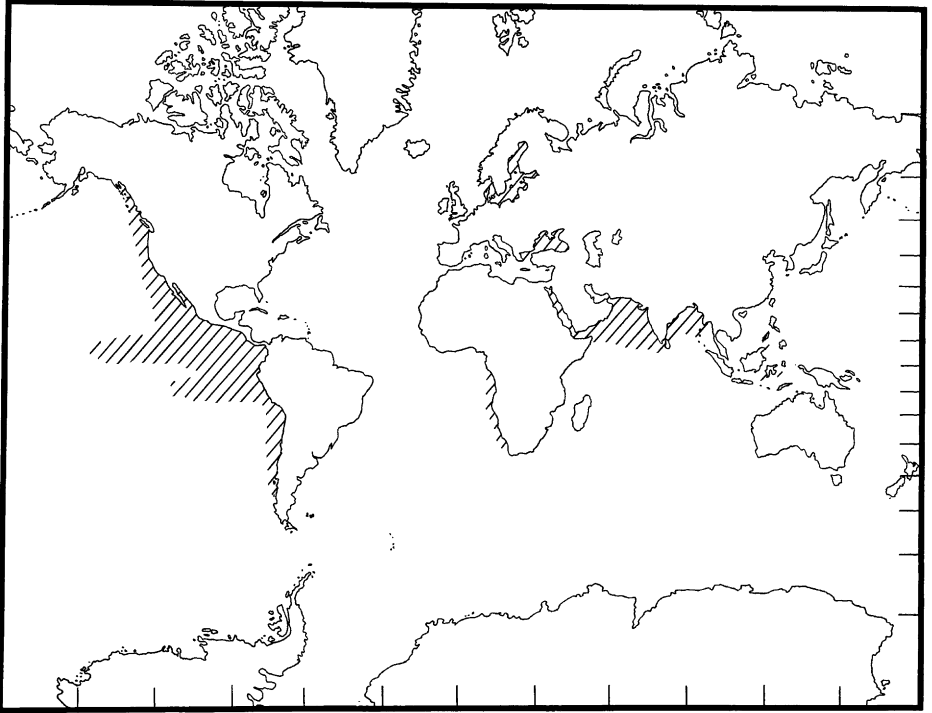


Fig. 1. Map showing distribution of oxygen-minimum zones in the world's oceans (adapted from Kamykowski and Zentara, 1990).

For oxygen-minimum zones to influence the evolution of the deep-sea fauna, species must be affected by environmental hypoxia and anoxia. For marine macrobenthic invertebrates, respiration is generally not affected until oxygen concentrations reach levels of 2 ml l^{-1} or less (Herreid, 1980; Rosenberg et al., 1991; Diaz and Rosenberg, 1995). Below these concentrations, benthic invertebrates show a graded response to increasingly hypoxic conditions. The initial response is often an increase in respiration or activity, followed by migration out of the affected zone, by mobile fauna. Benthic organisms, unable to leave the affected area, may show a range of responses. These include decreased activity not related to respiration (thus lowering metabolism), increased body surface area, decreased depth of distribution, and emergence from tubes or burrows (Diaz and Rosenberg, 1995; Levin et al., 2000; Lamont and Gage, 2000). When conditions become extremely hypoxic, some organisms, such as polychaetes, have the ability to switch to anaerobic metabolic pathways (Mangum and van Winkle, 1973; Warren, 1984). However, no macrofauna can live in persistently severely hypoxic or anoxic environments (Diaz and Rosenberg, 1995). Even if some species can survive prolonged periods of anoxia, they do not complete their life-cycles (Diaz and Rosenberg, 1995).

The macrofauna inhabiting hypoxic sediments, in or around oxygen-minimum zones, in deep water appear to be more tolerant of hypoxic conditions than their shallow-water relatives (Diaz and Rosenberg, 1995). Studies of the oxygen-minimum zones off the coasts of Peru, California and Oman have shown that abundant communities can exist at oxygen concentrations from 0.6 to 0.2 ml l⁻¹ (Rosenberg et al., 1983; Mullins et al., 1985; Levin et al., 2000). On the seamount Volcano 7, which penetrates the oxygen-minimum zone in the eastern Pacific, an abundant but low diversity community of macrofauna has been sampled where oxygen concentrations have been measured at 0.11–0.16 ml l⁻¹, (Wishner et al., 1990; Levin et al., 1991). Levin and Gage (1998) have reviewed the relationships between oxygen concentration, organic matter and the diversity of the deep-sea macrobenthos in the North Atlantic, East Pacific and Indian Oceans. Their findings also have indicated that the effects of hypoxia on macrobenthic diversity are relatively minor down to oxygen concentrations of < 0.45 ml l⁻¹ (Levin and Gage, 1998).

Species inhabiting oxygen-minimum zones may survive very hypoxic and occasionally anoxic conditions because of the very high quantities of organic matter available in these regions. This may have allowed species to evolve energetically expensive adaptations to cope with life in a low-oxygen environment (Diaz and Rosenberg, 1995). Such large amounts of organic matter may not be available to animals in shallow-water hypoxic environments, and so they may not be able to adapt to conditions of extreme hypoxia (Diaz and Rosenberg, 1995).

Despite hypoxia-tolerant species inhabiting oceanic oxygen-minimum zones, studies have revealed that low oxygen availability has a dramatic impact on benthic communities (Levin and Gage, 1998). Many studies on the fauna inhabiting oxygen-minimum zones have shown a decrease in community abundance and biomass at depths associated with lowest oxygen concentrations (e.g., Peru, Rosenberg et al., 1983; California, Mullins et al., 1985; Volcano 7, Wishner et al., 1990,1995; Levin et al., 1991). In several cases, a peak in abundance has been observed at the upper and/or lower boundaries of the oxygen-minimum zone (e.g., Mullins et al., 1985; Wishner et al., 1990,1995; Levin et al., 1991). This is not apparent off the coast of Oman, though the lower boundary of the oxygen-minimum zone is associated with increased levels of biological activity (Smith et al., 2000).

Community structure is also greatly influenced by the presence of oxygen-minimum zones. In many cases, species diversity has been shown to decrease and species dominance to increase within the cores of oxygen-minimum zones (e.g., Rowe, 1971; Rosenberg et al., 1983; Mullins et al., 1985; Wishner et al., 1990; Gooday et al., 2000; Levin et al., 1991,2000). The taxonomic composition of the benthic community also changes within oxygen-minimum zones. For example, polychaete and nematode worms tend to dominate the macrofaunal and metazoan meiofaunal communities at the cores of oxygen-minimum zones (e.g., Rowe, 1971; Rosenberg et al., 1983; Mullins et al., 1985; Wishner et al., 1990,1995; Levin et al., 1991,2000). Many taxa, especially those with calcified shells or exoskeletons, tend to be absent from the cores of oxygen-minimum zones (e.g., Rosenberg et al., 1983; Levin et al., 2000). Some calcareous taxa do occur in oxygen-minimum zones, such as foraminiferans and the mussel *Amygdallum* sp., though these are generally exceptional specialists of such

environments (e.g., Levin et al., 2000; Gooday et al., 2000). The “life styles” exhibited by species inhabiting oxygen-minimum zones also tend to be different to those living above or below the depths associated with reduced oxygen. Within the macrofauna, low oxygen communities tend to be dominated by surface-feeding organisms rather than those feeding below the sediment surface (Levin et al., 2000). Observations also have indicated that some taxa have a tendency to construct and inhabit surface structures, such as mudballs or nests (e.g., Gage, 1995; Levin and Edesa, 1997; Levin et al., 2000). Many of these trends have been observed in all size categories of the benthic fauna (e.g., Levin et al., 1991; Gooday et al., 2000).

Relatively few taxa have adapted to conditions in the core of oxygen-minimum zones, which include hypoxia, high sulphide concentrations and other limiting physical conditions. Large amounts of undegraded organic matter mean an abundant food supply for those species that inhabit these regions (e.g., Levin and Gage, 1998; Gooday et al., 2000). The strong gradient in oxygen and organic matter concentrations, at the upper and lower interfaces of oxygen-minimum zones, lead to a zonation of species distribution and are also responsible for the peaks in abundance and diversity at the upper and lower boundaries (see above). Oxygen-minimum zones must, therefore, influence speciation in the deep sea, either through geographic restriction of populations or through selection for tolerance to oxygen deficiency (see below).

It is apparent, from studies on deep water (and shallow water) environments, that different taxa have different tolerances to hypoxia. Differences in tolerance to hypoxia occur at a range of taxonomic levels, from species within the same genera or families to the level of phylum. The metazoan meiofauna in general have been found to be more tolerant of hypoxic conditions than the macrofauna, both in deep-sea and shallow-water habitats (Elmgren, 1975; Josefson and Widbom, 1988; Levin et al., 1991). In these cases, it is probably the nematodes that are responsible for the greatest penetration into oxygen deficient environments, as they are extremely tolerant of hypoxia and even periods of anoxia (Levin et al., 1991; Diaz and Rosenberg, 1995; Gooday et al., 2000). The influence of oxygen-minimum zones on nematode abundance can be comparatively small, and in some cases they exhibit higher densities within oxygen-minimum zones than outside them (Levin et al., 1991). Other members of the metazoan meiofauna, especially the harpacticoid copepods, are much less tolerant of hypoxic conditions (Levin et al., 1991; Diaz and Rosenberg, 1995). Some taxa within the protozoan meiofauna are also highly tolerant of reduced oxygen conditions (e.g., rotaliid foraminiferans; Rosenberg et al., 1983; Gooday et al., 2000). As with nematodes, these groups can reach their highest abundances in the core of oxygen-minimum zones (e.g., Gooday et al., 2000).

Within the macrofauna the polychaetes are the most hypoxia tolerant taxon, followed by the bivalves and then the crustaceans (Diaz and Rosenberg, 1995; Jacobs and Lindberg, 1998; Levin and Gage, 1998). This is apparent in the deep-sea studies outlined above and also in studies on shallow-water habitats (e.g., Gray et al., 1988; Llansó, 1992). Observations also have shown that different stages in the life history of a species can have different tolerances to hypoxia (see below). The specific influences of oxygen-minimum zones, on micro- and macro-evolutionary processes, in different taxa, are likely to be related to the different levels of oxygen tolerance displayed by them.

2.2. *The past*

If levels of oxygenation affect species distribution, it is possible that past variations in oxygen concentrations have influenced the evolution and diversity of the deep-sea fauna. To examine this possibility, a relationship must be established between the diversity of marine species in the fossil record and past fluctuations in oxygenation of the marine environment. This is possible through the use of palaeoecological and geochemical methods (Allison et al., 1995).

Palaeoecological methods involve examination of the taxonomic composition of fossil faunas, fossil morphology and bioturbation associated with sedimentary deposits. Rhoads and Morse (1971) hypothesised that benthic faunal diversity decreased with declining oxygen levels. Furthermore, calcareous shelled taxa were preferentially eliminated from low oxygen conditions. Thus, past oxygen levels may be assessed by the taxonomic composition of fossil faunas. The model proposed by Rhoads and Morse (1971) has been refined over the last 25 yr (e.g., Savrda et al., 1984; Levin et al., 1991), but it is accepted that the systematic composition of a fossil fauna can indicate past levels of environmental oxygenation. However, physical factors other than oxygen concentration can have a strong influence on faunal composition. Also, the environmental preferences of present day taxa may not be the same as the preferences of ancestral taxa (Allison et al., 1995). Morphology of burrows of soft-bodied infauna also can be used to assess levels of palaeo-oxygenation. In increasingly hypoxic conditions, the burrows of the infauna become smaller and shallower to the extent that burrow diameter can be used as a simple indicator of oxygen levels (Savrda and Bottjer, 1986). In anoxic conditions it is likely that no metazoans will be able to exist, leading to the deposition of unbioturbated, laminated sediments (e.g., Gorsline et al., 1996; Rohling et al., 1997).

Several geochemical methods can be used to estimate palaeo-oxygen levels. The occurrence of high total organic-carbon content (TOC) in sediments occurs when anoxia inhibits the decay of surface-derived organic matter deposited on the seabed (Curtis, 1980). This method has been used to estimate levels of palaeo-oxygenation, but it has been subject to question as other physical/biological conditions can lead to enrichment of sediments with organic carbon, especially high surface productivity (e.g., Pedersen and Calvert, 1990). Other methods include analysis of the presence or absence of elements that are preferentially concentrated in sediments under particular conditions of oxygenation. For example, cerium is concentrated in sediments under oxic conditions relative to other rare earth elements (e.g., Wright et al., 1987). Uranium is concentrated in sediments under anoxic conditions (e.g., Wignall and Myers, 1988). Increasing levels of hypoxia also are related to increasing levels of pyritization in sediments. This has been quantified as the degree of pyritization (DOP) and has also been used to determine levels of palaeo-oxygenation (Raiswell and Berner, 1985). This method, however, is complicated by sedimentation rates during deposition and by weathering of rocks (because of rapid oxidation of pyrite) (e.g., Allison et al., 1995).

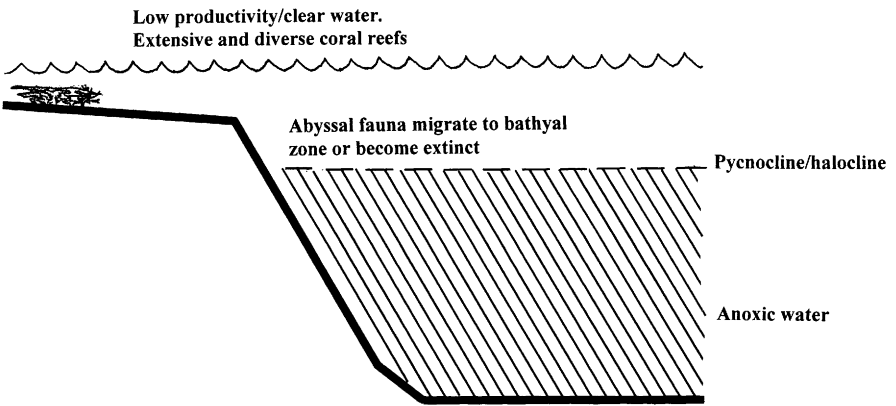
Because of the limitations of any one technique for assessing palaeo-oxygen levels, the best approach is the use of a combination of palaeoecological and geochemical

methods (Allison et al., 1995). Using a combination of techniques, it is possible to assess the influence of palaeo-oxygen levels on events that have occurred during the evolution of marine taxa. It is apparent from the fossil record that extinctions and radiations of marine taxa are episodic. These extinctions and radiations form the basis of biostratigraphy and in many cases major bio-events coincide with major litho-events (changes in rock facies) and inferred changes in climate (Barnes et al., 1996). Table 1 details some points in the stratigraphic record where major changes in the marine fauna and flora coincide with significant changes in palaeo-oxygen levels. It is apparent that major extinction or radiation events among marine taxa are often associated with periods of widespread putative anoxia in the marine environment, or the onset of fully oxygenated conditions. These periods are associated with periods of global warming or cooling and periods of sea level rise or fall, respectively (Barnes et al., 1996).

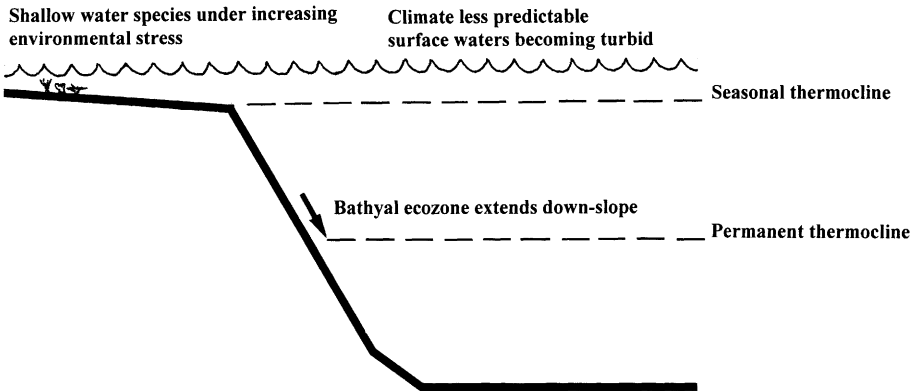
Such events have been studied by palaeontologists investigating periods of extinction and radiation in a number of marine fossil faunas. For example, marine conodonts and trilobites underwent a number of marked extinctions during the Ordovician and Silurian (Jeppsson, 1990; Chatterton et al., 1990; Armstrong, 1996; Berry, 1996; see Table 1) when major climatic changes are thought to have led to cyclical changes in the physical structure of the oceans. Atmospheric and oceanic conditions may have fluctuated between two states (see Fig. 2). During warm phases (the S-state), the oceans were characterised by high sea levels and a salinity-stratified and poorly ventilated ocean (Bralower and Thierstein, 1984). During cool phases (P-state), high-latitude temperatures fell to $< 5^{\circ}\text{C}$ and dense, cold, oxygenated waters descended into the deep oceans (Schopf, 1980). This coincided with thermal stratification in the oceans, and a fall in sea level, as water became locked up in the ice caps (Armstrong, 1996). In the Late Ordovician, evidence suggests that the Earth passed from a prolonged S-state, a short P-state, and back to an S-state (Armstrong, 1994).

Following patterns of extinction and radiation of conodonts and other taxa in the fossil record, models for the extinction, radiation and re-emergence of taxa during cycles of global warming and cooling through the Late Ordovician and Early Silurian have been developed (Jeppsson, 1990; Armstrong, 1996). During periods of global warming (S-state, Fig. 2), without deep, cold, circulation originating from the poles, the deep sea may have become anoxic (e.g., Railsback et al., 1990). Elements of the abyssal fauna unable to migrate up the continental slope, into the bathyal zone, may have become extinct (Armstrong, 1996). High sea levels on the continental shelves led to the development of extensive coral reefs, with a diverse reef and shallow water fauna (shallow speciation or cladogenesis). The cooling of the climate led to a transformation from the S-state to the P-state (Fig. 2). A seasonal, shallow thermocline developed, replacing the pycnocline/halocline, along with the development of a deeper, permanent thermocline. Bathyal taxa may have expanded their distribution down the continental slope, and a period of speciation occurred (Armstrong, 1996). The shallow extensive shelf reefs and other fauna (and flora) became increasingly stressed as sea levels fell, water became more turbid, and climatic conditions on the shelf became less predictable. The completion of these processes came about with the establishment of the P-state. Low temperatures at high latitudes led to the sinking of

S-State



Transition S-state to P-state



P-state

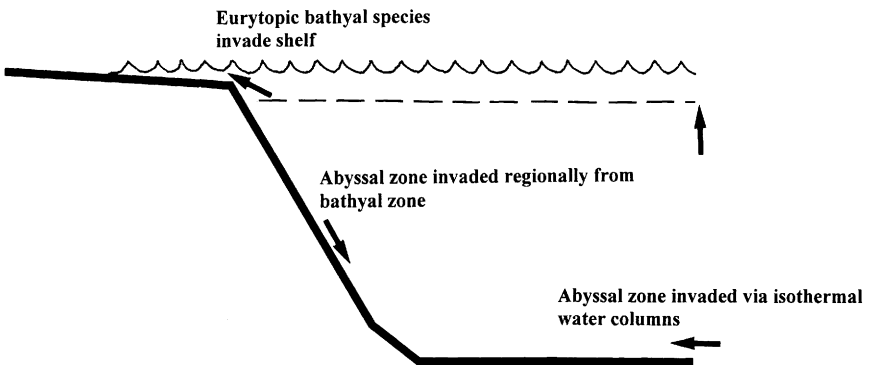


Fig. 2. Model for fluctuations from warm ocean (S-state) to cold ocean (P-state) conditions (adapted from Jeppsson, 1990; Armstrong, 1996).

dense, cold, oxygen-rich seawater to abyssal depths, allowing the invasion of this area by bathyal taxa (Fig. 2). Many shelf species became extinct or restricted in their distribution to warm refugia. These extinctions may have been enhanced by competition with eurytopic bathyal species, previously restricted to below the thermocline, which invaded the shelf (Armstrong, 1996). A return to global warming conditions would allow the eurytopic (previously bathyal) species to expand on to the shelf and deeper bathyal species to migrate on to the shelf. Shallow-water species that had survived the P-state in refugia reappeared in the fossil record (Armstrong, 1996).

The model proposed for the Ordovician–Silurian extinctions (Jeppsson, 1990; Armstrong, 1996) can be applied to other extinction/radiation events in the fossil record, from the Cambrian to the Triassic (see Jeppsson, 1990). It also can be applied to more recent events, such as major extinctions, of deep-sea taxa, that occurred during the Cretaceous and the Late Palaeocene/Early Eocene (Douglas and Woodruff, 1981; Kaiho, 1988; Kennett and Stott, 1991; Speijer, 1994). The driving forces for such global cyclic events are unclear at present, but appear to be related to cycles of atmospheric temperature fluctuation and carbon uptake and release by the oceans (Jeppsson, 1990).

There are a number of problems with the application of such models to the deep sea. Firstly, tectonic plate subduction means that such models invariably rely on fossil evidence from shallow water faunas, especially for more ancient events. Anoxic or dysoxic conditions may have arisen in such faunas through the growth of oxygen-minimum zones that may not have expanded to full ocean depth (e.g., White, 1987). Furthermore, exchange of oxygenated waters with the deep sea may occur through vertical thermohaline circulation at low latitudes, as in the Mediterranean (e.g., Young et al., 1997b; Wilson, 1998). Sinking of cold water at the poles is not necessarily the only route for oxygen into the deep sea.

For the Mesozoic extinctions of the Cenomanian/Turonian (see Table 1), a few core/rock sections are available for study (Jacobs and Lindberg, 1998). Fossil benthic Foraminifera, in one such section from Japan have been used to indicate palaeo-oxygen levels through examination of the wall thickness of calcareous species (Kaiho and Hasegawa, 1994). These fossils were deposited at an estimated 600 m depth (upper bathyal zone). This study indicates that oxygen levels may have reached as low as 0.1 ml l^{-1} and were probably the cause of significant extinctions of Foraminifera in this region. This area was on a western ocean boundary where oxygen minima, associated with upwelling, do not usually occur (Kaiho and Hasegawa, 1994). Organic, carbon-rich, sediments originating at this time have been recovered from the shelf, and deep sea in both the Atlantic and Pacific oceans. The only area from which organic-rich sediments have not been recovered are the centre of the Pacific gyres, which are characterised by low productivity and sedimentation (reviewed by Jacobs and Lindberg, 1998). This raises two salient points to the present discussion. Firstly that anoxia in the deep sea, at a regional scale, may be related to patterns of surface productivity. Secondly, conditions of oxygenation were not uniform throughout the world. During the Mesozoic, the deep Atlantic Ocean and Tethys Seas had limited connection to other oceans, so these basins in particular may have been subject to anoxic/dysoxic conditions (Jacobs and Lindberg, 1998). This emphasises that

Table 1

Periods of geological time record with inferred major bio-events and fluctuations in oxygen concentrations in marine environments (extracted from Murray, 1985; Barnes et al., 1996)

Era	Period	Epoch	Age	Bio-event	Oxygen
Cenozoic	Quaternary	Holocene			
Cenozoic (Tertiary)	Neogene	Pliocene	Piacenzian Zanclian		
		Miocene	Messinian Tortonian Serravalian Langhian Burdigalian Aquitanian		
	Palaeogene	Oligocene	Chattian Rupelian		
		Eocene	Priabonian Bartonian Lutetian Ypresian		
		Palaeocene	Thenetian Danian	Extinctions of deep-sea taxa.	Depletion of oxygen in deep-sea
Mesozoic	Cretaceous	Upper	Maastrichtian	Extinctions of plankton, final extinction of ammonites, belemnites and some bivalve groups	Diminishing greenhouse conditions (oxygen increase)
			Campanian	Moderate turn over of marine faunas	Oxygen depletion event
			Santonian	Moderate turnover of marine faunas	End of oxygen depletion event
			Coniacian	Extinctions of molluscan groups and corals	End of oxygen depletion event
			Turonian Cenomanian	Major extinction event, plankton, molluscs and corals	Shifts between global warming and cooling
		Lower	Albian Aptian Barremian Hauterivian Valanginian Ryazanian	Extinctions of ammonites	Widespread marine oxygen depletion
	Jurassic	Upper	Tithonian Kimmeridgian Oxfordian		

Table 1 (continued)

Era	Period	Epoch	Age	Bio-event	Oxygen	
Palaeozoic	Permian	Middle	Callovian Bathonian Bajocian Aalenian			
		Lower	Toarcian Pliensbachian Sinemurian Hettangian			
		Triassic	Upper	Rhaetian Norian Carnian		
			Middle	Ladinian Anisian		
			Lower	Scythian		
			Tartarian	Highest order extinction event (80% familial extinction)	Dysaerobic conditions widespread	
		Carboniferous (Pennsylvanian)	Silesian	Kazanian	Major extinctions (Tethyan Bryozoa, trilobites, brachopods)	
				Ufimian		
				Kungarian		
				Artinskian		
				Sakmarian	Extinction of Arctic-Tethyan Foraminifera, development of eastern tethyan fauna	
				Asselian		
Stephanian						
Westphalian Namurian						
Carboniferous (Mississippian)	Dinantian	Namurian	Major extinctions of ammonites and other groups			
		Visean				
Devonian	Devonian	Tournaisian	Major extinctions of ammonites	Spreading of black shales		
		Famennian	Major extinctions in ammonites and many other groups	Anoxic events		
		Frasnian	Major extinction event many fossil groups	Intensive anoxic event		
		Givetian				
		Eifelian	Major extinctions in many groups, turnover in conodont taxa	Onset of anoxic conditions		

Table 1 (continued)

Era	Period	Epoch	Age	Bio-event	Oxygen
			Emsian Siegenian Gedinnian	Loss of diversity in many marine groups	Anoxic event
	Silurian	Pridoli Ludlow Wenlock			
		Llandovery		Extinction among conodonts, maximum diversity of graptolites	Increase in anoxia of deep-sea
	Ordovician	Ashgill Caradoc Llandeilo Llanvirn		Major extinction – all fossil groups	Fluctuation from anoxic- oxic conditions
		Arenig		Major extinction of conodonts, graptolites and trilobites	Increased oxygenation in deep-sea
		Tremadoc		Major radiation of conodonts, nautiloids, trilobites and graptolites	Deposition of black shales
	Cambrian	Merioneth	Trempealeuan Franconian Dresbachian		
		St Davids	Mayan Amgan		
		Comley	Toyonian Botomian Atdabanian Tommotian Manykayan	Mass extinction of shallow water reef fauna and other taxa	Anoxia and flooding of nearshore reefs

present-day oceans have very different (oxygen) histories, and this may have had different influences on regional deep-sea diversity.

A more recent extinction event in the deep-sea fauna occurred in the Palaeocene/early Eocene, which has been recorded in Foraminifera (Douglas and Woodruff, 1981; Kaiho, 1988; Thomas, 1989; Kennett and Stott, 1991). This event was very widespread and possibly even global in extent (Jacobs and Lindberg, 1998). Furthermore, the extinction appears to have been largely restricted to benthic deep-sea species rather than shallow-water planktonic species (Kennett and Stott, 1991). Isotopic analysis has been carried out on foraminiferans from Antarctic cores, containing sediments laid down between 1000 and 2500 m depth (Thomas, 1989). These have indicated that

periods of extinction were associated with high temperatures (Kennett and Stott, 1991). The foraminiferan fauna surviving, during this period, were characteristic of low-oxygen/high organic-carbon conditions (Thomas, 1989). During this time, there was a brief period where conditions of deep-ocean circulation and ventilation changed markedly, producing low-oxygen conditions, in at least some, or many regions around the world (Thomas, 1989; Kennett and Stott, 1991). Ocean ventilation may have been achieved through the sinking of dense, saline waters at lower latitudes (Thomas, 1989). Even if this were the case, oxygen concentrations in deep water must have been reduced, as deep-water temperatures would have been relatively high.

Anoxic events have been recorded on a regional basis as recently as < 10,000 yr before present. Analysis of cores from the Adriatic have shown that increases in productivity, coupled with a decrease in deep-sea ventilation, led to anoxic and azoic conditions in deep water for approximately 900 yr (Rohling et al., 1997). Small changes in sea-surface temperature, atmospheric humidity and surface salinity probably reduced or eliminated the sinking of dense surface waters into the deep Adriatic. This event may have occurred throughout the deep sea in the eastern Mediterranean (Rohling et al., 1997).

Cycles of expansion and contraction of oxygen-minimum zones, on such a large scale, may have contributed significantly to the patterns of diversity observed in the deep-sea fauna today. The abyssal fauna, in particular, will have suffered from very high extinction rates during periods of deep-sea hypoxia or anoxia. The levels of these extinctions must have depended on the extent and severity of hypoxia or anoxia at abyssal depths. In extreme cases, only taxa within refugia or those able to move up the continental rise and slope survived to reinvade the abyssal zone, in later periods of deep oxygenation. Note, this is in contrast to the theory put forward by Madsen (1961), who suggested abyssal faunas in the past, were eliminated, by adverse temperatures, when the deep oceans were inundated with cold polar waters. It agrees, however, with the view put forward by Murray (1895) that the deep sea had been anaerobic in the past and had been only recently colonised. The vast area of the abyssal zone occupied by an impoverished fauna would be subject to invasion by eurybathic taxa through isothermal water columns, such as those at the poles (Wilson, 1998), or isohaline water columns, such as in the Mediterranean (Young et al., 1997b). In particular, species with dispersive lecithotrophic or planktotrophic larvae, with a wide tolerance to pressure, may have been able to colonise the abyssal zone very rapidly (Tyler et al., 1995; Young et al., 1997a; Tyler and Young, 1998). This may partially explain the low diversity of the abyssal fauna compared with that of the slope and shelf in some of the world's oceans. It also may suggest why many elements of the abyssal fauna are relatively recent, as suggested by Madsen (1961; also see below).

Compared to the abyssal and shelf faunas, the bathyal fauna may have shown lower extinction rates during fluctuations between S-state and P-state oceans. Periods of movement up the slope, during S-state phases, and periods of invasion of deeper areas of the slope and areas of the shelf, during P-state phases, also have provided the bathyal fauna with repeated speciation events. Armstrong (1996) suggested that during the invasions of deeper slope areas, during the onset of P-state phases, decrease population densities, as greater areas of habitat became available, promoted

parapatric speciation. Many characteristics of slope environments, discussed in relation to maintenance of high diversity (see above) and the intrinsic characteristics of the life histories of many bathyal taxa, are also likely to have promoted speciation during such transitions. Repeated opportunities for speciation, in bathyal taxa, are likely to be reflected in evidence from fossil records or from morphological or molecular systematics. This also places great importance for the bathyal zone as a source of colonisers for the shelf and abyssal zones (e.g., Zezina (1997, but see below)).

The lower species diversity of shelf faunas compared to bathyal faunas (except in warm water coral reef refugia and in areas where oxygen-minimum zones impinge on the continental slope) may reflect higher extinction rates in shallow water. This is because of the long-term environmental fluctuations described above, and the fact that we are currently in a P-state phase. Changes in patterns of onshore–offshore diversity over geological timescales are well recorded for many fossil groups (e.g., Jablonski and Bottjer, 1988; Sepkoski, 1991). Observations indicate that many taxa (especially higher taxa) originated in nearshore environments and subsequently colonised deeper, offshore, habitats (and subsequently radiated). Many of these groups subsequently retreated into the deep sea, leaving few or no representatives in shallow-water (Jablonski and Bottjer, 1988; Sepkoski, 1991). Gradients in long-term extinction rates between shallow-water and bathyal environments have been suggested as the principle cause of changes in onshore–offshore patterns of faunal diversity through geological time (e.g., Sepkoski, 1991).

Changes in ocean ventilation may explain some of the conclusions drawn in regard to the recent evolution of specific groups of deep-sea organisms. Isopods are a group that have been well researched in the deep sea (e.g., Hessler and Thistle, 1975; Hessler and Wilson, 1983; Poore and Wilson, 1993; Wilson, 1998). The suborder Asellota is important principally through the contributions of the superfamily Janiroidea (Paraselloidea) which contains 22 families, 14 of which are almost exclusively restricted to the deep sea (Wilson, 1998). Of the 14 families within the Janiroidea, 7 are endemic to the deep sea, whilst the other seven only have shallow-water representatives at high latitude, where the water column is isothermal (e.g., Hessler and Thistle, 1975; Hessler and Wilson, 1983; Wilson, 1998). In discussion the origin and radiation of the Janiroidea in the deep sea, Hessler and Thistle (1975) indicated that the present day members of several families probably originated from indeterminate shallow water localities and invaded the deep sea through isothermal/isohaline water columns. Furthermore, they suggested that the lack of eyes in shallow water species from 12 of these families indicates a reinvasion of shelf habitats by some of these deep-water taxa (Hessler and Thistle, 1975; Hessler et al., 1979). It would appear that the Janiroidean isopods have been present in the deep sea for a long time (Wilson, 1998) and provide a good example of a group of animals that have shifted their distribution up and down the shelf, creating opportunities for multiple speciation events.

Studies of the isopod suborder Flabellifera (see Wilson, 1998) indicate a different pattern of expansion into the deep sea. This group has a low diversity in the deep sea, with no endemic deep-sea families (Wilson, 1998). Wilson (1998) considered it likely that representatives of this suborder invaded the deep sea sometime during the mid-Tertiary, after the generation of isothermal water columns at high latitudes

(following the Palaeocene anoxic events described above). This is also probably responsible for differences in patterns of regional occurrence between the Asellota and Flabellifera. The flabelliferans are more speciose in the deep sea in the Southern Hemisphere than in the northern, whilst the asellotans do not show such a distribution (Wilson, 1998). It is likely that the flabelliferans are in a state of ongoing invasion of the deep sea through vertical transmigration, whilst the distribution of the Asellota was determined largely prior to the Tertiary (Wilson, 1998).

The echinoderms and particularly the holothurians are well represented amongst the deep-sea megafauna (Gage and Tyler, 1991). Gebruk (1994) suggested that the elasipodid holothurians originated from shallow-water ancestors that inhabited the Tethys Sea. Species invaded the bathyal zone from this region, and their distribution extended to the Antarctic from where they invaded the abyssal zone via the isothermal water column, when conditions had become sufficiently cold to set up a P-state ocean (Gebruk, 1994). This pattern fits with the kind of recolonisation of the abyssal zone expected during transitions from an S-state to a P-state. The invasion of the abyssal zone by elasipodid holothurians may have been aided by their possession of dispersive lecithotrophic larvae (Young et al., 1997a). Similar patterns of invasions of the abyssal zone also have been suggested for many other taxa (e.g., the nuculanid bivalves; Madsen 1961).

France and Kocher (1996) cite oxygen as a factor in the evolution of amphipods within the *Eurythenes gryllus* species complex, in the deep sea. Their observations, based on analysis of 16s rDNA sequence data, have indicated that abyssal populations of *E. gryllus* (> 3200 m depth) are genetically similar. This suggests a single, recent, invasion event of the abyssal zone. This would fit a colonisation of the abyssal zone following the onset of cool (P-state) conditions via isothermal water columns at high latitudes by *Eurythenes* sp., in a similar manner to the flabelliferan isopods and the elasipodid holothurians. In the case of *Eurythenes* sp., dispersal is more likely to have occurred via the highly mobile adult stage, as amphipods brood their young. In contrast, bathyal populations (species) showed a much higher degree of genetic differentiation, suggesting multiple speciation events and isolation between (and within) ocean basins (France and Kocher, 1996), as would be expected under the model proposed by Jeppsson (1990) and Armstrong (1996).

The model put forward by Jeppsson (1990) and Armstrong (1996) is different to the deep-allopatry hypothesis of White (1987). In this model, it is proposed that oceanic oxygen minima did not expand to abyssal depths but acted to isolate populations in disjunct, oxygenated refugia. White (1987) suggested that populations were pushed offshore by expanding oxygen minima (see Fig. 3). The model presented by Jeppsson (1990) is more extreme, but is plausible based on evidence for global anoxic events such as those in the Ordovician/Silurian and Cretaceous periods. Incidents of deep-sea hypoxia, rather than anoxia, also may have occurred in the Palaeocene/Eocene (see above), though judging from the levels of extinction, this event must have been severe (Kennett and Stott, 1991). Furthermore, Jeppsson (1990) suggested that a third intermediate ocean-state may have arisen when cold conditions at high latitudes produced water that sank but was not sufficiently dense to replace bottom water (presumably high salinity, dense water originating at lower latitudes). In such a case,

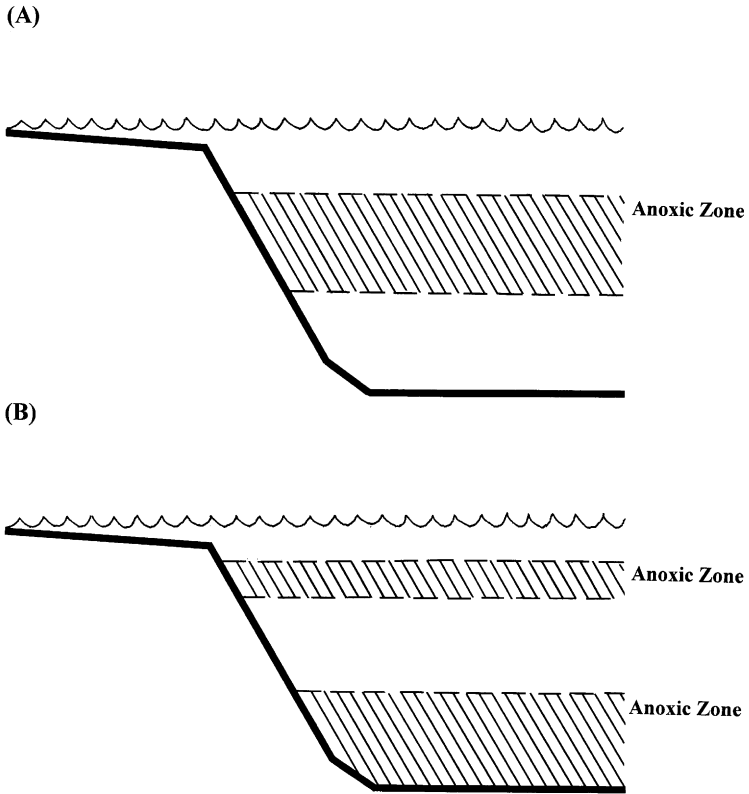


Fig. 3. Alternative models for ocean structure in the past. (a) Expansion of oxygen-minimum zones to produce a “mid-water” anoxic zone as in White (1987); (b) intermediate condition between S-state and P-state where mid-water and shallow water are oxygenated as in Jeppsson (1990).

water originating from high latitudes may have formed a middle layer (see Fig. 4). The deepest areas of the benthos would have remained anoxic, but the lower shelf and bathyal regions may have become well oxygenated. Such a scenario would present similar opportunities for allopatric speciation as in the model proposed by White (1987). It is possible that different permutations of all these models may have occurred during evolutionary history.

Superimposed on these events were shorter term cycles, such as the 41,000 yr cycle in deep-sea ostracod diversity that has been related to orbitally forced changes in surface productivity (Cronin and Raymo, 1997). Other complexities, such as the drifting of the continents and uneven reversal of hypoxic/anoxic conditions around the globe (e.g., Jeppsson, 1990) also are likely to complicate the broad picture of the role of oxygenation in the evolution of species in the deep sea (White, 1987). Indeed, such geographic variation, in the advance and recession of anoxia or hypoxia in the

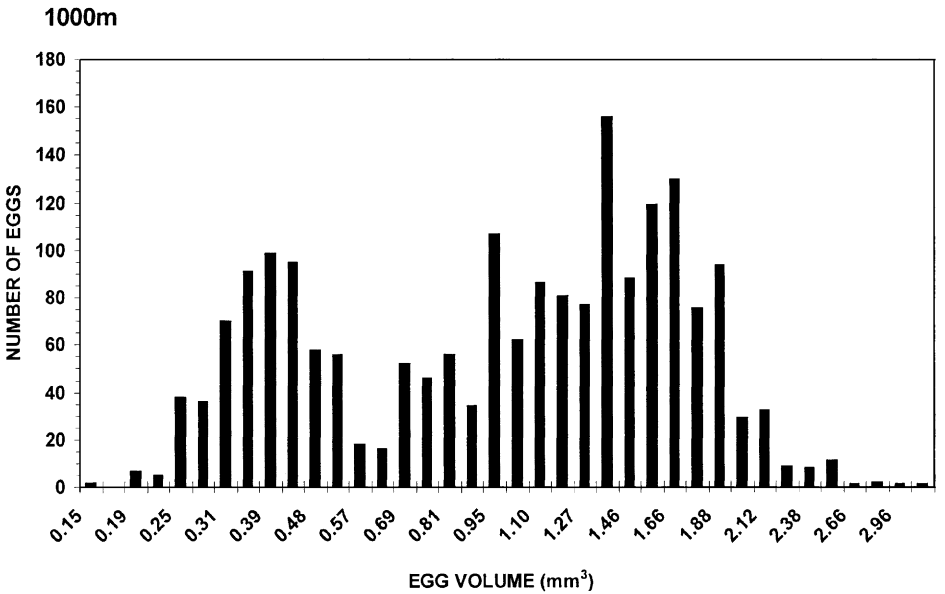
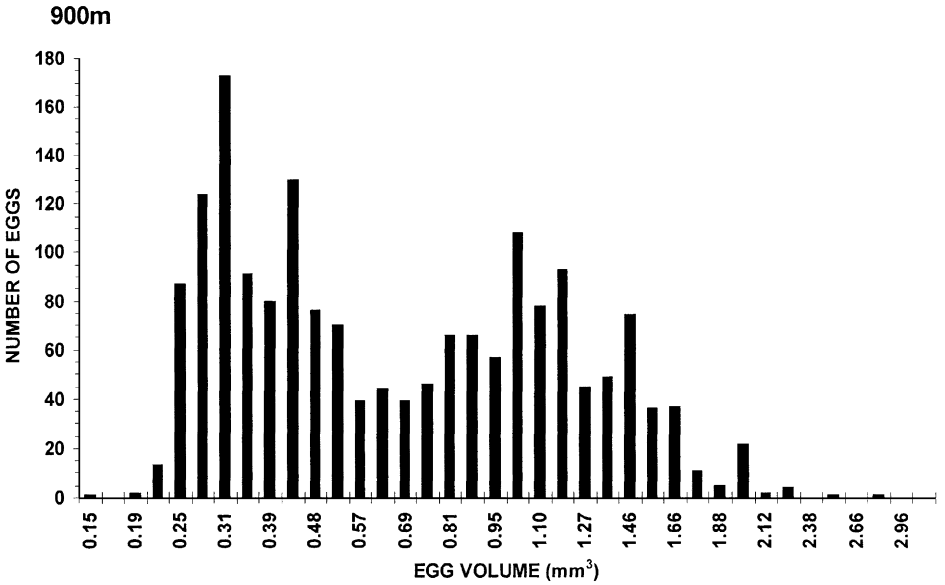


Fig. 4. *Munidopsis scobina*. Size frequency of eggs from ovigerous non-parasitised individuals from 900 and 1000 m depth off the coast of Oman in the Arabian Sea. From Creasey (1998) with permission from the author.

abyssal/lower bathyal zone, is another mechanism for allopatric speciation. Also, recent evolution and patterns of diversity are affected by the multiplicity of physical factors and biological interactions as outlined above. This model provides a mechanism that may have contributed to the broadest patterns of evolution of high species diversity in the deep sea and patterns of species diversity with depth. Studies of the influences of environmental changes on ocean ventilation and changes in the deep-sea fauna, in the past, may provide important clues to present day deep-sea climatic change.

3. The present influence of oxygen-minimum zones on evolutionary processes in deep sea populations

3.1. *Oxygen minima as a barrier to gene-flow*

During times of global warming, species adapted to life in hypoxic conditions may have been more widespread (White, 1987). The distribution of such species would become restricted to the oxygen-minimum zones associated with upwellings and other high productivity/poor circulation areas, as cooler atmospheric conditions developed. This would, and probably still does, present opportunities for allopatric speciation and explains the high proportion of endemic species in some faunas characteristic of oxygen-minimum zones, today (e.g., eastern tropical Pacific; White, 1987 and refs. therein). Oxygen-minimum zones are island-like habitats in the sense that they are only located in regions of upwelling and poor circulation and are separated from each other by large geographic distances, continental barriers and by oxygenated water.

An example of genetic differentiation between populations inhabiting oxygen-minimum zones is the myctophid, *Triphoturus mexicanus*, which has a discontinuous distribution along the west Coast of the Americas. A northern population is located from San Francisco to southern Mexico, and a southern population is located from Guatemala to Chile (Moser, 1996). These populations show significant levels of genetic differentiation ($F_{ST} = 0.230$ calculated by Creasey and Rogers, 1999 from data in Afanas'yev et al., 1990) despite *T. mexicanus* having pelagic eggs and larvae (Moser, 1996). Genetic differentiation between these populations is sufficiently high that their taxonomic status is uncertain. However, the observed discontinuity in distribution and resultant population differentiation may have arisen prior to the emergence of the Panamanian Isthmus and may have been maintained by hydrographic barriers (Afanas'yev et al., 1990).

Some species have their distribution disrupted by the presence of the oxygen-minimum zone. Saltzman and Wishner (1997) studied the vertical distribution of copepods, in the oxygen-minimum zone, around Volcano 7. They observed that the copepod *Rhincalanus nasutus* was absent from the core of the OMZ but present both above and below it. Such a pattern of species distribution has been recorded in studies of zooplankton distribution in the Arabian Sea (Vinogradov and Voronina, 1962). In such cases, hypoxic conditions within the oxygen-minimum zone act as a barrier to distribution within a species. Whether the oxygen-minimum zone can retard

reproduction and larval dispersal between such disjunct populations has not been investigated, but it does remain a possibility. This is especially the case in areas where the oxygen-minimum covers a very large geographic area, such as the northern Indian Ocean. There is little evidence for the occurrence of disjunct populations of benthic species located above and below oxygen-minimum zones. This is possibly because many species in the bathyal zone are already restricted to a specific bathymetric range along the depth gradient (see Gage and Tyler, 1991). At present, there have been no investigations on genetic differentiation between populations separated along isobaths by oxygen-minimum zones.

3.2. *The environmental gradient and selection in oxygen-minimum zones*

The sharp zonation in community species composition at the boundaries of oxygen-minimum zones is a response to a strong physical gradient. The extent to which a species therefore penetrates an oxygen-minimum zone is a measure of its adaptation to low concentrations of oxygen and high concentrations of hydrogen sulphide, as well as its ability to out-compete other species in such a stressed environment. Because bacterial degradation and consumption of organic material are retarded within oxygen-minimum zones, there is an abundance of food for growth and reproduction. Oxygen minima also may provide a refuge from predators sensitive to hypoxia. Oxygen-minimum zones therefore provide a favourable environment for the proliferation of species that can adapt to conditions of hypoxia and high hydrogen sulphide levels.

A wide variety of morphological and behavioural characteristics are subject to selective processes in adaptation to low oxygen concentrations. Examples of this can be seen in the vent-endemic vestimentiferan and polychaete tube-worms and in polychaete worms and spider crabs in the oxygen-minimum zone in the Arabian Sea (Creasey et al., 1997; Levin et al., 1997; Lamont and Gage, 2000; Levin et al., 2000). Many species found in the Arabian Sea oxygen-minimum zone, also inhabit dwelling structures. In polychaetes these takes the form of tubes or concretions (e.g., cirratulid mudballs, Levin and Edesa, 1997), while a mussel (*Amygdalum* sp) constructs a byssus/mud “cocoon” (Gage, 1995; Levin et al., 1997). The exact function of such dwellings is uncertain, but they probably help their occupants regulate the environmental conditions in which they live. Such morphological and behavioural “adaptations” to oxygen-poor environments may, in some cases, represent examples of preadaptation. Observations of the way in which the oxygen-minimum zone influences the selection of such morphological characters are difficult, as such processes have occurred over long periods of time. Examination of the population genetics of species inhabiting the boundaries of oxygen-minimum zones is more likely to reveal processes of natural selection actually in progress, especially where the genes in question code for functional proteins involved in aerobic or anaerobic metabolic pathways.

Studies on allozyme loci in terrestrial and marine species have suggested that environmental selection for particular alleles may play a role in evolution. Evidence for selection of alleles, driven by low oxygen availability, is sparse. Monti et al. (1986) observed changes in genotype frequencies, for the enzyme locus malate dehydrogenase

(*Mdh*), within populations of the shallow water bivalve, *Ruditapes decussatus*, in response to increased environmental temperature and hypoxia. In the deep sea, Jollivet et al. (1995) have examined environmental selection for alleles of several enzymes in polychaetes of the family Alvinellidae. They have shown a correlation between the thermostability of the alleles for glucose-6-phosphate isomerase (*Gpi*), aspartate-amino transferase (*Aat*) and phosphoglucosmutase (*Pgm*) with the temperature in which a particular species is found. Jollivet et al. (1995) also suggested that oxygen concentrations in these environments may play a significant role in selection of genotypes for these enzyme loci.

Evidence also has been found for more complex forms of adaptation that may lead to increased resistance to environmental hypoxia. A cline in the distribution of alleles at the lactate dehydrogenase locus (*Ldh-B*) has been observed for the marine teleost *Fundulus heteroclitus*, along the east coast of the United States (Powers et al., 1983). The important physical variable along this cline was temperature. Lactate dehydrogenase catalyses the reaction from lactate to pyruvate to counteract the build up of lactic acid in muscles during exercise. At low temperatures, the genotype *Ldh-B^bB^b* has a higher activity than *Ldh-B^aB^a*. Heterozygotes have an intermediate activity level. At low temperatures in a swimming chamber, *Ldh-B^bB^b* fish can sustain a 20% higher swimming speed than in *Ldh-B^aB^a* fish. *Ldh-B^bB^b* fish have a higher ATP:haemoglobin ratio and a greater delivery of oxygen to swimming muscles (DiMichele and Powers, 1982). Thus, in these species, lactate dehydrogenase has an indirect effect on oxygen consumption and metabolic rate. The frequency of specific genotypes and overall genetic variation in some marine organisms also has been related to metabolic efficiency and oxygen consumption (e.g., Zouros and Pogson, 1994).

Evidence from population genetic studies for adaptation to hypoxic conditions within oxygen-minimum zones is sparse through a lack of study. Creasey et al. (2000) observed a reduced heterozygosity in a population of the squat lobster, *Munidopsis scobina*, sampled close to the perceived oxygen-minimum zone in the Arabian Sea, compared to a population from deeper, and presumably better oxygenated, waters. Such a reduced heterozygosity may arise as a result of selective mortality of individuals with genotypes unfavourable for survival in hypoxic conditions. Alternatively, these observations may have arisen simply by chance or because of a lower effective population size with increasing proximity to the oxygen-minimum zone because of a high rate of random mortality among individuals.

In the Arabian Sea, significant genetic differentiation has been observed between adult populations of the spider crab, *Encephaloides armstrongi*, sampled from within the oxygen-minimum zone and a juvenile population found above the oxygen-minimum zone (Creasey et al., 1997). This differentiation was mainly because of the occurrence of alleles for aspartate amino transferase (*Aat*) and phosphoglucose isomerase (*Pgi*) at much higher frequencies in the juvenile population than in the adult populations. Such a pattern of genotype frequencies between adult (oxygen-minimum zone) populations and juvenile (non-oxygen-minimum zone) populations may be a result of the selective mortality of individuals, with unfavourable genotypes, during ontogenetic migration into, and occupation of, the oxygen-minimum zone. In such a case the selectively unfit genotypes for adult stages would have to be positively

selected in the juvenile stages, leading to a balancing selection or overdominance situation (e.g., Hartl and Clark, 1989, see also Zouros and Foltz, 1984; Zouros and Mallet, 1989). This would prevent the selective elimination of genotypes unfavourable in the adult populations of spider crabs living in the oxygen-minimum zone. Alternatively, a low sample size of juvenile individuals may have led to incorrect estimates of allele frequencies for the juvenile population, or an extremely low effective population size in *E. armstrongi* may have led to a large temporal variance in allele frequencies.

Therefore, there is evidence (especially from allozyme studies) for selection in functional genes related to environmental parameters such as oxygen concentration. It is highly likely that the strong gradient in oxygen concentrations and other physical parameters associated with the boundaries of the oxygen-minimum zone act as a selective force leading to genetic divergence and isolation of populations living within, or close to, such boundaries. The separation of life-history stages inside and outside of the oxygen-minimum zone may lead to overdominance or other forms of balancing selection. Because of the mobility of the boundaries of oxygen-minimum zones (e.g., Levin et al., 1991), selection for genotypes insensitive to wide fluctuations in oxygen concentration may take place, as well as selection for genotypes that favour survival in a narrow range of oxygen concentrations. The strength of such selective processes is likely to vary amongst different taxa as tolerance to hypoxia is different (see above).

3.3. *The indirect influence of oxygen-minimum zones on population structure*

Selection for environmentally favourable genotypes in populations found within or on the boundaries of oxygen minima is likely. It is also possible that oxygen minima can have less direct effects on speciation processes in deep-sea organisms, through influences on life history. In the case of the spider crab, *Encephaloides armstrongi*, from the Arabian Sea, population and genetic studies indicate that the life history, dispersal patterns and spatial genetic structure of this species are very complicated (Creasey et al., 1997). Evidence indicate that juvenile crabs are spatially separated from adult animals, and they appear to develop above the oxygen-minimum zone in relatively shallow depths of 150 m. This means that different stages in the crab's life history are subject to very different physical conditions (see above) and that the crab larvae are probably subject to dispersal prior to settlement in currents flowing above the oxygen-minimum zone (Creasey et al., 1997). Such a life-history pattern probably results from a differential resistance to hypoxia at different stages of development.

The adult populations of *Encephaloides armstrongi* show significant genetic and size differentiation over small geographic distances. Such differentiation was restricted to the male crabs, and there was a striking bias in sex ratio, with male crabs outnumbering female crabs by 3.3:1. Population studies, along with photographic evidence, indicate that *E. armstrongi* probably exhibits sex-specific dispersal behaviour, possibly related to reproduction (Creasey et al., 1997). Biased sex ratio leads to a reduction in effective population size (Avice, 1994), and this in itself influences the genetic structure of populations, especially over generations (e.g., Hedgecock, 1994). Sex-related dispersal behaviour also influences the spatial genetic structure of popula-

tions. In such cases, the perceived dispersal pattern of individuals may not have predictable influences on spatial genetic structure of populations of a given species, especially in genes with transmission through one sex compared with those that are transmitted biparentally (e.g., green turtles, *Chelonia midas*; Bowen et al., 1992). As spatial genetic structure is directly related to speciation processes in all organisms (e.g., Palumbi, 1992), such behaviour is significant in relation to speciation processes.

In *Encephaloides armstrongi*, poor sample size in females, because of the biased sex ratio, had an inevitable impact on observations of differential spatial genetic structure (Creasey et al., 1997). The observation of a patchy distribution of very high numbers of *Encephaloides* sp. below the oxygen-minimum zone (see Bett, 1995) may explain the skewed sex ratio of the populations within the oxygen-minimum zone. In this region (830–1230 m depth), the very high densities of crabs (up to 130 m^{-2}) may be caused by mating aggregations. Again, if this were the case, it is likely that the crabs have to move out of the oxygen-minimum zone for reproduction. This would be another example of the way in which the oxygen-minimum zone is capable of influencing the distribution of populations within it. Data on the distribution and population genetics of *E. armstrongi* are incomplete and require further investigation.

In a second investigation on the oxygen-minimum zone, in the Arabian Sea, two populations of the squat lobster, *Munidopsis scobina*, were sampled from just below the oxygen-minimum zone at 900 and 1000 m, depth (Creasey et al., 2000). Significant differences in the size distribution of adult *M. scobina* were observed between these two populations (Creasey, 1998; Creasey et al., 2000). At the 900 m station, closer to the core of the oxygen-minimum zone, individuals were significantly larger than at the 1000 m depth station. This may reflect a migration upslope as the squat lobsters develop, as observed for other deep-sea Crustacea (e.g., Attrill et al., 1990). Alternatively, it also may reflect a larger food supply and faster growth rates for individuals located at a closer proximity to the base of the oxygen-minimum zone (Creasey et al., 2000). Such increased growth rates may lead to a faster maturation of populations closer to the oxygen-minimum zone, and this in itself may lead to differences in the timing of reproduction at different depths, if reproduction is synchronous. Such a change in reproductive timing may lead to temporal allopatry in populations along the depth gradient below the oxygen-minimum zone, and this may provide a mechanism for speciation.

Evidence that the oxygen-minimum zone in the Arabian Sea influences reproduction has been provided by an examination of size frequency in egg and brood volumes of *Munidopsis scobina* populations sampled from 900 and 1000 m depth (Creasey, 1998). In both populations, the size frequency of eggs was distinctly bimodal, but the distribution in size frequency between the two sites was significantly different, with the mean egg volume of the population sampled at 900 m being lower than that of the population sampled at 1000 m (Creasey, 1998; see fig. 4). Such data provide evidence that the timing of the onset of reproduction, overall developmental times or even developmental modes of eggs were different between the two sites. If such differences are not an artefact of sampling only two populations, they are likely to be a result of the gradient of physical conditions associated with the lower boundary of the oxygen-minimum zone and may be environmental (phenotypic) or genetic (i.e. result of

selection — see above). Such differences in reproduction between individuals sampled at different depths below the oxygen-minimum zone almost certainly will influence the spatial genetic structure of such populations and influence speciation as described above.

4. Conclusions

Recent studies have indicated that the deep-sea benthic fauna is characterised by an extremely high species richness. The diversity of the deep-sea benthic fauna follows a parabolic pattern with depth, with peak diversity occurring at bathyal depths, at least in some oceans (e.g., North Atlantic). Recent explanations of high diversity in the deep sea have concentrated on processes maintaining diversity, especially patch dynamics.

Studies on oxygen-minimum zones in the present day show that hypoxic conditions strongly influence the distribution of the benthic fauna. It is, therefore, likely that past fluctuations in oxygen concentrations in the oceans are likely to have influenced the evolution of the benthic fauna. Following models from palaeontological studies it is proposed that past fluctuations in atmospheric conditions from warm phases to cold phases resulted in cycles of hypoxia/anoxia and oxygenation in the deep sea. Such cycles caused periodic extinctions of the abyssal fauna as well as warm water shallow fauna but had less influence on the bathyal zone. Through these periods the bathyal zone acted as a source area for reinvasion of the abyssal and shelf zones, when conditions permitted. This may explain the high diversity of the bathyal fauna. Evidence from biogeographic and molecular studies support recent invasions of the abyssal zone from high-latitude isothermal water columns and, on a more regional scale, from the bathyal zone. Such studies also support multiple invasion/reinvasion events between the bathyal and shelf zones. As different taxa display different levels of resistance to hypoxia, the exact influence on their evolution by fluctuations in oxygen concentration also will vary. It is feasible that the dominance of certain taxonomic groups within the deep sea, especially in the macrobenthos, may partially reflect the cumulative influence of previous episodes of ocean hypoxia or anoxia. Furthermore, differences in the history of such environmental perturbations in different oceans may have resulted in differences in present day faunas. Further studies on the molecular evolution, systematics and biogeography of deep-sea taxa are necessary to confirm many of these possibilities.

At present oxygen-minimum zones may act as a barrier to gene-flow between populations of marine organisms, though genetic data confirming this is equivocal at present. If this is the case, oxygen-minimum zones are likely to influence speciation in such marine organisms both in the present and in the recent past. Organisms inhabiting oxygen-minimum zones show morphological adaptations to life in a hypoxic environment. Biochemical genetic studies on marine species, including those in the deep sea, indicate that selection for alleles favourable for survival in hypoxic conditions can occur. Selection for traits that increase survival in hypoxic conditions are a mechanism for speciation in organisms that are influenced by oxygen minima.

Oxygen-minimum zones also can influence speciation processes in marine organisms by indirect effects on life-history traits, such as growth rates, reproduction and larval development.

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