Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic macrofauna

Article *in* Oceanography and Marine Biology · January 1995

2 authors:

Robert Diaz
Virginia Institute of Marine Science
118 PUBLICATIONS **19,689** CITATIONS
SEE PROFILE

Rutger Rosenberg
University of Gothenburg
189 PUBLICATIONS **29,995** CITATIONS
SEE PROFILE

Oceanography and Marine Biology: an Annual Review 1995, **33**, 245–303
© A. D. Ansell, R. N. Gibson and Margaret Barnes, Editors
UCL Press

MARINE BENTHIC HYPOXIA: A REVIEW OF ITS ECOLOGICAL EFFECTS AND THE BEHAVIOURAL RESPONSES OF BENTHIC MACROFAUNA

ROBERT J. DIAZ & RUTGER ROSENBERG
Virginia Institute of Marine Science, School of Marine Science,
College of William and Mary, Gloucester Point, VA 23062, USA
and Göteborg University, Kristineberg Marine Research Station,
450 34 Fiskebäckskil, Sweden

Abstract In this review the effects of hypoxia on benthic fauna are summarized and detailed information is given on (1) the impact on community structure and function in fjords, estuaries, coastal and offshore areas (2) behavioural changes (3) recovery processes (4) ecosystem energy flow implications, and (5) tolerance in experimental studies.

There is no other environmental variable of such ecological importance to coastal marine ecosystems that has changed so drastically in such a short period as dissolved oxygen. While hypoxic and anoxic environments have existed through geological time, their occurrence in shallow coastal and estuarine areas appears to be increasing, most likely accelerated by human activities. Ecological problems associated with the occurrence of low oxygen are increasing on a global scale. The oxygen budgets of most major estuarine and coastal ecosystems have been adversely affected mainly through the process of eutrophication, which acts as an accelerant or enhancing factor to hypoxia and anoxia, and when coupled with adverse meteorological and hydrodynamic events, hypoxia increases in frequency and severity. The area of hypoxic and anoxic bottom water is even increasing within systems that historically are considered oxygen stressed. Many ecosystems that are now severely stressed by hypoxia appear to be near or at a threshold. Should oxygen concentrations become slightly lower, catastrophic events may overcome the systems and alter the productivity base that leads to fisheries species. Examples of such events are becoming increasingly common. At what point permanent damage will result is difficult to say. To date there is no large system that has recovered after development of persistent hypoxia or anoxia. The only exception may be small systems where pollution inputs have ceased and recovery initiated from surrounding non-affected areas.

The expanding occurrence of hypoxia and anoxia continues to bring about significant structural changes in benthic communities and to affect benthic–pelagic coupling. Restoring ecosystem balance and reversing the trend of increasing hypoxia and anoxia will require dealing with the global problem of coastal eutrophication and determining how to reduce the production of organic matter in sensitive estuarine and coastal areas.

Introduction

Oxygen is a key element in the metabolic processes of fishes and invertebrates. Although oxygen concentration in the sea can be much lower than saturation, respiration in most marine invertebrates does not appear to be significantly affected until extremely low concentrations are reached. For many benthic invertebrates this concentration is about $2\,\mathrm{ml\,l^{-1}}$, or even less (Herreid 1980, Rosenberg et al. 1991).

Hypoxic and anoxic basins are well known features of the world's oceans (Richards 1965, Kamykowski & Zentara 1990). In general, the Pacific and Indian Oceans have lower dissolved oxygen concentration and greater areas exposed to hypoxic water than the Atlantic Ocean (Fig. 1; for further details see Richards 1957, Wyrtki 1966, Kamykowski & Zentara 1990 and references therein). Hypoxia and anoxia are usually associated with the bottom, but an Oxygen Minimum Zone (OMZ) can occur at intermediate depths in the water column, typically in the open oceans or along coastlines. In some deep-sea areas the OMZ can impinge upon the bottom, exposing fauna to steep gradients of dissolved oxygen (Thompson et al. 1985, Wishner et al. 1990, Levin et al. 1991).

Hypoxic and anoxic environments are not recent phenomena. There is an extensive literature on paleoenvironmental records of ancient oxygen related biofacies, mainly due to an interest in reconstructing ancient marine basins (see Savrda & Bottjer 1991 and others in Tyson & Pearson 1991a).

All marine sediments are anoxic below a certain depth from the sediment surface and, consequently, sulphidic sediments have a worldwide distribution. The boundary zone separating surficial sediments dominated by aerobic processes from subsurface anaerobic dominated sediments is defined as the redox potential discontinuity, RPD (Fenchel 1969). Oxygen penetrates by physical diffusion only a few millimetres into the sediment in muddy and silty habitats (Revsbech et al. 1980), but burrowing and irrigation activity of infauna can distribute oxygen much deeper into the sediment (Aller 1982). Other factors that affect the position and thickness of the RPD are: oxygen content of bottom water, sedimentation of organic matter, sediment grain size, and temperature (Fenchel & Riedl 1970, Pearson & Rosenberg 1978, Vismann 1991).

In the absence of oxygen, microbes can utilize other compounds as electron acceptors, i.e. NO_3^-, MnO_4, FeOH, SO_4^{2-}, and CO_2 which are reduced to N_2, Mn^{2+}, Fe^{2+}, HS^-, and CH_4, respectively. Sulphide, in the form of hydrogen sulphide (H_2S), because of its wide occurrence and high toxicity to metazoan life, is the most important of these reduced compounds generated by bacterial metabolism in anoxic sediment. The combined effects of hypoxia and H_2S on marine organisms are difficult to separate (Vismann 1991). Since hypoxia and H_2S generally occur together and both stress marine organisms, it is likely that their effects are at least additive. Some meiofaunal organisms are, however, permanent inhabitants of the sulphide biome in anoxic sediments (Fenchel & Riedl 1970), and colourless sulphur bacteria are commonplace in oxygen and hydrogen sulphide micro-gradients (Jørgensen & Revsbech 1985).

Organic sediment enrichment occurs through vertical and advective accumulation of organic carbon. On bottoms where accumulation is predominant, oxygen may be reduced to low concentrations. This occurs mainly in enclosed sea areas, or where water column stratification causes stagnant conditions. In such areas the highest oxygen demand can be in the water close to the bottom rather than in the sediment (Rydberg et al. 1990). Hypoxia is often seasonally associated with the peak in the annual temperature cycle, which occurs around August in the northern hemisphere (Rosenberg 1980).

The increasing input of anthropogenic nutrients to many coastal areas over the past several decades has been suggested as the main contributor to more recently declining trends in bottom water oxygen concentrations (Turner & Rabalais 1994). In the Adriatic Sea, for example, hypoxia has reached its present state gradually over a period of about 20 years as a direct result of increased phytoplankton blooms that increased the sedimentation of organic matter (Justic

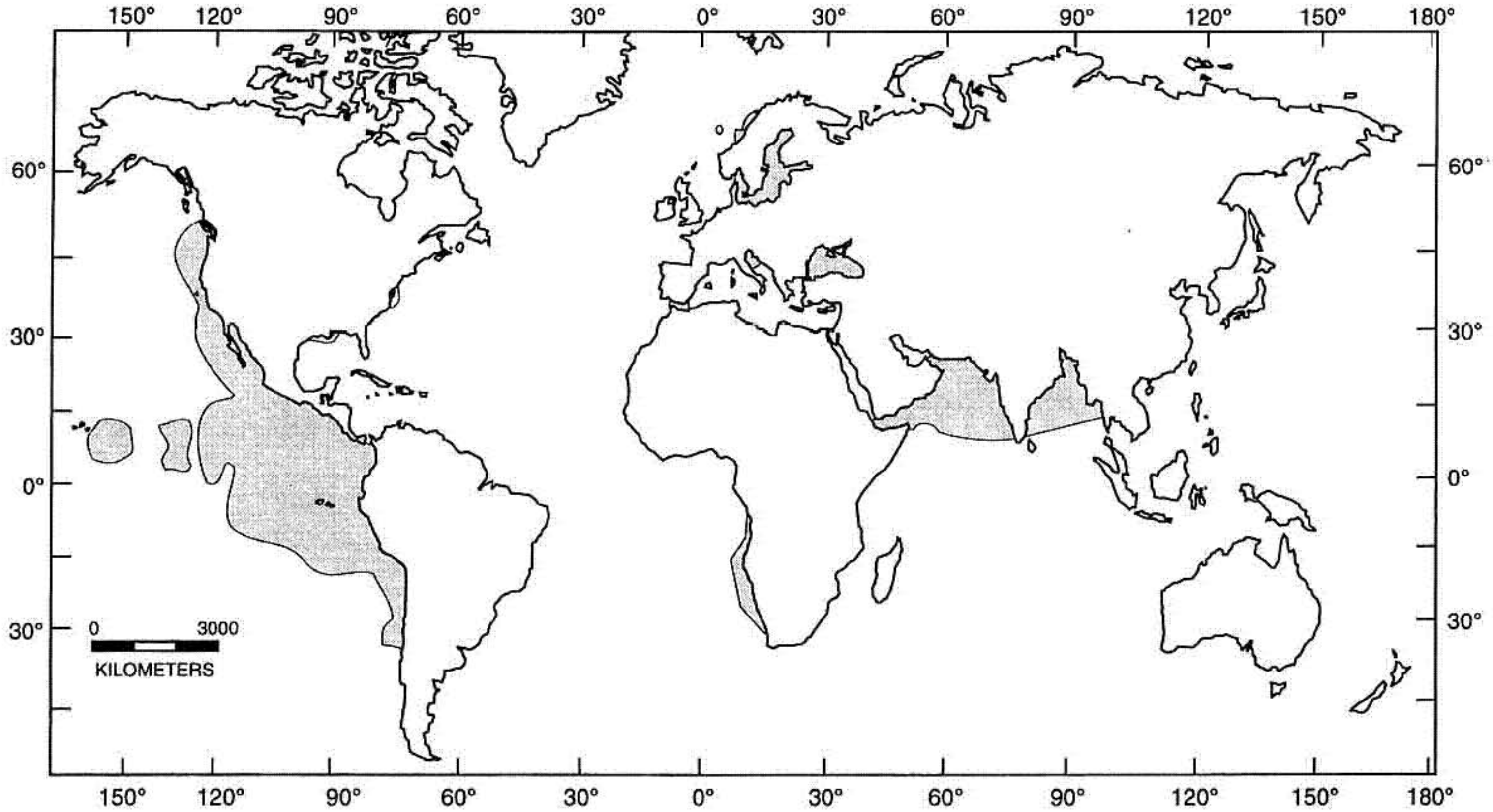

Figure 1 Map of major areas with observations of severe hypoxia ($<0.2\,\mathrm{ml\,l^{-1}}$) in marine and estuarine regions of the world oceans as recorded in the NODC, Washington DC dataset as of December 1986 (modified from Kamykowski & Zentara 1990).

Table 1 Summary of benthic effects for hypoxic systems around the world. Several of these systems also experience anoxia. In the case of many fjords, and coastal and oceanic oxygen minimum zones (OMZ) there is an anoxic zone within which no macrofauna occur. The absence of fauna from these anoxic zones is not considered a community response but a consequence of stable anoxia. Hypoxia is typed as: Aperiodic, events that are known to occur at irregular intervals greater than a year; Periodic, events occurring at regular intervals shorter than a year, related to tidal stratification/destratification cycles (Haas 1977); Seasonal, yearly events related to summer or autumnal stratification; Persistent, year round hypoxia. Levels of hypoxia are: Moderate, oxygen decline to about $0.5\,\mathrm{ml\,l^{-1}}$; Severe, decline to near anoxic levels, could also become anoxic. Time trends of hypoxia, area and or intensity, for the systems are: – = Improving conditions; + = Gradually increasing; ++ = Rapidly increasing; 0 = Stable; . = No temporal data. Benthic community response is categorized as: None, communities appear similar before and after hypoxic event; Mortality, moderate reductions of populations, many species survive; Mass Mort., drastic reduction or elimination of the benthos. Benthic recovery is: No Change, dynamics appear unrelated to hypoxia; Some, recolonization occurs but community does not return to prehypoxic structure; Slow, gradual return of community structure taking more than a year; Annual, recolonization and return of community structure within a year.

		System level response to hypoxia						
No.	System	Hypoxia type	Hypoxia level	Time trends	Benthic com. response	Benthic recovery	Fisheries stocks	References
1	Deeper Texas Shelf	Aperiodic	Moderate	0?	Mortality	Annual	Stressed	Harper et al. 1981, 1991
2	German Bight, North Sea	Aperiodic	Mod./Severe	+	Mass Mort.	Annual	.	Dethlefsen & Westernhagen 1983
3	New York Bight, New Jersey	Aperiodic	Severe	.	Mass Mort.	Slow	Surface clam losses	Boesch & Rosenberg 1981, Garlo et al. 1979, Sindermann & Swanson 1980
4	Shallower Texas Shelf	Aperiodic	Severe	+	Mass Mort.	Slow	Stressed	Harper et al. 1981, 1991
5	Sommone Bay, France	Aperiodic	Severe	+?	Mass Mort.	Slow	Collapse of cockle fishery	Desprez et al. 1992
6	North Sea, W. Denmark	Aperiodic	Severe	+	Mortality	Annual	Stressed	Dyer et al. 1983, Westernhagen & Dethlefson 1983
7	Peru/Chile, El Niño, shallow	Aperiodic	Severe	0?	Mass Mort.	???	Stressed	Rosenberg et al. 1983, Arntz & Fahrbach 1991
8	York River, Virginia	Periodic	Mod./Severe	0	None	No Change	Stressed	Pihl et al. 1991, Diaz et al. 1992
9	Rappahannock River, Virginia	Periodic	Severe	+	Mortality	Annual	Stressed	Llansó 1992
10	Seto Inland Sea, Japan	Seasonal	Moderate	.	Mortality	Annual	.	Imabayashi 1986
11	Louisiana Shelf	Seasonal	Mod./Severe	+	Mortality	Annual	Stressed	Boesch & Rabalais 1991, Rabalais et al. 1991
12	Saanich Inlet, British Columbia	Seasonal	Mod./Severe	0	Mortality	Annual	.	Tunnicliffe 1981
13	Bornholm Basin, S. Baltic	Seasonal	Mod./Severe	+**	Mass Mort.	Slow	.	Tulkki 1965, Leppäkoski 1969
14	Oslofjord, Norway	Seasonal	Mod./Severe	+	Mortality	Annual	Reduced	Petersen 1915, Mirza & Gray 1981, Rosenberg et al. 1987
15	Kattegat, Sweden-Denmark	Seasonal	Mod./Severe	++	Mass Mort.	Slow	Collapse Norway lobster	Baden et al. 1990a, Josefson & Jensen 1992, Rosenberg et al. 1992
16	German Bight, North Sea	Seasonal	Severe	+?	Mortality	Annual	Stressed	Niermann et al. 1990
17	Main Chesapeake Bay, Maryland	Seasonal	Severe	+	Mortality	Annual	Stressed	Holland et al. 1987
18	Port Hacking, Australia	Seasonal	Severe	.	Mortality	Annual	.	Rainer & Fitzhardinge 1981
19	Tolo Harbor, Hong Kong	Seasonal	Severe	.	Mass Mort.	Annual	.	Wu 1982
20	Tome Cove, Japan	Seasonal	Severe	.	Mortality	Annual	.	Tsutsumi 1987

		System level response to hypoxia						
No.	System	Hypoxia type	Hypoxia level	Time trends	Benthic com. response	Benthic recovery	Fisheries stocks	References
21	Laholm Bay, Sweden	Seasonal	Severe	++	Mortality	Annual	Stressed	Baden et al. 1990b, Rosenberg & Loo 1988
22	Gullmarsfjord, Sweden	Seasonal	Severe	+	Mass mort.	Annual	Stressed	Josefson & Widbom 1988
23	Swedish West Coast Fjords	Seasonal	Severe	++	Mortality	Some	Stressed	Josefsen & Rosenberg 1988
24	Pamlico River, North Carolina	Seasonal	Severe	.	Mass Mort.	Annual	.	Tenore 1972
25	Limfjord, Denmark	Seasonal	Severe	+	Mass Mort.	Annual	None	Jørgensen 1980
26	Kiel Bay, Germany	Seasonal	Severe	+	Mass Mort.	Annual	Stressed	Arntz 1981, Weigelt 1990
27	Lough Ine, Ireland	Seasonal	Severe	0	Mass Mort.	Annual	.	Kitching et al. 1976
28	Hillsborough Bay, Florida	Seasonal	Severe	.	Mass Mort.	Annual	.	Santos & Simon 1980
29	Gulf of Trieste, Adriatic	Seasonal	Severe	++	Mass Mort.	Slow	Stressed	Stachowitsch 1991
30	Elefsis Bay, Aegean Sea	Seasonal	Severe	.	Mass Mort.	Annual	.	Friligos & Zenetos 1988
31	Black Sea NW Shelf	Seasonal	Severe	++	Mass Mort.	Annual	Reduced	Zaitsev 1993
32	Århus Bay, Denmark	Seasonal	Severe	+	Mass Mort.	Slow	.	Fallesen & Jørgensen 1991
33	Sullom Voe, Shetland	Persistent	Severe	0	Mass Mort.	No Change	.	Pearson & Eleftheriou 1981
34	Byfjord, Sweden	Persistent	Severe	0*	Mortality	Some	Pelagic only	Rosenberg 1990
35	Black Sea (except NW shelf)	Persistent	Severe	+	No Benthos	No Change	Pelagic only	Tolmazin 1985, Mee 1992
36	Idefjord, Sweden–Norway	Persistent	Severe	+#*	Mortality	Some	.	Rosenberg 1980
37	Baltic Sea, Central	Persistent	Severe	++	Mortality	Some	Stressed	Andersin et al. 1978
38	Fosa de Cariaco, Venezuela	Persistent	Severe	.	Reduced	No Change	.	Nichols 1976
39	Caspian Sea	Persistent	Mod./Severe	0	Mortality	Some?	.	Zenkevitch 1963
40	Peru/Chile Upwelling Deep	Persistent	Mod./Severe	0	Biomass increase	No Change	Enhanced?	Arntz & Fahrbach 1991, Rosenberg et al. 1983
41	Santa Maria Basin, California	Persistent	Mod./Severe	0	Reduced	No Change	.	Hyland et al. 1991
42	Central California OMZ	Persistent	Mod./Severe	0	Biomass increase	No Change	.	Mullins et al. 1985
43	Volcano 7, Pacific OMZ	Persistent	Mod./Severe	0	Biomass increase	No Change	.	Levin et al. 1991
44	Gulf of Finland, Deep	Persistent	Mod./Severe	–	Reduced	Slow	.	Andersin & Sandler 1991

* Stable oxygen gradient associated with organic enrichment.

** These systems are currently in a persistent hypoxic state.

\# Recent improvements in oxygen concentrations due to pollution abatement.

1987). This "new" primary production locally increases the flux of organic carbon to the bottom (Wassmann 1990, Justic et al. 1993) and increases oxygen demand at the bottom, first through bacterial and then other metazoan respiratory processes (Graf et al. 1982). In the presence of a stratified water column, a gradient of declining oxygen concentrations will result from a combination of water column and benthic oxygen demand setting up hypoxic conditions. Before mortality, animals will show different levels of tolerance or resistance. In a hypoxic zone, stress on benthic animals may be shown in various ways, for example by exhibiting altered behavioural patterns, decreased feeding and reproduction activity, and by changes in physiological functions (see reviews by Vernberg 1972, Davis 1975, Herreid 1980). It has also been demonstrated, in a model by Pearson & Rosenberg (1978), how benthic communities generally are distributed and how their feeding mode changes in relation to organic enrichment and changing oxic–anoxic conditions in the sediment.

Oxygen deficiency may very well be the most widespread anthropogenically induced deleterious effect in the marine environment that causes localized mortality of benthic macrofauna. Over the past 10 to 15 years the number of coastal areas with seasonal hypoxia in the bottom water has spread rapidly and the main cause for this is suggested to be eutrophication (Rosenberg 1985, Colombo et al. 1992, Vollenweider et al. 1992, Justic et al. 1993, Orel et al. 1993). A future global warming may accelerate these effects and enlarge the areas that are affected (Kennedy 1990, Beukema 1992). Table 1 lists the areas experiencing oxygen deficiency and reporting benthic effects.

Up to the 1950s, mass mortality of marine animals caused by lack of oxygen was summarized by Brongersma-Sanders (1957). The importance of oxygen as an ecological factor for maintaining populations, of mostly fisheries related species, is emphasized in early reviews, such as Davis (1975). He reviewed oxygen requirements of Canadian freshwater and marine species with the intention of determining water quality criteria relative to minimum dissolved oxygen concentrations.

Our objective in this review is to evaluate the ecological importance of hypoxia and how it alters benthic community structure and energy flow processes. Our examples are drawn both from field and experimental data. We will show that benthic macrofauna have a rather high tolerance to hypoxia and that many species react to declining oxygen concentration with various behavioural responses before they eventually die. This review concentrates on benthic macrofauna, but a few comparisons with meiofauna are made. The literature on ecological effects of hypoxia and anoxia on meiofauna is limited (but see Coull 1969, Tietjen 1969, Elmgren 1975, Van Es et al. 1980, Josefson & Widbom 1988, Murrell & Fleeger 1989, Levin et al. 1991, Coull & Chandler 1992, Hendelberg & Jensen 1993). Overall, it seems that meiofauna in general are less affected by hypoxia and anoxia than macrofauna and megafauna.

Terminology and measurement

The terminology of oxygen deficient environments varies between geologists, physiologists, chemists, and ecologists. A recent and thorough review of this subject can be found in Tyson & Pearson (1991a). In our review we use the terms hypoxia and anoxia to define low oxygen environments. We found that these were the most widely used terms in the ecological and physiological literature. Hypoxia begins at $2.0\,\mathrm{ml\,l^{-1}}$ of oxygen and extends to $0.0\,\mathrm{ml\,l^{-1}}$, the point of anoxia. Approximate equivalencies for comparison with other oxygen units (at 20 psu (practical salinity units, equal to ‰), 25°C, 1 atmosphere pressure) are: $1\,\text{ml}\,\text{l}^{-1} = 1.4\,\text{mg}\,\text{l}^{-1} = 1.4$ ppm $= 23.9$ mmHg $= 23.9$ torr $= 3.18$ kPa $= 45.7$ mM $= 89.3\,\text{mg}\,\text{at}\,\text{l}^{-1} = 4.3\%$ O_2 vol. = 14% air saturation. For shallow estuarine or marine habitats, normal dissolved oxygen concentrations range from 100% air saturation (about $8\text{–}10\,\text{ml}\,\text{l}^{-1}$), to $2.0\,\text{ml}\,\text{l}^{-1}$. For this review, we consider this range to be normoxia. For comparison, atmospheric oxygen concentration is about $200\,\text{ml}\,\text{l}^{-1}$. When expressing oxygen concentration as percentage saturation, we refer to air saturation as 100%. Saturation concentration in the sea is dependent mainly on temperature, salinity and pressure (water depth and in experimental situations, barometric pressure). Solubility of oxygen in water is reviewed by Kester (1975) and solubility tables are presented in Weiss (1970), Colt (1984) and Benson & Krause (1984).

The measurement of dissolved oxygen is complicated by the reactive nature of oxygen and is still mainly based on the Winkler method (Winkler 1888). His method remains the standard for calibration of modern dissolved oxygen sensor technologies, with improvements to the original method of Winkler increasing the accuracy of dissolved oxygen measurements. Polarographic oxygen electrodes have made the *in situ* field measurement of dissolved oxygen possible. For recent examples see Sanford et al. (1990), Diaz et al. (1992), Summers & Engle (1993) and Rabalais et al. (1994). Microelectrodes (Revsbech & Jørgensen 1986) and other emerging sensor technologies are advancing rapidly, which should make the measurement of oxygen more reliable and precise (Gundersen & Jørgensen 1990). It is not the purpose in this review to describe and evaluate different methods for measurement of dissolved oxygen (for this see Gnaiger & Forstner 1983).

Because of the relationship between hypoxia, primary production, and water temperature, it may be possible to use satellite sensors to predict if conditions favourable for the formation of hypoxia will occur. Leming & Stuntz (1984), using data from the Coastal Zone Color Scanner, found a correlation between surface chlorophyll concentrations and areas of bottom water hypoxia on the inner Louisiana–Texas continental shelf. This type of remote sensing for identifying potential hypoxia "hot spots" around the world seems promising, but must be critically evaluated. Rabalais et al. (1991) found no relationship between surface chlorophyll concentrations and bottom hypoxia. Other remote sensing techniques for detecting the presence and ecological consequences of hypoxia and anoxia involve the use of sediment profile cameras, which provide *in situ* vertical section photographs of bottom sediments. Sediment profile cameras and surface cameras have been used to map the areal extent of hypoxic bottoms in several systems (Rhoads & Germano 1982, 1986, Valente et al. 1992, Rosenberg & Diaz 1993).

Most studies of hypoxia and anoxia that profile the water column report strong declining gradients of dissolved oxygen and nutrients within the benthic boundary layer. (Rosenberg & Loo 1988, Gundersen & Jørgensen 1990). Within this layer, turbulence and eddy diffusion provide the energy for mixing (Wright 1989). At the sediment/water interface there is a thin diffusive boundary layer, approximately 1 mm thick, through which molecular diffusion is the dominant transport mechanism for dissolved materials (Gundersen & Jørgensen 1990). In addition to water column demands, benthic biological and chemical oxygen demands accelerate the consumption of oxygen within these boundary layers. An example of a strong vertical oxygen gradient is found in the Limfjord, Denmark, where oxygen concentrations were 6.0, 2.9 and $0.4\,\text{ml}\,\text{l}^{-1}$ at 0.5, 0.3–0.2, and 0.05 m above the bottom, respectively (Jørgensen 1980). Exceptions to this monotonic declining trend in dissolved oxygen were shown by Rabalais et al. (1994) for the Louisiana shelf. Many of their profiles show a slightly elevated level of oxygen at the sea bed, then a decrease above the sea bed and then an increase towards the surface. This apparent anomaly is likely related to photosynthetic production of oxygen at the sea bed by benthic primary producers (Rabalais et al. 1994). If the eventual effects on the fauna are to be correlated with the prevailing oxygen concentration, then oxygen must be precisely measured in the microhabitat in which the animals live.

Measurement of oxygen close to the bottom can best be obtained by *in situ* use of oxygen electrodes. Moreover, long-term continuous recording of dissolved oxygen is essential to evaluate the field effects of hypoxia and anoxia on benthic fauna. Continuous recordings by reliable oxygen electrodes are preferred to measurements at intervals because periodic and aperiodic oscillations in oxygen concentration occur in many habitats (Sanford et al. 1990, Diaz et al. 1992, Summers & Engle 1993). Single point measurements of oxygen can be particularly misleading for interpreting biological effects in shallow, well mixed systems that experience diurnal cycles. Often, measurements should also be made at night during the time of lowest oxygen concentration (Summers & Engle 1993). Even when hypoxic and anoxic water masses that develop in deeper water appear temporally stable, internal waves or wind driven seiches can result in aperiodic intrusions of low dissolved oxygen water into adjacent normoxic habitats (Sanford et al. 1990, Breitburg 1992).

The ecological effects of hypoxia and anoxia on benthos appear to be a function of the amplitude and temporal variation in oxygen concentration as well as the absolute oxygen concentration. Diurnal and semi-diurnal internal tides on the summit (730–800m) of the Volcano 7 seamount in the eastern Pacific displaced water masses and exposed the benthos to periodically varying low oxygen (range of $0.08–0.16\,\mathrm{ml\,l^{-1}}$), rather than to constant hypoxic conditions. This small difference in oxygen was sufficient to elicit a strong faunal response (Levin et al. 1991). In most field studies, however, the magnitudes of temporal and spatial changes in hypoxia are not known. When the history of hypoxic exposure is not known, infaunal effects should not be ascribed to a particular oxygen level (Rosenberg et al. 1992).

Effects of benthic hypoxia on marine communities

In this section benthic community and population level responses (species, abundance, and biomass) induced by oxygen deficiency are summarized. The first section deals with the response patterns along oxygen gradients, and mortality in relation to declining oxygen levels in fjords, estuaries and near coastal areas. Open coastal areas, the Black Sea, and the Baltic proper will be discussed in the second section and a discussion of oxygen minimum zones comprises a third section. Faunal behaviour in relation to declining oxygen concentrations and recovery of organisms subsequent to improved oxygen conditions will be dealt with in separate sections.

There is a complicated interplay between oxygen concentration and sediment geochemistry that regulates the response of organisms to declining dissolved oxygen concentrations. For example, prolonged hypoxia or anoxia allow sulphate-reducing bacteria, typically found deeper in the sediments during normoxia, to survive in surface sediments where they can produce potentially lethal concentrations of hydrogen sulphide (Jørgensen 1980, Bagarinao 1992) and alter other geochemical cycles.

Examples of species recorded in, and eliminated from, hypoxic areas are presented in Table 2.

Table 2 Examples of species found to be resistant to moderate and severe hypoxia, and species that seem to be eliminated during such conditions (sensitive species). Numbers in brackets refer to the marine systems and accompanying references in Table 1. Reference for numbers from 50 upwards are listed at the end of the table.

Species resistant to severe hypoxia	Species resistant to moderate hypoxia	Species sensitive to hypoxia
Arctica islandica (15, 26)	*Capitella capitata* (20, 30, 50)	*Diastylis rathkei* (15)
Astarte borealis (13, 26)	*Abra alba* (15, 53)	*Nephrops norvegicus* (15)
Corbula gibba (15, 26, 27, 34, 60)	*Abra nitida* (16, 53)	*Echinarachnius parma* (3)
Ophiura albida (15, 16)	*Amphiura filiformis* (15, 52, 53)	*Brissopsis lyrifera* (15)
Halicryptus spinulosus (13, 26)	*A. chiajei* (15, 53)	*Ampelisca agassizi* (11)
Malacoceros fuliginosus (30, 56)	*Streblospio benedicti* (9)	*Ampharete grubei* (51)
Metridium senile (57) .	*Mediomastus ambiseta* (9)	*Macoma calcarea* (32)
*Phoronis müller*i (15, 34)	*Mercenaria mercenaria* (59)	*Gammarus tigrinus* (59)
Ophiodromus flexuosus (34)	*Spisula solidissima* (3, 59)	*Spisula solida* (65)
Pseudopolydora pulchra (27)	*Lumbrinereis verrilli* (1)	*Asterias forbesii* (3)
Paraprionospio pinnata (9, 11)	*Scoloplos armiger* (61)	*Crangon crangon* (25)
Loimia medusa (9, 55)	*Asychis elongata* (62)	*Carcinus maenas* (25)
Modiola phaseolina (35)	*Nereis diversicolor* (25)	*Magelona phyllisae* (1)
Nephtys hombergi (35, 52)	*Pectinaria koreni* (25, 52)	*Nereis pelagica* (64)
Ragacitis pulchra (29)	*Nereis micromma* (1)	
Calliactis parasitica (29)		
Streblospio benedicti (54)		
Goniadella gracilis (3)		
Astarte castanea (3)		
Mytilus edulis (25)		
Munida quadrispina (12)		
Heteromastus filiformis (13, 15, 31)		
Arenicola marina (61)		
Saduria entomon (37, 63)		
Magelona sp. H (10, 11, 66)		

50 Rosenberg 1972
51 Henriksson 1969
52 Nilsson & Rosenberg 1994
53 Rosenberg et al. 1991
54 Llansó 1991
55 Llansó & Diaz 1994
56 Tyson & Pearson 1991b
57 Wahl 1984
58 Shumway et al. 1983
59 Winn & Knott 1992
60 Pearson & Eleftheriou 1981
61 Schöttler & Grieshaber 1988
62 Dauer et al. 1992
63 Hagerman & Szaniawska 1988
64 Theede et al. 1973
65 Theede et al. 1969
66 Gaston 1985

Fjords, estuaries, and near coastal areas

In stagnant or semi-stagnant areas (fjords, sea lochs, protected embayments) the dissolved oxygen concentration critical to most benthic organisms appears to be around $1.4\,\mathrm{ml\,l^{-1}}$ (Rosenberg et al. 1992). In areas that experience seasonally varying hypoxia (estuaries and open coasts) the critical oxygen concentration is closer to $0.7\,\mathrm{ml\,l^{-1}}$ (Llansó 1992), with the reduction from 0.7 to $0.4\,\mathrm{ml\,l^{-1}}$ being particularly important (Llansó & Diaz 1994). The difference in faunal response between these two types of environments is related to the stability and duration of hypoxia.

Norwegian fjords with poor bottom water circulation typically experience lowest oxygen levels in November (Rygg et al. 1985). Hypoxia and anoxia in these fjords are not necessarily associated with increased organic enrichment, but this might be a factor in some instances. In the Langesundfjord, for example, the benthos at the deepest sites (>100m) displayed patterns of species, abundance and biomass (SAB curves) most consistent with stress from seasonal anoxia that could be related to organic enrichment (Gray et al. 1988). The organic enrichment- and low oxygen-tolerant *Heteromastus filiformis* (Rosenberg 1976) was the most abundant species at the deep hypoxic stations (Gray et al. 1988).

Organic enrichment of the Oslofjord, Norway, has created a gradient of oxygen stress that has worsened through time. Prior to 1900 there is little evidence of low oxygen problems in the inner Oslofjord, the Bunnefjord, with the area supporting a commercial fishery for *Pandalus borealis*. By 1915, Petersen (1915) found a deep station in the inner Bunnefjord to be depauperate. Other stations in the middle Oslofjord, the Vestfjord, had well developed communities. The deep waters (>75m) in the Vestfjord have declined in oxygen from 2.8$\text{ml}\,\text{l}^{-1}$ in the 1930s, to 1.7$\text{ml}\,\text{l}^{-1}$ in the 1960s, to 0.9$\text{ml}\,\text{l}^{-1}$ in the 1970s (Mirza & Gray 1981). These areas with declining oxygen values have reduced benthic communities. Annual renewal of at least part of the bottom water, however, maintains communities at a pioneering successional state with high abundance of opportunistic species (Mirza & Gray 1981).

The Skagerrak coast of western Sweden has many semi-enclosed fjordic areas that experience hypoxic or anoxic water below the halocline for most of the year. Significant declining trends in bottom water oxygen concentrations have been demonstrated for several of these basins since the 1950s and 1960s (Rosenberg 1990). Comparison of infaunal communities in three of these fjordic areas between 1976 and 1986 showed significant reductions in: (a) total mean abundance and biomass (excluding some large and rare species), (b) abundance and biomass of molluscs, and (c) abundance of suspension feeders and carnivores. Community similarity also changed between the two periods (Josefson & Rosenberg 1988). Hypoxia was recorded in these areas, but no detailed information is available concerning oxygen concentration prior to the two sampling periods. The authors stated that the reductions were most likely due to hypoxia induced by large-scale eutrophication.

In the Gullmarsfjord, the largest of the Swedish fjords, the yearly minimum oxygen concentration has declined gradually over the years in the deeper areas, but remained above 2$\text{ml}\,\text{l}^{-1}$ until 1980. During the winter of 1979–80, oxygen levels dropped to exceptionally low values. In November 1979 oxygen concentration was 0.83$\text{ml}\,\text{l}^{-1}$ and continued to decline to a low in January 1980 of 0.21$\text{ml}\,\text{l}^{-1}$ (temperature: 5–6°C) at 115m depth. The macrobenthic communities were fairly stable in abundance and biomass from 1977 up to November 1979, but by January 1980 the entire macrobenthic community was eliminated (Josefson & Widbom 1988). Meiofauna did not seem to be affected at the same station in January 1980, but later that year, when the bottom water had been reoxygenated, meiofauna diversity was reduced (Austen & Widbom 1991). The reduction of macrofauna was abrupt and occurred after oxygen concentrations declined below 0.83$\text{ml}\,\text{l}^{-1}$. A combination of factors was responsible for the apparent lack of a gradual response and subsequent threshold response of the infauna. The communities had been pre-stressed by previous years of seasonal hypoxia with sensitive faunal groups (echinoderms and crustaceans) already absent, or in low abundance, prior to 1979. The low temperatures (5–6°C), also tended to increase tolerance to low dissolved oxygen of the pre-stressed community.

Shallow bottoms (15–30m) in the inner parts of the Gullmarsfjord, the Saltkällefjord, were heavily affected by organic enrichment and subsequent periodic anoxia in the 1960s. The benthic macrofauna was reduced at some stations and missing at others (Leppäkoski 1968). While recordings of oxygen concentrations were not made, it was inferred that lack of oxygen was responsible for the differences in fauna.

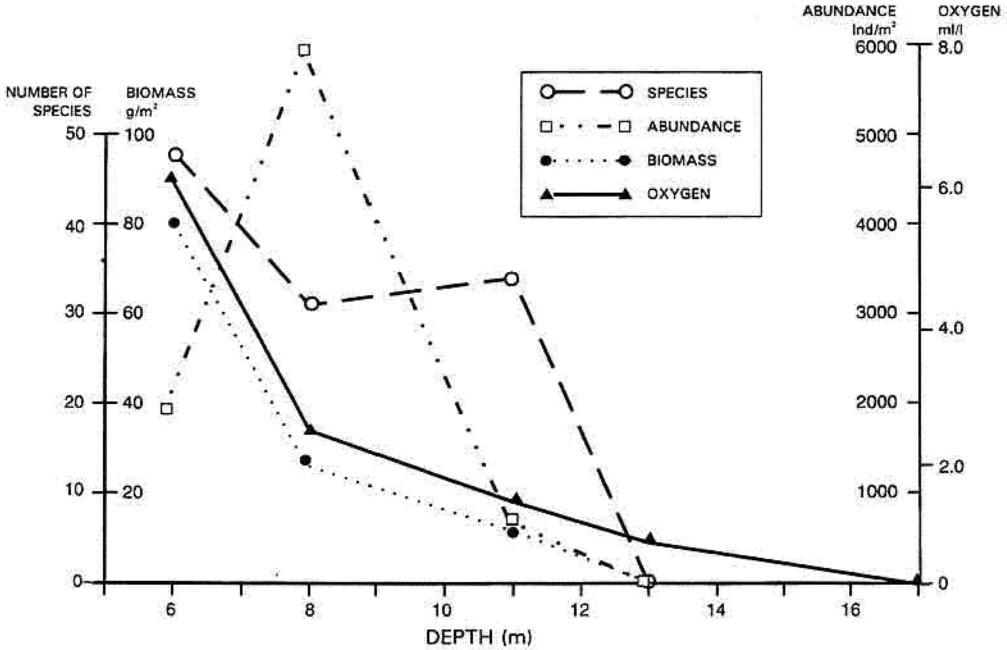

Figure 2 Number of species, abundance and biomass (wet weight) in relation to declining oxygen concentrations with depth. Example from a persistent anoxic fjord, the Byfjord Sweden (modified from Rosenberg 1977).

The Byfjord on the Swedish west coast is permanently anoxic below 15–20 m water depth. The number of species, abundance, and biomass of macrofauna in the Byfjord decline with depth, which itself was highly correlated with declining oxygen concentrations (Rosenberg 1977) (Fig. 2). The temporal and spatial stability of the vertical gradients in oxygen concentrations has led to strong faunal gradients in the Byfjord. Among the species listed by Rosenberg (1977) as abundant in hypoxic fjord habitats are: *Phoronis mülleri, Ophiodromus flexuosus, Scalibregma inflatum, Polydora ciliata, Nassa reticulata, Aporrhais pespelicani* and *Corbula gibba.*

In Lough Ine, a sea loch in Ireland that experiences annual hypoxia and anoxia, *Corbula gibba* is the most hypoxia tolerant species. Below 30 m only *C. gibba* survived past August and by September no macrofauna were present. Mass mortality induced by the summer hypoxic/anoxic water eliminates benthos below about 25 m, but recolonization occurs during the winter. Dominant species in the severe hypoxic habitats are *Pseudopolydora pulchra* and *Corbula gibba*, which recolonize by pelagic larvae (Kitching et al. 1976).

In the innermost part of a fjord in the Shetland Isles, Sullom Voe, Pearson & Eleftheriou (1981) found that seasonal development of a thermocline could result in hypoxic bottom conditions. During hypoxia in the summer of 1977 in that area all macrofauna died with the exception of *C. gibba*.

Large areas ($330\,\mathrm{km}^2$) of the Limfjord in Denmark experience periodic summer hypoxia. The oxycline can be sharp with high values ($>5.7\,\mathrm{ml\,l^{-1}}$) at 0.5 m above the bottom but only $0.4\,\mathrm{ml\,l^{-1}}$ at 0.05 m above the bottom (Jørgensen 1980). Benthic fauna experience pulses of annual mass mortality and recolonization. High densities of the sulphur bacteria *Beggiatoa* spp. were also found to cover muddy bottoms throughout the year with average biomass of

5–20 $g\,m^{-2}$ (Jørgensen 1977). The presence of *Beggiatoa* spp. is indicative of sulphide diffusion into surface sediments and at least some oxygen in the near bottom water.

Kiel Bay, an inlet to the Baltic, has seen a significant declining trend in deep-water oxygen concentrations since the 1950s (Weigelt 1990). It was not until late summer of 1981 (salinity 20–26psu, temperature 10–14°C), however, that a severe oxygen reduction occurred in all parts of Kiel Bay and Mecklenburg Bay (Ehrhardt & Wenck 1984). Anoxia and H_2S were widespread below the halocline at depths >20m (Weigelt 1991). The anoxia lasted for several weeks and resulted in mass mortality of the benthic infauna. An estimated 30000 tonnes (99% of the total biomass) of macrofauna were lost over an area of about 750 km^2. Other hypoxic–anoxic events in 1967 and 1983 were not as widespread, or as detrimental to the fauna, with losses of about 65–67% over smaller areas (600–700 km^2) (Weigelt 1991). Among the few survivors of the hypoxia–anoxia were *Arctica islandica*, *Astarte* spp., *Corbula gibba*, and *Halicryptus spinulosus* (Weigelt & Rumohr 1986, Weigelt 1987). Arntz (1977) found *Astarte elliptica*, *Mya truncata*, and *Arctica islandica* to be particularly resistant to hypoxia in that region. Currently the dominant faunal groups in Kiel Bay are hardy hypoxia–anoxia tolerant bivalves and the priapulid *Halicryptus spinulosus* (Weigelt 1987, 1991). All the long-term declines in macrofauna within the Kiel Bay system have been attributed to oxygen depletion. Most of the species that increased following the 1981 oxygen event were either hypoxia tolerant or had opportunistic life histories (Weigelt 1991).

In a general review of the benthic ecosystem in this part of the Baltic, Arntz (1981) described how declining oxygen concentrations can result in "ecological catastrophes". Arntz (1981) found the deepest benthic habitats to be extremely sensitive to hypoxia for two reasons; this is where hypoxia first develops and the distribution of deep dwelling, long-lived equilibrium species tends to be restricted to these bottoms. While hypoxia is not a problem above the halocline, the salinity at shallower depths is too low for the survival of these equilibrium species. The physical stability of deeper high salinity habitats is an important factor in the development of these advanced successional communities (Rhoads 1974, Rhoads & Germano 1986, Schaffner 1990), which also may be the most sensitive to hypoxia.

The shallow Cabbage Tree Basin in Port Hacking (southeastern Australia) is a relatively pristine estuarine ecosystem that experiences brief periods of hypoxia and anoxia when high freshwater inflow or temperature stratifies the water column. Hypoxia was first recorded in 1951 and may be a naturally occurring phenomenon (Rochford 1953, in Rainer & Fitzhardinge 1981). Rainer & Fitzhardinge (1981) determined that hypoxia and anoxia were the most important factors in limiting species distributions. Along the declining oxygen gradient, biomass and average community structure parameters, except evenness, declined. Changes in substratum characteristics or depth could not account for these community patterns. Four of 49 species that occurred at a 5m deep station, which experienced hypoxia of near 10% saturation, were common. At the deepest station (8m), which went anoxic, none of the 11 species present occurred in high numbers. The mean biomass at the anoxic station was 1.6 $g\,WW\,m^{-2}$, 35 $g\,WW\,m^{-2}$ at the hypoxic station, and 290 $g\,WW\,m^{-2}$ at a nearby normoxic station.

In Tomoe Cove, a small semi-enclosed cove on the northwest coast of Amakusa Shimoshima Island, Japan, oxygen concentrations dropped dramatically during summer stratification (July and August) at about 10m depth. Minimum oxygen concentrations of 10% saturation were measured at depths of 10m and a temperature of 27°C. Subsequently a high sulphide content (0.75 $mg\,g^{-1}$) was recorded in the surface sediments and the samples smelled of H_2S. The benthic faunal abundance and number of species decreased sharply during the hypoxic period and at the peak of hypoxia no macrobenthos was recorded (Tsutsumi &

Kikuchi 1983, Tsutsumi 1987). The polychaetes *Capitella capitata*, *Pseudopolydora* spp., and *Prionospio cirrifera*, and the bivalve *Theora fragilis* quickly recolonized defaunated areas after hypoxia. These species are not considered especially tolerant to oxygen deficiency, rather they are suggested to be opportunists with life history traits that facilitate recolonization of vacant habitats (Gray 1979). In summary, the benthic fauna was eliminated at an oxygen saturation $<10\%$ that prevailed for some weeks.

Megafauna of the deep fjordic Saanich Inlet in British Columbia experience hypoxia ($<1.0\,\mathrm{ml\,l^{-1}}$) and anoxia for much of the year. Annual flushing reoxygenates the inlet and produces a complicated normoxic–hypoxic–anoxic mixture throughout the 220m water column (Tunnicliffe 1981). The megafauna assemblages exposed to hypoxia maintain a higher diversity and abundance than does much of the upper photic zone. Peaks of faunal abundance occurred at 75 and 100m, which corresponds to the edge of the hypoxic water. This boundary effect or edge effect, of increased abundance is common in oceanic and coastal OMZs (Mullins et al. 1985). In Saanich Inlet, however, diversity within the hypoxic zone (85–100m, $<1.0\,\mathrm{ml\,l^{-1}}$ for half the time) was also high. This is not a condition seen in other OMZs (Mullins et al. 1985, Levin et al. 1991). Persistence of a megafaunal community of high abundance and diversity in Saanich Inlet is pertinent to behavioural and physiological adaptations that allow survival in hypoxia and anoxia. Regulation of competitive dominance in this substratum-limited community through anoxia-induced mortality (Tunnicliffe 1981), and not food quality, may be most important in maintaining high diversity.

Oxygen concentrations $<2.9\,\mathrm{ml\,l^{-1}}$ have been reported in about 40% of the 130 estuarine and near coastal areas throughout the continental USA that have adequate data (Whitledge 1985). We know, however, that benthic fauna can generally tolerate oxygen concentrations down to at least $2\,\mathrm{ml\,l^{-1}}$ without major effects. But every major estuarine system within the USA has areas that seasonally experience mild to severe hypoxic or anoxic conditions. However, persistent hypoxic or anoxic conditions have not been reported from any US estuarine or coastal system.

Relative to hypoxia, Chesapeake Bay is the most studied system in North America. Newcombe & Horne (1938) were the first to report recurring oxygen depletion in the deeper portions of the Chesapeake. This now appears to be related to the long-term development of the Chesapeake Bay watershed, initiated by European settlement in the seventeenth century (Cooper & Brush 1991). The spatial distribution and severity of hypoxia and anoxia vary from year to year and are related to a combination of factors, including meteorology and the amount of freshwater runoff, both of which directly affect the magnitude of primary production and the stratification of the water column (Officer et al. 1984, Seliger et al. 1985). In the main stem of Chesapeake Bay, hypoxic conditions persist through the late spring and summer until autumn winds cause vertical mixing and turn-over of bottom water.

Seasonal defaunation and/or declines in benthic abundance have been recorded by Holland et al. (1977, 1987) during seasonal hypoxia in Chesapeake Bay. This recurring seasonal hypoxia, in the upper mesohaline Chesapeake Bay, has been linked to the decline in abundance of larger, more long-lived benthic species (Holland et al. 1977, 1987) and the dominance of the benthos by smaller short-lived species (Mountford et al. 1977).

The deeper waters of the major tributaries of Chesapeake Bay experience periodic hypoxic events that can last from days to weeks (Haas 1977, Kuo & Neilson 1987, Diaz et al. 1992). By periodic hypoxia we mean short-term or intermittent hypoxic events that last on the order of days and reoccur at irregular times of the year. The factors that cause these periodic events vary from tributary to tributary (Kuo & Neilson 1987). In the York River the strength of tidal mixing regulated by the spring-neap tidal cycle is the principle factor (Haas 1977). In the Rappahannock River, and probably the Potomac River, a combination of tidal mixing and the proximity to the main stem hypoxic waters, which supply oxygen deficient bottom water to the tributaries, are the principle factors (Kuo & Neilson 1987, Kuo et al. 1991).

The ecological consequences of periodic hypoxia are varied. This type of less temporally severe hypoxia may be a mechanism for regulating benthic population dynamics (Breitburg 1992, Dauer et al. 1992, Llansó 1992). In the Rappahannock River, Llansó (1992) found temporal and spatial patterns in macrobenthic abundance and species composition to be related to intermittent hypoxia. Communities were dominated by opportunistic polychaete species, and the magnitude of response to hypoxia was species specific. *Streblospio benedicti* and *Mediomastus ambiseta* became extinct locally with the onset of severe hypoxia, while *Loimia medusa* and *Paraprionospio pinnata* were present in affected habitats through recurring hypoxic events. Llansó (1992) also found that the timing of hypoxia relative to recruitment was critical to survivorship. The summer recruitment peaks for *Podarkeopsis levifuscina* and *Pseudeurythoe paucibranchiata* both declined with the onset of an hypoxic event. The intensity and duration of hypoxia are also factors that can affect population dynamics (Llansó 1991).

In the York River, periodic hypoxia at depths >9m is less severe than Rappahannock River hypoxia and macrobenthic community structure does not appear to change spatially or temporally in response to hypoxic events (Dauer et al. 1992, Diaz et al. 1992). This may be due to the long-term conditioning of the community by hypoxia stress. The dominant species are now those known to be tolerant to low dissolved oxygen (Llansó 1991, 1992, Neubauer 1993). In the 1960s the York River macrobenthic community at 10m was dominated by *Nephtys incisa*, *Acteocina canaliculata*, and *Micropholis atra*, but by the mid-1970s euryhaline opportunistic *Paraprionospio pinnata* and *Pseudeurythoe* spp. were dominant (Boesch et al. 1976). In part, long-term changes documented in the York River macrobenthic community may be due to hypoxia.

Demersal fishes and the blue crab, *Callinectes sapidus*, quickly repopulated areas after periodic hypoxic events in the York River (Pihl et al. 1991). *Squilla empusa* remained in the deep hypoxic areas until their tolerance was exceeded, at which point they migrated to and remained in shallow water. Food availability seemed to be the main reason that motile species would stay or return to hypoxic waters (Arntz 1981, Pihl et al. 1992). During hypoxic events, infaunal prey such as *Micropholis atra*, *Leptosyanapta tenuis* and spionid polychaetes were seen to migrate to the sediment surface, and spionid polychaetes were also seen swimming in the water column, probably in response to hypoxic stress (Diaz et al. 1992). The movement of infauna to the sediment surface was also seen during more severe hypoxia in the Rappahannock River (Llansó 1992).

The successful exploitation of oxygen stressed infauna in the York River by bottom-feeding predators is related to the level of hypoxia (0.2–$0.8\,\mathrm{ml\,l^{-1}}$), its short duration (6–14 days), and the relatively small area affected (only depths >9m). The larger scale hypoxia and anoxia that develop in the upper Chesapeake Bay do not allow for such a "positive" energy transfer. In these areas macrobenthic community structure is drastically affected (Holland et al. 1987) and utilization of the stressed habitats by invertebrates and fishes do not occur again until the autumnal turnover.

Over the past 30 years there has been a gradual, but variable, increase in the pool of hypoxic water that seasonally develops in the upper Chesapeake Bay with the intrusion of hypoxic water onto shallower bottoms (Officer et al. 1984, Seliger et al. 1985, Seliger & Boggs 1988). At the fringe of the hypoxic water mass, short-term variability in dissolved oxygen concentrations is associated with large amplitude wind- and tide-forced lateral internal oscillations of the pycnocline (Sanford et al. 1990). This results in the advection of more saline hypoxic water onto the shallower (3–17 m) bottoms of the Bay. Mobile fauna quickly move out of the advected hypoxic waters, but not all individuals successfully escape (Breitburg 1992). Breitburg (1992) found that a number of factors, including age and behaviour, reduced the mobility or increased physiological susceptibility to hypoxia. Hypoxia stress, then, can act as a selective force upon populations. Aperiodic stress from the intrusion of deep water hypoxia onto shallower bottoms will result in more eurytopic communities. This is a community response that is similar to those seen in response to the periodic hypoxia in the York River.

The presence of a eurytopic community is not always strictly related to a single stress factor. From the 1950s, gross sewage and heavy metal pollution of Los Angeles–Long Beach Harbours, California, resulted in hypoxia and anoxia in the inner portions of these harbours (Reish 1955, Reish et al. 1980). While oxygen concentration was undoubtedly a factor in the observed community changes, it was not possible to distinguish it from the effects of pollution.

The inner and middle continental shelf of the northern Gulf of Mexico (from the Mississippi River delta to the Texas border) is the largest area in North America affected by hypoxia (Rabalais et al. 1991). An area of 8000–9500 km^2 now experiences seasonal summer hypoxia. Hypoxic bottom waters are found at depths from 5 to 60 m and can extend up to 20 m above the bottom (Rabalais et al. 1991). Although possibly the first occurrence, hypoxia was first recorded in the summer of 1973 between 6 and 37 m on the central Louisiana continental shelf (Harper et al. 1981). The hypoxic layer extended 2–7 m above the bottom and contained areas that were anoxic. A reduction in the abundance of benthic fauna was observed during this event, but it was not until the summer of 1978 that hypoxia caused extensive mortality (Harper et al. 1981). Hypoxia has occurred almost annually since 1973; extensive mortalities and low trawl catches were reported for 1979 (Pavela et al. 1983), 1981 (Gaston 1985), 1982 (Leming & Stuntz 1984), 1983 and 1984 (Renaud 1986b).

The 1981 hypoxia in this area dramatically reduced many of the numerically dominant macrobenthic species (*Phoronis mülleri*, *Mediomastus californiensis*, *Cirratulus* cf. *filiformis*). Species richness was also lowered by hypoxia, with the elimination of many amphipod and some polychaete species (Harper et al. 1981, Gaston 1985). Defaunated bottoms were quickly recolonized after hypoxia by *Paraprionospio pinnata* (Gaston 1985, Harper et al. 1991). In general, the community composition of the hypoxia-stressed bottoms of the Louisiana–Texas shelf has shifted to a younger, smaller sized, short-lived fauna.

The coast of Texas is only aperiodically affected by hypoxia (Harper et al. 1981, Rabalais et al. 1991). In the summer of 1979 (May–August), a hypoxic event occurred during a long-term benthic monitoring programme of the inner Texas continental shelf (1977–84, Harper et al. 1981). This provided detailed insight into how hypoxia affects inner continental shelf benthos. The phytoplankton bloom, which produced the organic matter that fuelled this hypoxia, is thought to have originated on the Louisiana shelf and moved west with prevailing currents (Harper et al. 1991). A tropical storm broke up the hypoxia in August. In subsequent years hypoxia did not occur, but there was a declining trend in minimum oxygen concentration that ended with a brief period of hypoxia in 1983. During the 1979 hypoxia, divers smelled hydrogen sulphide in bottom waters, and observed dead infauna lying on the sediment surface and bacterial mats covering large areas of the bottom (Harper et al. 1991). Motile species appeared to have migrated away from the affected habitats and not to have suffered mortality (Pavela et al. 1983). This is not always the outcome. Another bloom-associated hypoxic event occurred off Galveston, Texas, in June 1984 which caused mortalities of motile fishes and crabs (Harper & Guillen 1989).

Prior to the 1979 hypoxia on the Texas shelf, the dominance of *Paraprionospio pinnata* was declining and *Ampelisca agassizi* populations were increasing. Hypoxia then eliminated *Ampelisca* and post-hypoxia outbreaks of *Paraprionospio pinnata* briefly dominated the benthos. Deeper offshore habitats (21 m) experienced mild hypoxia, as low as $1.1\,\mathrm{ml\,l^{-1}}$, with high macrobenthic mortality but recovered within a year. In slightly shallower nearshore habitats (15 m) hypoxia was severe, with oxygen values as low as $0.5\,\mathrm{ml\,l^{-1}}$, and the occurrence of mass macrobenthic mortality. Recovery of nearshore communities did not occur within a year. The original polychaete dominants were reduced in abundance and a succession of several different taxa followed, each of which was dominant for one to three months. This pattern persisted for two years after the 1979 severe hypoxic event. At shallower nearshore habitats, *Paraprionospio pinnata* and other polychaete populations were low after initial post-hypoxia peaks, possibly as a result of shrimp predation. The 1980 shrimp catch was one of the largest recorded and many of the numerical dominants in the nearshore habitats were molluscs, which are less susceptible to shrimp predation than polychaetes (Harper et al. 1991).

Offshore areas

The Black Sea, with an average depth of 1270m, is the largest mass of "naturally occurring" permanently anoxic water on Earth. About 90% of its $5.4\times10^5\,\mathrm{km}^3$ volume is anoxic beginning at depths of 150–250m. Below about 100m, the Black Sea is permanently hypoxic (Caspers 1957, Bacesco 1963, Zenkevitch 1963). The Ukrainian northwestern Black Sea shelf is critically eutrophic with increasing frequency of phytoplankton blooms over shallow shelf seas (Tolmazin 1985, Mee 1992). Periodic hypoxia and anoxia is widespread encompassing all of the Sea of Azov and up to 95% of the Ukrainian northwestern shelf. These periodic events are distinct from the permanent anoxic layer and lead to mass mortalities of benthic populations which colonize the area during normoxic periods (Zaitsev 1991, 1993) (Fig. 3). In 1991, anoxia along the Romanian coast eliminated an estimated 50% of the demersal fish populations. Since the 1960s increasing hypoxia and anoxia have been blamed for the replacement of the highly valued demersal fish species with planktonic omnivores. Of the 26 commercial species fished in the 1960s only six still support a fishery (Mee 1992).

Macrobenthic fauna occupy about 23% of the total area of the Black Sea (Caspers 1957, Zenkevitch 1963). The lower depth limits for macrobenthic life in the Black Sea are 125 m in the western region, 115–124m in the northwest region, 127–135m off the Crimea, 135–165m off the Caucasus, 130–135m off the south coast, and 170–200m off the Bosphorous. Polychaetes are the group penetrating to greatest depths in the hypoxic water followed by molluscs. Crustaceans are poorly represented except in shallow waters. Zenkevitch (1963) and Bacesco (1963) list the following species with the deepest distributions: *Modiola phaseolina* 180m, *Amphiura stepanovi* 165m, *Nephtys hombergi* 162m, followed by *Cerianthus vestitus*, *Melinna palmata*, *Terebellides stroemi*, *Abra alba*, *Cardium simile*, *Mytilus galloprovincialis*, and phoronids extending down to about 130m. Bacesco (1963) concluded that only a few molluscs occurred below 120m depth, and only polychaetes were found below 150m. The most tolerant taxa were syllid worms and *Nephtys hombergi*, followed by *Terebellides stroemi* and *Melinna palmata*. Biomass of infauna declines dramatically below about 100m depths (Bacesco 1963) (Fig. 3). Biomass was close to zero deeper than 130m, below an oxygen concentration of $1.4–0.9\,\mathrm{ml\,l^{-1}}$, at temperatures of 8–9°C and salinities of 17 and 23psu. Mass mortalities of benthic fauna, e.g. *Mya arenaria*, have also been reported from shallow areas. These reductions may be due to toxic algae or to oxygen deficiency

(Gomoiu 1983). The deep areas of the Caspian Sea also have low oxygen concentrations. Zenkevitch (1963) reports that benthic biomass is very low (often a fraction of 1 gwwm^{-2}) in depositional areas where oxygen is low.

A trend of declining oxygen concentrations was documented from the 1930s to the late 1960s in the deep basins of the Baltic Sea (Fonselius 1969). Beginning in the 1960s and lasting up to the present, large deep bottom areas of the Baltic Sea have been mostly permanently hypoxic or anoxic and devoid of benthic macrofauna (Andersin et al. 1978). Below the halocline, at about 70m, approximately 100000km^2 of the bottom is more or less permanently hypoxic. No significant change in the bottom water oxygen content has occurred up to 1993. Low salinities (7–16psu) below the halocline also contribute to the reduced number of marine species in these areas.

Andersin et al. (1978) described a general reduction of the benthic communities in the

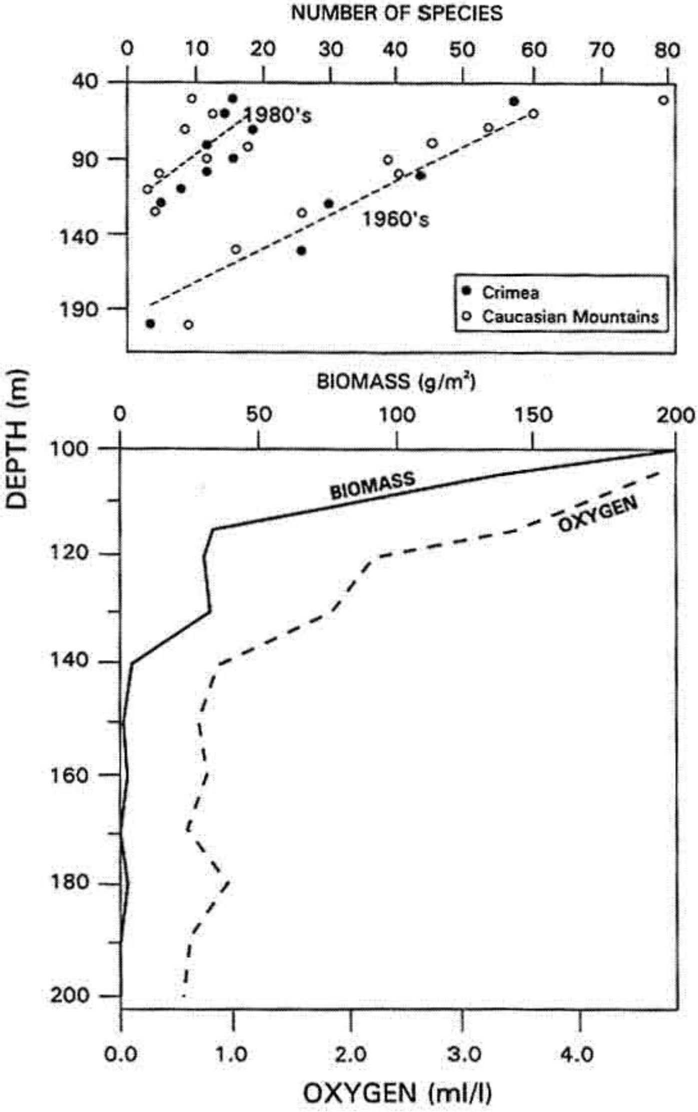

Figure 3 Long term changes in benthic fauna from 1960s to 1980s in the Black Sea in relation to depth and declining oxygen concentration is shown in the top figure (Modified from Zaika 1990 in Mee 1992). Macrofaunal biomass (wet weight) changes in relation to declining oxygen concentration with depth in the Black Sea is shown in the bottom figure (modified from Bacesco 1963).

central Baltic basin (Baltic proper) up to the mid-1970s. The general decline in depth distribution of the fauna of the Gulf of Finland is illustrated in Figure 4. It has been speculated that the biomass "missing" in the anoxic areas may be about 1.7×10^6 tww (Rosenberg 1980). Elmgren (1975) described the changes in number of species, abundance and biomass of both macro- and meiofauna along the depth gradient of declining oxygen concentrations. He noted a gradual decline in the macrofauna towards deeper bottoms containing less dissolved oxygen. The common Baltic polychaete *Harmothoe sarsi*, however, appears particularly resistant to hypoxia (Andersin et al. 1978). The number of meiofauna taxa was higher than for macrofauna at all sampling depths >45m. The proportion of nematodes, the most hypoxia and anoxia tolerant meiofaunal taxon (Hendelberg & Jensen 1993), increased with depth.

Periodic hypoxia in the mesohaline (13–17psu) Bornholm Basin in the south Baltic was reported from 1948 to 1971 by Tulkki (1965) and Leppäkoski (1969, 1971). These authors described how benthic communities were reduced and even eliminated during periods of hypoxia or anoxia and how bottoms were recolonized following a subsequent return of normoxia. The species most tolerant to hypoxia, usually the only species to be found at a station, were: *Astarte borealis*, *Halicryptus spinulosus*, *Scoloplos armiger* and *Capitella capitata*. In addition to these, Leppäkoski (1971) lists the polychaetes *Heteromastus filiformis* and *Trochochaeta multisetosa* as tolerant of hypoxia. It may be possible that some of these species colonized the area following a temporary increase in oxygen. Leppäkoski (1969) did find, however, that all individuals of *Astarte borealis* collected from 1963 to 1967 were old, implying that they survived the periodic hypoxic events.

The bottom water in the Kattegat, between Denmark and Sweden, has been affected by annual late summer–autumn hypoxia since 1980. During hypoxic years the oxycline was sharp, with lowest oxygen values close to the bottom (Rosenberg & Loo 1988, Rosenberg et al. 1992). In September 1988, the worst year on record, approximately 3000km^2 of the bottom was hypoxic and hypoxic water extended up to about 20m above the bottom. Macrobenthos was frequently affected at depths around and below the halocline at 16–22m. In some years, abundance and biomass were reduced to low numbers by mass mortality (Rosenberg & Loo 1988, Baden et al. 1990a). Table 3 shows heavy mortality and poor recolonization of infauna at a 22m deep station during and following hypoxia. The oxygen

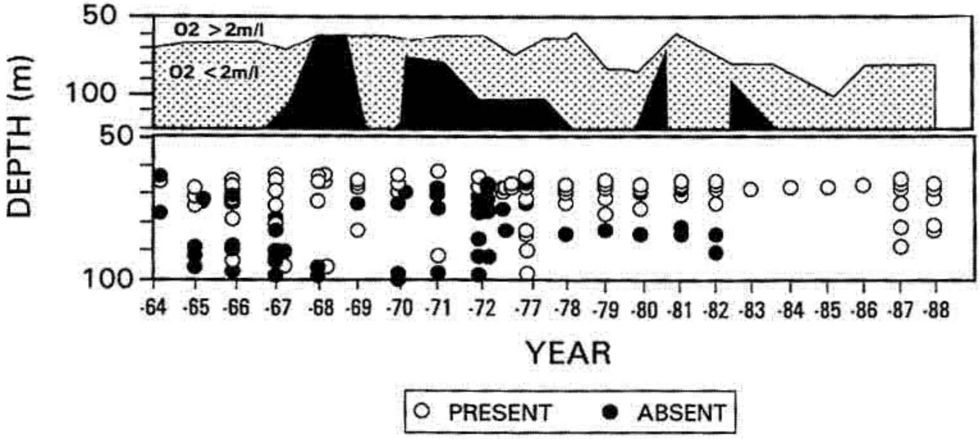

Figure 4 Vertical distribution of macrobenthos in the deep areas of the western Gulf of Finland (Baltic Sea) is shown in the bottom figure. Water column oxygen (normoxia = white, hypoxia = stippled) and H_2S (black) concentration profiles are shown in the top figure (modified from Andersin & Sandler 1991).

concentrations recorded here in 1988 were $3.1\,\mathrm{ml\,l^{-1}}$ in June, $1.0\,\mathrm{ml\,l^{-1}}$ in August, $0.9\,\mathrm{ml\,l^{-1}}$ in September, $3.1\,\mathrm{ml\,l^{-1}}$ in October, and 1.8 in November 1988. These measurements suggest that the benthos were exposed to concentrations of about $1\,\mathrm{ml\,l^{-1}}$ of oxygen about two months prior to sampling late in September 1988. Short-term oscillations in oxygen concentration over that period cannot, however, be excluded. The species that best survived this hypoxic event were the bivalves *Arctica islandica* and *Corbula gibba*, the polychaetes *Heteromastus filiformis* and *Myriochele* sp., and the phoronid *Phoronis mülleri* (Table 3).

Table 3 Abundance per $\mathrm{m^2}$ of some dominant species in relation to actual oxygen concentration and saturation at the bottom at time of sampling the fauna at station L5 (22 m depth) below the halocline in the SE Kattegat during 1986–90. Total number of species and total abundance are also given. (Adapted from Rosenberg et al. 1992).

Species	1986 Oct.	1987 Aug.	1987 Sep.	1987 Oct.	1988 Sep.	1988 Nov.	1989 Apr.	1989 Sep.	1989 Oct.	1990 Mar.	1990 Sep.
Oxygen conc., $\mathrm{ml\,l^{-1}}$	2.2	1.0	0.6	2.4	0.9	1.8	5.0	0.2	2.6	3.9	1.0
Oxygen saturation, %	35	15	7	39	10	29	48	2	41	74	16
Diastylis rathkei	277	153	460	140	100	0	0	0	0	0	0
Amphiura filiformis	80	160	67	77	67	0	0	0	0	0	0
Ophiura albida	47	43	67	77	20	0	0	0	0	0	350*
Abra alba	3663	2630	1657	477	0	0	1017*	0	0	0	0
Euchone papillosa	43	77	190	53	3	0	0	3	0	0	0
Scoloplos armiger	33	50	57	130	43	0	0	0	0	0	0
Terebellides stroemi	7	27	93	13	7	0	0	0	0	0	0
Arctica islandica	113	97	100	110	100	70	83	90	87	107	93
Corbula gibba	123	150	130	37	23	60	53	63	100	217	60
Phoronis mülleri	110	13	87	307	467	390	180	283	190	307	303
Heteromastus filiformis	95	0	7	0	250	140	80	43	217	257	527
Myriochele spp.	230	177	284	513	630	367	90	280	383	440	577
Total no. of species per $0.3\,\mathrm{m^2}$	41	36	41	46	30	26	21	25	20	30	42
Total abundance per $\mathrm{m^2}$	5337	4237	3690	2397	2100	1380	1647	977	1143	1560	2300

* Juveniles.

A 37 m station in the Kattegat, dominated by two brittle stars, was sampled in October and November 1985 (30 days apart). Fishermen reported dead *Nephrops norvegicus* in that area in the middle of that period when the oxygen concentration was $1.8\,\mathrm{ml\,l^{-1}}$ about 1 m above the bottom, but probably less at the bottom (see Rosenberg & Loo 1988 their Fig. 2). During this episode *Amphiura filiformis* was significantly reduced in abundance and biomass, whereas *A. chiajei* was not. This suggests that *A. filiformis* is more susceptible to low oxygen concentrations than *A. chiajei* (Rosenberg & Loo 1988).

In October 1987 dead *Abra alba* were photographed lying on the surface with their valves open and mantle edge visible, indicating recent mortality. The oxygen concentration at that time was $3.4\,\mathrm{ml\,l^{-1}}$. During grab sampling one month earlier, most of the population was alive, but some recently dead specimens were noted. The oxygen concentration was then $0.8\,\mathrm{ml\,l^{-1}}$ (Baden et al. 1990a). The finding of recently dead bivalves in October was most probably a result of the low oxygen concentrations prior to the sampling.

The examples given above show localized effects at some sites in the Kattegat. However, in September 1988 bottom trawling was conducted at 12 stations in the Kattegat over an area of approximately 3000 km^2 where the oxygen concentrations were approximately 1 ml l^{-1} (15% saturation). Each trawl, which lasted 1 h, caught 200–400 kg of dying infauna, indicating large scale effects of hypoxia (Baden et al. 1990a).

In 1984, 24 of Petersen's stations sampled in 1912 in the Kattegat were resampled for macrofauna. Total biomass was significantly reduced in the northern and western Kattegat, and in general the majority of species were found to be smaller in size in 1984 compared with 1912 (Pearson et al. 1985). This may be an effect of increasing periodic hypoxia in the area. In 1989, some of these stations were resampled by Josefson & Jensen (1992). They recorded a 70–80% reduction in biomass and poor recruitment compared to the 1984 survey at four stations where oxygen concentrations in 1988 had been <1 ml l^{-1}. Overall, temporal variation in benthic communities in the Kattegat was greatest where the seasonally most severe hypoxia occurred (Rosenberg et al. 1992).

The Norway lobster (*Nephrops norvegicus*) population was also affected by the hypoxia in that area. In 1984, rather high catches were recorded (mean 10 kg h^{-1}) where oxygen concentrations were >2 ml l^{-1}. Following that year, oxygen concentrations during summer–autumn dropped below 2 ml l^{-1} and poor catches were recorded. From September 1988 onwards no lobsters were found in the south Kattegat (Baden et al. 1990a). The diet of demersal fish in that area changed with declining oxygen concentrations. During periods of oxygen deficiency the consumption of epibenthic crustaceans was reduced and shifted towards a greater proportion of hypoxia-tolerant infaunal species (Pihl 1994).

In the North Sea, west of Denmark and the German Bight, seasonal bottom water hypoxia was recorded below the summer thermocline in August 1981, 1982, and 1983. The hypoxia lasted about four weeks each year, with September storms dispersing the hypoxic water masses. The severity of hypoxia increased each year (Rachor & Albrecht 1983) with oxygen concentrations dropping to <0.7 ml l^{-1} by 1983. In 1981, mass mortality of epibenthos was observed near the Danish west coast (Dyer et al. 1983), but no effects on macrobenthos were observed (Rachor & Albrecht 1983). During the 1992 hypoxia, Dethlefsen & Westernhagen (1983), Westernhagen & Dethlefsen (1983) and Dyer et al. (1983) documented widespread acute mortality of epibenthos. In 1983, macrofauna was reduced by as much as 30–50% in some affected areas (Niermann et al. 1990). During the hypoxic years communities were dominated by species such as *Magelona* spp. and *Edwardsia* spp. The long-term reductions in populations of *Nucula nitidosa* and *Abra nitida* in the German Bight appear to be related to the worsening hypoxic conditions (Rachor 1985).

The oxygen concentration in the bottom water of the Adriatic Sea declined between 1911 and 1984 (Justic 1987). In September 1983 a severe hypoxic event occurred with day-to-day reduction in benthic species as documented photographically by Stachowitsch (1984, 1991). The area affected was estimated to have been at least 250 km^2, and biomass was estimated to have been reduced by 20, 57, 80 and 93% over the first four days of the hypoxic event (Fig. 5). The most resistant species were the anemones *Ragactis pulchra* and *Calliactis parasitica*, which normally are attached to shells of hermit crabs. High temperatures (about 18°C) may have been an important factor in the rapid mortality seen. The detailed reports of Stachowitsch are, unfortunately, not accompanied by oxygen recordings.

An area of the Mediterranean Sea that now experiences annual hypoxia and anoxia is Elefsis Bay at the north end of Saronidos Gulf, Western Aegean Sea. Elefsis Bay is a semi-enclosed embayment of 67 km^2. Nutrients discharged from the Keratsini Athens sewage outfall and industry sources cause severe ecological stresses in the Bay. By 1973, hypoxia and anoxia were occurring in the deeper areas, below about 30 m, from July through August

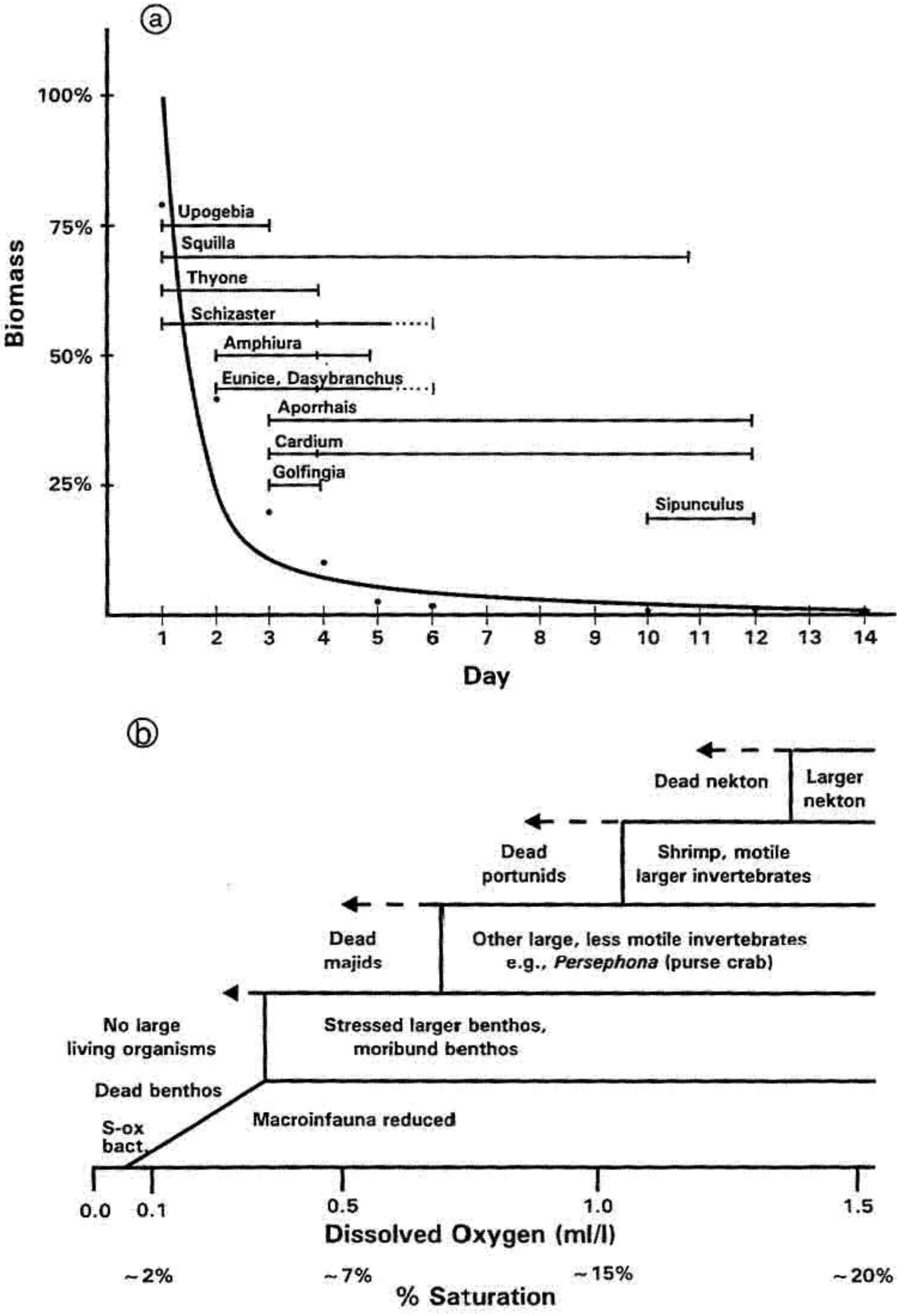

Figure 5 (a) Estimated decline in biomass (curve) and timing of macrobenthos elimination during the 1983 Gulf of Trieste hypoxic event (modified from Stachowitsch 1991). (b) Graded response of nekton, megafauna and infauna to delining oxygen concentrations (modified from Rabalais in preparation).

(Friligos 1976). By 1977 the annual summer hypoxia and anoxia had more than doubled in the area, and bottoms as shallow as 20m were affected. Hypoxia and anoxia are now the primary factors regulating seasonal changes in benthic communities and the timing of annual recruitment in affected areas. On average, 16 species per $0.2\,m^2$ recruited into habitats experiencing anoxia, while normoxic habitats recruited 61 species per $0.2\,m^2$. However, the magnitude of recruitment was similar in oxygen stressed and normoxic habitats at about 5100–6100 individuals per m^{-2} (Friligos & Zenetos 1988).

Oceanic and continental slope environments

The eastern Pacific is characterized by a shallow mixed layer (Wishner et al. 1990) and a pronounced oxygen minimum (Wyrtki 1966). In 1988, the core of the OMZ ($<0.5\,ml\,l^{-1}$) around the Volcano 7 seamount intersected the bottom from a depth of 70 to 1300m, with lowest oxygen ($<0.1\,ml\,l^{-1}$) from 300 to 1100m. OMZ bottom boundaries are regions of enhanced biological activity. The enhanced flux of high quality, undegraded organic matter to the bottom under an OMZ is partly due to primary production sinking through midwater depths where hypoxia has reduced populations of midwater consumers (Gowing & Silver 1983). When upwellings are associated with the OMZ there is also an increase in primary production (Walsh 1981). This high organic matter flux typically supports an unusually high abundance of benthic species that are tolerant to hypoxia (Wishner et al. 1990, Levin et al. 1991).

At the edge of an OMZ, benthic fauna experience steep gradients in oxygen and organic matter. Along the California coast north of Point Conception, Hyland et al. (1991) found that communities in muddy sediments on the shallow edge of the OMZ, in the Santa Maria Basin in $1.3\,ml\,l^{-1}$ of oxygen, had less than half the abundance and species of nearby normoxic stations with oxygen levels of $2.7\,ml\,l^{-1}$. Deeper into the OMZ ($0.6\,ml\,l^{-1}$), abundance and species number were further reduced to about one-fourth of the normoxic stations. Along the edge of the central California coastal OMZ, off Point Sur, Mullins et al. (1985) found increased biogeochemical activity. Macrofauna and benthic foraminiferans displayed edge effects at both the upper and lower OMZ depth boundaries (Fig. 6; Mullins et al. 1985). The lowest oxygen measured was $0.27\,ml\,l^{-1}$ at 700–750m (Broenkow & Greene 1981 in Mullins et al. 1985). The primary factor responsible for this faunal distribution pattern (edge effect) is the hypoxia, but Mullins et al. (1985) hypothesize combinations of bottom currents, bacterially mediated nutrient recycling and food supply are also important controlling factors. Levin et al. (1991), at the Volcano 7 seamount, found that megafauna and macrofauna were severely reduced in a near-anoxic zone ($<0.1\,ml\,l^{-1}$), but just tens of metres in depth from that near-anoxic area, the fauna attained high abundance in a severe hypoxic zone (0.11–$0.16\,ml\,l^{-1}$). These authors found that populations of microbes and meiofauna, except harpacticoids, reached peak abundance within the near-anoxic zone.

Off Point Sur, California, the boundaries of the OMZ ($0.5\,ml\,l^{-1}$) occur at 500–525m and 1000–1025m. These boundaries have been temporally and spatially stable for at least the past 25 years (Mullins et al. 1985). Data from Volcano 7 from 1984 and 1988 indicate similar stable OMZ conditions (Wishner et al. 1990). Sampling eight times from 1986 to 1989 in the OMZ ($0.6\,ml\,l^{-1}$) of the Santa Maria Basin, California, Hyland et al. (1991) determined that communities were stable and had lower variation in community structure through time when compared with normoxic communities at $2.7\,ml\,l^{-1}$ oxygen just above the OMZ.

The upwelling system along the Peru–Chile coast is well studied (Rosenberg et al. 1983,

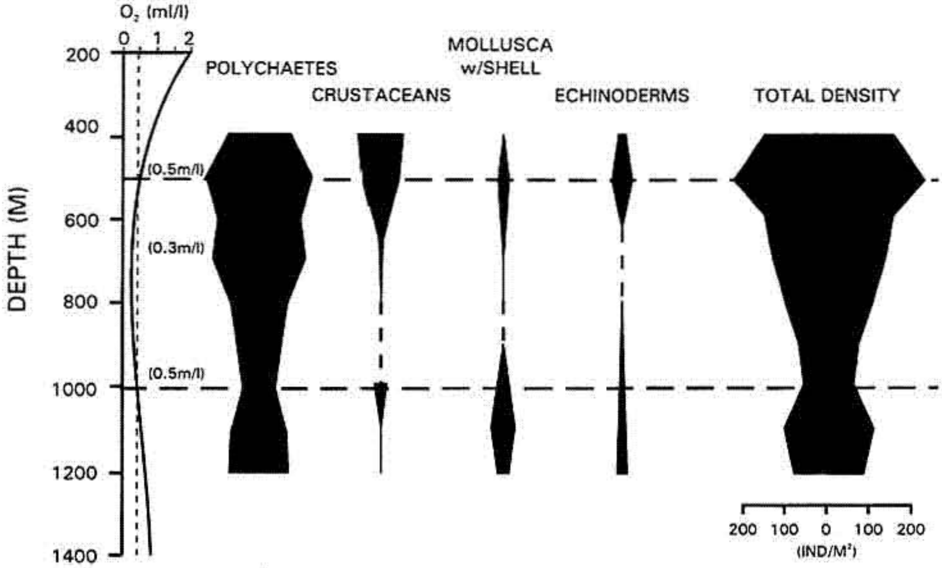

Figure 6 Major-taxon density (number of individuals per m^2) vs water depth and oxygen concentration across central California oxygen minimum zone, OMZ. Dashed lines highlight boundaries and core of OMZ (modified from Mullins et al. 1985).

Arntz & Fahrbach 1991 and references therein) and serves as a model system for hypoxic and anoxic effects on benthos. Generally, oxygen is $<0.8\,\mathrm{ml\,l^{-1}}$ from 20 to 700m depth. Enrichment of the bottom by sedimentation of high quality organic matter leads to enhanced benthic biomass in hypoxia from 2.0 to about $0.6\,\mathrm{ml\,l^{-1}}$ (80m). Below about $0.2\,\mathrm{ml\,l^{-1}}$, macrobenthic biomass was reduced, but microbial biomass (*Thioploca* spp.) increased (Rosenberg et al. 1983). Beyond 700m, Thiel (1978) found deep-sea benthic biomass off Peru to be higher than in other non-upwelling areas, possibly a result of downslope transport of organic matter. Fish catches are negatively correlated with occurrence of filamentous bacteria and positively correlated with macrobenthic biomass. Benthic and demersal fish biomass increase above and below the hypoxia (Rosenberg et al. 1983).

The temporal and spatial stability of dissolved oxygen within upwelling and OMZ systems, combined with a supply of high quality organic matter appear to be a key in successful adaptation of fauna to hypoxic conditions (Rosenberg et al. 1983, Mullins et al. 1985, Forbes & Lopez 1990, Levin et al. 1991). The importance of high quality organic matter in the development of benthic communities under upwellings and OMZs can be seen in the modifications of the original Rhoads & Morse (1971) biofacies model for anoxic and hypoxic habitats proposed by Thompson et al. (1985). Basically, it differs from the model of Rhoads & Morse (1971) by lowering the upper limit of oxygen from 1.0 to $0.3\,\mathrm{ml\,l^{-1}}$ for the dysaerobic zone (Rhoads et al. 1991). The availability of large quantities of high quality organic matter results in an increased tolerance of species through energetic compensation. Even though more energy is used in surviving within the hypoxic environment, the availability of easily digested and nutritious organic matter allows populations of tolerant species to flourish.

Tolerance to hypoxia and H_2S from experiments

Physiological experiments

The physiological response of marine organisms to hypoxia is a broad subject, to which several review and summary papers are devoted (see Mangum & van Winkle 1973, Herreid 1980, Warren 1984). Here we will summarize results from papers dealing with tolerance of marine infauna to hypoxia. In these experiments, unfortunately, few efforts were made to treat the organisms as if they were in their natural benthic habitat. Consequently, the ecological implications of these results are difficult to assess.

In a series of experiments conducted in the late 1960s and early 1970s, more than 20 benthic species were examined for tolerance to hypoxia and/or H_2S (Theede et al. 1969, von Oertzen & Schlungbaum 1972, Theede 1973, Dries & Theede 1974). The methods used in these experiments were similar. Most organisms were obtained from the south Baltic, but some came from the North Sea. The experiments were performed in glass cylinders with filtered sea water and no sediment. The oxygen was lowered by bubbling nitrogen gas into the water, to which animals were added. Such procedures not only shock the organisms but also alter the pH and carbonate balance of the water. In addition, the absence of sediment means that organisms were tested without their natural environment.

At a salinity of 17 psu and a temperature of 10°C survival of species in oxygen concentrations $<0.15\,\mathrm{ml\,l^{-1}}$ varied between a few hours and three months (Dries & Theede 1974). The species with highest tolerances were arctic bivalves, followed by boreal bivalves, polychaetes, echinoderms, and then crustaceans (Fig. 7). In another experiment, comparisons were made between tolerance to hypoxia alone ($0.15\,\mathrm{ml\,l^{-1}}$) and to hypoxia plus H_2S "in a concen-

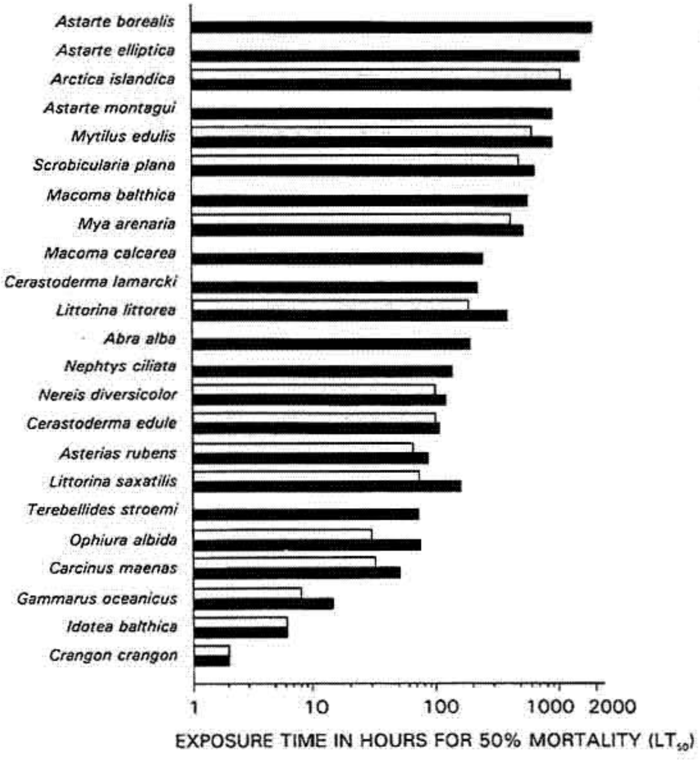

Figure 7 Resistance of marine invertebrates to oxygen deficient sea water (black bars) and in some cases with the addition of H_2S (grey bars)(experiments without sediment) (modified from Theede 1973, Dries & Theede 1974).

tration approximately comparable to that of certain areas in the North Sea, Baltic Sea and Black Sea" (Theede et al. 1969, Theede 1973). These authors conclude that high resistance to H_2S parallels that to hypoxia. Theede et al. (1969) found the tolerance in experiments with hypoxia at 10°C to be approximately 20% higher compared with hypoxia plus H_2S (Fig. 7). These experiments suggest that the addition of H_2S had a minor but notable effect on the survival of benthic animals. In similar parallel experiments with five bivalves exposed to hypoxia (0.1–0.15 ml l^{-1}) and H_2S (2–14 mg l^{-1}), it was concluded that resistance of these species to hypoxia was similar to resistance to H_2S (von Oertzen & Schlungbaum 1972). In other experiments dealing with physiological parameters, but using similar methods to those detailed above, Oeschger (1990) and Oeschger & Storey (1990) mention that the priapulid *Halicryptus spinulosus* and the bivalves *Astarte borealis* and *Arctica islandica* can withstand anoxic conditions for long periods.

Llansó (1991), found *Streblospio benedicti*, which is at times dominant in hypoxic estuarine habitats of North America, tolerant of severe hypoxia (surviving at least 14 days at 0.4 ml l^{-1}). However, its low tolerance of anoxia (100% mortality in 2.3 days, LT_{50} 1.8 days) was typical for that of other polychaete species (Table 2 in Llansó 1991). Tolerance of *Streblospio benedicti* was not reduced by exposure to anoxia combined with 66 μM sulphide (Llansó 1991). Two polychaetes particularly sensitive to sulphide under hypoxic conditions are *Cirriformia tentaculata*, with survival reduced by five days in the presence of 200 μM sulphide (Bestwich et al. 1989), and *Arenicola marina*, survival reduced from 10 to 4.5 days with 10 μM (Groenendaal 1980).

The hypoxia tolerance of the polychaetes *Capitella capitata* and *Polyphysia crassa* was tested at 5–6°C. About 50% of these animals survived at 0.8–0.9 ml l^{-1} of oxygen for 13 and 8 days, respectively. At 1.5 ml l^{-1} most *Capitella capitata* survived >24 days (Rosenberg 1972). *Capitella* sp. 1 stopped burrowing and feeding at $<0.8\,\text{ml l}^{-1}$ when confronted with hypoxia. These behavioural changes may account for the relatively long survival times of adults in severe hypoxia (2 mm Hg) with no food or sediment (only 30% mortality after 35 days, Warren 1977). However, at least trace amounts of oxygen are needed for long-term survival (100% mortality after 30 days in <1 mm Hg, Warren 1977). The net effect of prolonged hypoxia on populations may then be indirect through starvation induced mortality and not from lack of oxygen. In hypoxia, small *Capitella* sp. 1 lose body volume at 3% d^{-1} and large worms at 20% d^{-1} (Forbes & Lopez 1990). It appears that in severe hypoxia small worms are better able to satisfy their metabolic demands with more efficient aerobic metabolism using the small amount of available oxygen than are large worms (Forbes & Lopez 1990).

Lower temperatures were positively correlated with increased survival during hypoxia. With few exceptions, survival was longest at 0°C followed by 5, 10, 15, and 20°C (von Oertzen & Schlungbaum 1972, Dries & Theede 1974). The influence of salinity was minimal for euryhaline species (Theede et al. 1969). Results from these authors also indicate that infauna inhabiting finer sediments (clay–silt) seem to have a higher tolerance than infauna from sandy sediments. Experiments repeated during different seasons suggest that if the individuals were tested at different points in their life histories, different tolerance times may result. For example, *Ophiura albida* showed only half the tolerance time (LD_{50}) to hypoxia in May to July compared with December to February (Dries & Theede 1974).

Larval tolerance of hypoxia in opportunistic species may be critical to their early recolonization of hypoxia stressed habitats, particularly in organically enriched habitats which are prone to develop hypoxia and anoxia due to high chemical and biological oxygen demand. Llansó (1991) found that larvae of *Streblospio benedicti* were unaffected when exposed to short-term hypoxia (92 h, 14% saturation). The response of *Mytilus edulis* larvae to hypoxia varies with developmental stage (Wang & Widdows 1991). Embryo and early prodissoconch larvae of *M. edulis* are tolerant of hypoxia and grow normally at oxygen concentrations as low as $1.0\,\mathrm{ml\,l^{-1}}$. Growth of later stage larvae was depressed by hypoxia, but hypoxia had little influence on settlement behaviour of pediveligers (Wang & Widdows 1991).

Experiments with sediments

When hypoxia is initiated at the sediment/water interface, H_2S concentrations increase in the oxic sediments above the redox potential discontinuity (RPD) layer and may reach toxic concentrations for the infauna. Toxicity of H_2S results from the inhibition of the electron transport chain in aerobic respiration (Torrans & Clemens 1982). Vismann (1991a) has reviewed the literature on sulphide tolerance and states that increased tolerance may be achieved by five different mechanisms: prevention of H_2S from entering the organism, possession of an H_2S insensitive cytochrome-c oxidase, reliance on anaerobic metabolism, detoxification of H_2S by endosymbiotic sulphide-oxidizing bacteria, and detoxification of H_2S in the animal tissue. Thus, to understand fully the effects of oxygen deficiency on infaunal organisms the concentration of H_2S must be taken into account. The additional stress caused by H_2S is, as for hypoxia alone, dependent on concentration, temperature (von Oertzen & Schlungbaum 1972) and duration of exposure. In this section we summarize experiments designed to simulate natural conditions, with animals tested within their native sediment.

Six infaunal species indicative of pollution in the Öresund, between Denmark and Sweden, were put in 1-l jars with native sediment (Henriksson 1969). The jars were sealed and all oxygen was consumed in two to three days. *Macoma balthica* showed the highest resistance, with 50% surviving after 18 days. The ranked tolerance in declining order of the other species was *Cardium lamarcki* → *Nereis diversicolor* → *Scoloplos armiger* → *Ampharete grubei* → *Terebellides stroemi*. Thus, it seems that bivalves (*Macoma* and *Cardium*) were more tolerant than polychaetes in this test with rapidly declining oxygen ending in anoxia.

Vismann (1990) exposed the polychaetes *Nereis diversicolor* and *N. virens* to hypoxia (*c.* 10% saturation) and to hypoxia combined with $172–187\,\mu\mathrm{M}$ sulphide continuously supplied to the water in a flow through system with natural sediment. No differences in survival were found between the treatments during the first six days, but subsequently *N. virens* in hypoxia+sulphide showed a higher mortality, whereas the worms exposed to only hypoxia survived for at least another five days; however, there was no replication. *N. diversicolor* survived both treatments during the initial 16 days, but during the following six days mortality was higher in hypoxia+sulphide. Such tolerance to hypoxia+sulphide corresponds to the sulphide tolerances determined by Miron & Kristensen (1993) and Theede et al. (1973) for both species. *N. virens* was the least tolerant of pore water sulphide with *N. diversicolor* and *N. succinea* possessing adaptive mechanisms to cope with sulphide. Such mechanisms were also described by Vismann (1990) and Oeschger & Janssen (1991). The presence of sulphide in moderate to high concentrations combined with hypoxia appears to be more toxic than hypoxia alone after prolonged exposure. The build-up of sulphide in the sediment during hypoxia may also reduce survival of infaunal species. Imabayashi (1986) indicated that juveniles of the bivalve *Theora lubrica* appear more susceptible to hypoxia and hydrogen sulphide than do adults.

The tolerance of three terebellid polychaetes (*Loimia medusa*, *Terebella lapidaria*, and *Terebellides stroemi*) to anoxia and severe hypoxia is similar and ranges from three to six days (Henriksson 1969, Warren 1984, Llansó & Diaz 1994). In moderate hypoxia ($0.7\,\mathrm{ml\,l^{-1}}$, 14% saturation) *Loimia medusa* survived at least 14 days (Llansó & Diaz 1994). In hypoxic experiments (4.7–6.2% saturation at about 10°C) with animals in 5 cm of sieved sediments, Larsen & Petersen (1991) found that most individuals of *Amphiura filiformis*, *Abra alba*, *Abra nitida*, and *Mysella bidentata* survived for at least 17 to 34 days.

Tolerance of benthic communities in their natural sediments with different redox potentials, one "non-sulphidic" and the other "sulphidic" at the sediment surface, to moderate (about 0.7 $\mathrm{ml\,l^{-1}}$) and severe hypoxia (about 0.4 $\mathrm{ml\,l^{-1}}$) was tested by Nilsson & Rosenberg (1994) (Fig. 8). In the "non-sulphidic" community, survival of individuals was reduced in severe hypoxia compared with moderate hypoxia and normoxia. In the "sulphidic" community abundance and the number of species were significantly reduced in the moderate and severe hypoxia compared with normoxia. Although the species composition was not the same in the two experiments the results suggest that higher H_2S concentrations in the sediment intensify the effect of hypoxia.

Rosenberg et al. (1991) exposed eight infaunal species (*Abra alba, A. nitida, Amphiura filiformis, A. chiajei, Arctica islandica, Cerastoderma edule, Mya arenaria* and *Ophiura albida*) to gradually declining oxygen concentrations in their native sediment. Salinity and temperature were constant during the experiments at 32 psu and 10–11°C. Hypoxia (0.63 $\mathrm{ml\,l^{-1}}$, 10% saturation) was reached after one to two weeks and was then maintained for the rest of

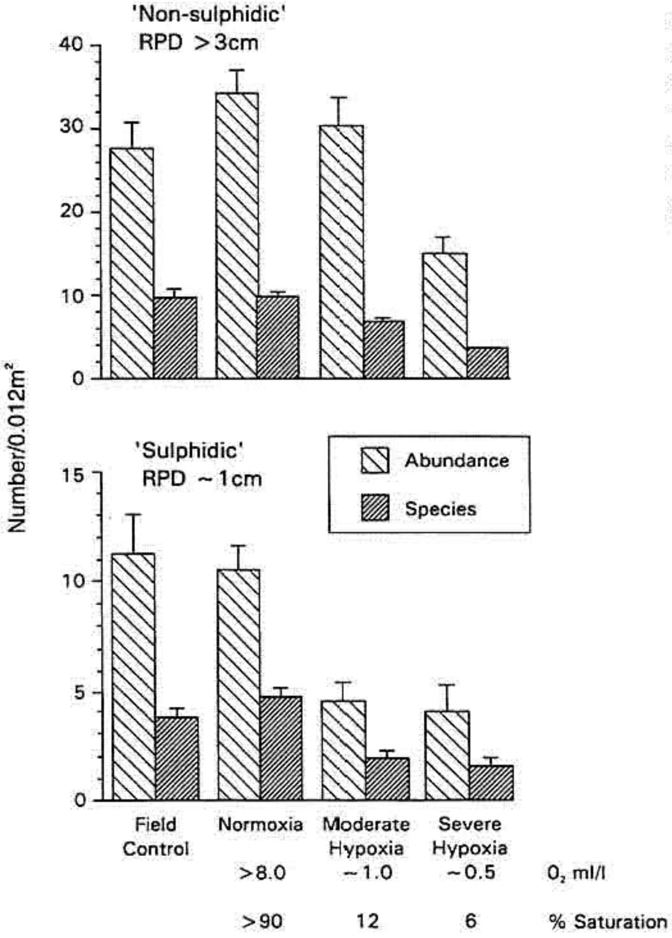

Figure 8 Average abundance and species number after natural communities were exposed to moderate and severe hypoxia in "non-sulphidic" and "sulphidic" sediments (modified from Nilsson & Rosenberg 1994).

the experiment. The majority of species tested survived for several days to several weeks in hypoxia. All differences between controls and treatments were significant with the exception of *Arctica islandica* trials. The lobster *Homarus gammarus* was tested in similar experiments but without sediment. After about 30 days, lobsters in hypoxia ($1.6\,\mathrm{ml\,l^{-1}}$) were sluggish, and all lobsters died on the 41st day when oxygen was $0.63\,\mathrm{ml\,l^{-1}}$.

Behavioural changes caused by hypoxia

Much of what we know about behavioural and physiological compensation to hypoxia in marine benthos is derived from intertidal species (see Warren 1984). Intertidal organisms are regularly subjected to hypoxia during low tide when they are isolated from the water column. The compensation mechanisms that have evolved are all directed towards short-term survival of hypoxia but also allow organisms to utilize habitats that experience periodic hypoxia or are permanently marginal relative to dissolved oxygen concentration.

While Mangum & van Winkle (1973) found that most species tested showed some compensation for surviving in reduced oxygen conditions, there does not appear to be any long-term physiological mechanism for surviving chronic stable hypoxia. In metazoans, the shift to anaerobic pathways during severe hypoxia and anoxia is energetically less efficient than aerobic pathways utilized during normoxia and consequently too costly to allow the completion of a life-cycle (Herreid 1980, Powell 1989). An exception may be those upwelling areas and OMZs where chronic and stable hypoxia is associated with highly nutritious organic matter (Mullins et al. 1985, Levin et al. 1991). Under these conditions, a low-oxygen-tolerant fauna may evolve and thrive (Tunnicliffe 1981, Rosenberg et al. 1983). In the upwelling system off Peru, Rosenberg et al. (1983) found six genera to be abundant and have high biomass in a permanently oxygen deficient area of the continental slope.

Fluctuating and short-term hypoxia is survivable through a combination of behavioural (Steimle & Radosh 1979, Jørgensen 1980, Stachowitsch 1984) and physiological adaptations (Herreid 1980, Innes 1985). With the onset of hypoxia, the dynamic balance between oxygen concentration and an organism's response shifts hierarchically (Table 4, p. 276). The first response to declining oxygen is an increase in respiration rate. Petersen & Petersen (1988) found that as oxygen concentration declined to 50–60% saturation a gobiid fish initiated increased respiration before avoidance behaviour. Mobile fauna then begin to migrate away from low-oxygen areas (Renaud 1986a,b, Pihl 1989, Baden et al. 1990a, Rahel & Kolar 1990, Pihl et al. 1991). Fauna, unable to leave or escape, initiate a series of sublethal responses related to the severity of hypoxia (Warren 1984). Feeding ceases and activities not related to respiration decrease. Increased periods of rest occur to depress metabolism. Under anoxia tube irrigation decreases (Warren 1984). For infaunal species decreased tube irrigation has the effect of allowing the accumulation of reduced compounds in sediments that were previously oxidized. As oxygen continues to decline and/or reduced compounds accumulate, the infauna migrate closer to the sediment surface (Ankar & Jansson 1973, Jørgensen 1980, Vismann 1990, Tyson & Pearson 1991b, Llansó 1992). The moribund individuals lying on the surface of the sediment are thus easy prey if pelagic predators are able to enter the hypoxic water column to feed (Pihl et al. 1992). Selective mortality occurs first among the more sensitive taxa, such as crustaceans and echinoderms (Harper et al. 1981, Stachowitsch 1984, Boesch & Rabalais 1991). If hypoxia persists or intensifies, extensive mortality is seen in all but the most tolerant species (Arntz 1981, Weigelt & Rumhor 1986, Rosenberg & Loo 1988, Llansó 1992).

Many epifaunal and infaunal species react to declining oxygen concentrations with a similar set of behaviours (Table 4). Mobile species first attempt to avoid hypoxia through migration. Infaunal species capable of limited mobility may also attempt an escape response (Diaz et al. 1992). Hypoxia causes the RPD layer to migrate closer to the sediment surface by reducing the oxygen gradient into the sediment. This forces tube dwelling and burrowing species to move closer to the sediment surface (Ankar & Jansson 1973, Rosenberg 1977) or to emerge from the sediment in search of higher oxygen concentrations (Egusa & Yamamoto 1961, Jørgensen 1980). The process of emerging from the sediment into hypoxic bottom water appears to be regulated by the oxygen microgradients within centimetres of the bottom (Tyson & Pearson 1991b) and by accumulation of H_2S within the sediments (Vismann 1991). Once on the sediment surface, different postures are assumed depending on the oxygen concentration.

Some bivalves react to hypoxia by stretching their siphons up into the water column, where more oxygen and/or some current may be found. In the Limfjord, Denmark, where a strong gradient in oxygen concentrations was found within the benthic boundary layer, with minimum values of 0.1–$0.7\,\mathrm{ml\,l^{-1}}$, *Mya arenaria*, *Cerastoderma edule* and *Abra alba* were observed with their siphons extended into the water column (Jørgensen 1980). *Mya arenaria* extended their siphons 20–30cm above the sea bed. In experiments at mean oxygen concentrations of $0.9\,\mathrm{ml\,l^{-1}}$, Rosenberg et al. (1991) determined that the water column siphon activity of *Abra alba* was 3.5 times greater than that of specimens in oxygenated waters. *A. alba* also had a significantly higher siphon activity than *A. nitida* when exposed to hypoxia. *Mulinia lateralis* remained active and continued to feed when exposed to hypoxia (Shumway et al. 1983). The amphipod *Corophium volutator* responded to oxygen saturation below 30% by constructing mud tubes that protruded from the sediment surface. These tubes may then serve to raise the point of contact above the sediment surface into more oxygenated water (Eriksson & Weeks 1994).

Responses of white (*Penaeus setiferus*) and brown (*P. aztecus*) shrimp to hypoxic water encompass the range of possible behavioural reactions. These shrimp first increase their general activity level (rapid eye-stalk movements and flexing of their antennal scales) and then retreat from hypoxia by walking or swimming. In addition, white shrimp unable to escape hypoxia exhibited abdominal flexures until they appeared exhausted (Renauld 1986b). White shrimp detected and avoided hypoxic water $\leq 1.1\,\mathrm{ml\,l^{-1}}$. Brown shrimp were more sensitive and avoided hypoxic water $\leq 1.4\,\mathrm{ml\,l^{-1}}$. Physiological stress from hypoxia and resultant abnormal behaviours may make shrimp more vulnerable to predators that are more tolerant of low oxygen levels.

Rosenberg et al. (1991) demonstrated a threshold response to decreasing oxygen concentration in the ophiuroids *Amphiura filiformis* and *A. chiajei* (Fig. 9). Under normoxia these ophiuroids live in a buried position with their discs at about 5cm from the sediment surface. During hypoxia they move rapidly to the sediment surface. More than half of the *A. filiformis* emerged at a concentration of $0.85\,\mathrm{ml\,l^{-1}}$, and at $0.54\,\mathrm{ml\,l^{-1}}$ for *A. chiaje*. Specimens on the sediment surface frequently stood on the tips of their arms with the disc elevated above the surface. They were also found lying upside-down. It was suggested that the significantly higher tolerance to hypoxia of *A. chiajei* was because this species has a respiration rate five times lower than *A. filiformis* (Buchanan 1964).

In growth experiments with juvenile *A. filiformis* and *Abra alba* in sediment, Larsen & Petersen (1991) found that at about 20% saturation, growth was approximately the same as in fully oxygenated water. Growth was reduced by 44% and 61% for these species, respectively, at 10% saturation. Forbes & Lopez (1990) found for *Capitella* sp. 1 that a reduction in oxygen from 5.4 to $1.5\,\mathrm{ml\,l^{-1}}$ decreased growth of large worms (>1.6mgww individual)

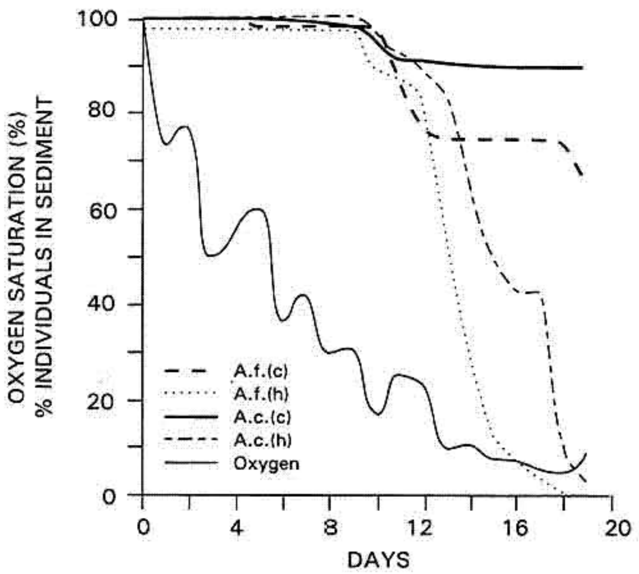

Figure 9 Emergence from the sediment of *Amphiura filiformis* (A.f.) and *A. chiajei* (A.c.) during deoxygenation of the overlaying water (h) and in the control (c) (modified from Rosenberg et al. 1991).

by up to 36% per day. Continued reduction of oxygen from 1.6 to 0.8 $\mathrm{ml\,l^{-1}}$ further decreased growth of large worms from 2% to 25% per day. Growth of small worms (<1.1 mg ww), however, was unaffected.

During a hypoxic event in the Kattegat, *Ophiura albida* were observed from a remotely operated submersible vehicle to be standing immobile on their arm tips at an oxygen concentration of 0.5–0.6 $\mathrm{ml\,l^{-1}}$ (7–10% saturation). In an adjacent bottom area, where the oxygen concentration was 1.4 $\mathrm{ml\,l^{-1}}$ (24% saturation, 15°C), the brittle stars were mobile with their discs on the sediment surface (Baden et al. 1990a). In the area where *O. albida* were on their arm tips, arms of what must have been *Amphiura filiformis* were actively waving up in the water column. It is not clear on the video if the discs were at the sediment surface (Rosenberg, pers. obs.). During hypoxia in the North Sea, *Ophiura albida* were also observed standing on their arm tips at an oxygen concentration of 0.6 $\mathrm{ml\,l^{-1}}$ (14°C) (Dethlefsen & von Westernhagen 1983). These authors found that *O. albida* had the same arm tip posture in the laboratory at an oxygen concentration of 1.35 $\mathrm{ml\,l^{-1}}$. Thus, it seems that an oxygen concentration less than about 1.4 $\mathrm{ml\,l^{-1}}$ can trigger this "arm-tipping" behaviour.

Sea cucumbers, when first confronted with hypoxia (60–70% saturation), swell to increase their surface area to volume ratio, which promotes oxygen uptake through their general body surface. The large coelom also provides a store of oxygen, which allows individuals to initiate an escape from the hypoxia. When faced with severe hypoxia (<15 torr) sea cucumbers will eviscerate to reduce their metabolic requirements (Astall & Jones 1991).

When initially exposed to hypoxic conditions, the polychaete *Loimia medusa* ceased feeding activities within 20h, but continued to irrigate their tubes. After 42–122h in 14.3% saturation, feeding resumed. General activity of *L. medusa* (tube irrigation, protrusion of the anterior thoracic region out of the tube, movement of tentacles and branchia) declined during the 14-days exposure to hypoxia (14.3 and 7.2% saturation). About 25% of the worms came out of their tubes during the 14-days experiment (Llansó & Diaz 1994). Under anoxic conditions *L. medusa* rapidly ceased feeding and tube irrigation activities, and started to evacuate their tubes after 24h (Llansó & Diaz 1994).

Metridium senile can survive extended periods of anoxia. Wahl (1984) described a set of behaviours for *M. senile* in anoxia that starts with retraction of tentacles and reduction of body surface when anoxia is first encountered. After 7 to 9 days of exposure to anoxia, energy consuming activities ceased. At approximately 10 days of exposure the anemone detached from its substratum. If oxygen levels increase before both ciliary activity stops and detachment occurs, 60% of the anemones recover.

In experiments with natural sediments, many infaunal species leave the sediment at oxygen concentrations below $0.7\,\mathrm{ml\,l^{-1}}$ (12% saturation). After several days at that concentration, the polychaete *Pectinaria koreni* emerged from the sediment with its tube. Later the tube fell over and the worm died. The echinoderms *Echinocardium cordatum* and *Amphiura filiformis*, and the small bivalve *Mysella bidentata* migrated to the sediment surface (Nilsson & Rosenberg 1994). Also, Ockelmann & Muus (1978) observed *M. bidentata* emerging from the sediment at 5% saturation, while at 8–10% saturation it again dug into the sediment.

In November 1977, a severe hypoxic event in the northern part of the Adriatic caused mass mortality of benthos. Divers found millions of dead shells as well as lobsters outside their dens and grouped on the highest parts of outcrops (Stefanon & Boldrin 1981). Stachowitsch (1984, 1991) provides a detailed and illustrative description of benthic infaunal and epifaunal behaviour during the September 1983 hypoxic event in the Adriatic. However, no oxygen recordings were made. Infauna emerged from the sediment and aggregated on the slightest bottom relief forming mounds of animals. This aggregation pattern was performed by *Amphiura chiajei* and *Astropecten bispinosus*. *Amphiura chiajei* and *Ophiura texturata* were also observed standing on their arm tips, and *Astropecten bispinosus* and *Ophiothrix quinquemaculata* were positioned upside-down on the sediment surface. During the period of observation the surface sediments became darker in colour, except on top of the mounds. This suggests that the oxygen concentration was higher a few centimetres above the flat sea bed. Through this behaviour the organisms were attempting to raise themselves above the hypoxic layer including the millimetre thin diffuse boundary layer where declining gradients of oxygen are steepest (Gundersen & Jørgensen 1990).

In the eastern Hiuchi-Nada and Bisan Strait, Seto Inland Sea, Japan, late summer (August 1983) thermal stratification initiates moderate hypoxia ($1.6\,\mathrm{ml\,l^{-1}}$, 33% saturation) over deep ($>20\,\mathrm{m}$) muddy habitats (Imabayashi 1986). In these habitats hypoxia appears to be regulating the settlement and survival of the deposit feeding bivalve *Theora lubrica*. *T. lubrica* produces planktonic larvae throughout the year, with continuous recruitment into both normoxic and hypoxic habitats. Survival of recruits in the periodic hypoxic habitats is low during hypoxia and high during normoxia. Those individuals that recruit during normoxia in the periodic hypoxic habitats grow rapidly, but only a few of the larger individuals survive the hypoxia.

Demersal trawling in hypoxic areas has shown that large numbers of infaunal species in areas of high abundance and biomass leave their protected positions in the sediment and lie exposed on the bottom. At a bottom water oxygen concentration of about $1\,\mathrm{ml\,l^{-1}}$ (15% saturation) in the Kattegat almost no fishes were caught, but $200–400\,\mathrm{kg\,h^{-1}}$ of benthic invertebrates (echinoderms: *Brissopsis lyrifera*, *Echinocardium cordatum*, *Cucumaria elongata*, *Ophiura* spp., *Amphiura filiformis*, polychaetes: *Polyphysia crassa*, *Aphrodite aculeata*, *Nephtys* spp.) were collected (Baden et al. 1990a). Similar mass migration of benthic infauna to the sediment surface was recorded during trawling in the North Sea (Dyer et al. 1983). Many species were the same as in the Kattegat, but no oxygen recordings were made during trawling. Low values (about $2\,\mathrm{ml\,l^{-1}}$) were, however, recorded in the area about that time. Also, during the 1976 aperiodic hypoxic event on the middle Atlantic continental slope off New Jersey large quantities of infauna were collected with trawls. Many of the infaunal species in the trawls were deep dwelling and rarely taken in grab samples (Boesch & Rosenberg

Table 4 Response patterns of benthic organisms to declining oxygen concentrations. Oxygen concentrations are in $ml l^{-1}$ or percent saturation (%).

Response	Oxygen	Example	Reference
Avoidance			
Initial increase in respiration or activity	50–60%	Gobiid fish	Petersen & Petersen 1988
	≈2	*Penaeus aztecus, P. setiferus*	Renaud 1986b
Mobile fauna begin migration		Fish	Dyer et al. 1983, Pihl 1989, Baden et al. 1990a,b, Pihl et al. 1991, Pavela et al. 1983
	1.5	*Squilla empusa*	Pihl et al. 1991
		Callinectes sapidus	Pihl et al. 1991
	2.0	*Penaeus aztecus*	Renaud 1986b
	1.5	*Penaeus setiferus*	Renaud 1986b
Infaunal swimming	0.8	*Paraprionospio pinnata*	Diaz et al. 1992
Fauna unable to leave or escape initiate a series of sublethal responses			
Depressed metabolism	≈1	*Carcinus maenas*	Hill et al. 1991
		Bunodosoma cavernata	Ellington 1981
		Metridium senile	Sassaman & Mangum 1972
Increase surface area:volume ratio	60–70%	*Holothuria forskali*	Astall & Jones, 1991
Cessation of intraspecific aggression	0.2	*Munida quadrispina*	Burd & Brinkhurst 1984
Cessation of feeding	0.4	*Streblospio benedicti*	Llansó 1991
	0.7	*Loimia medusa*	Llansó & Diaz 1994
	0.8	*Capitella* sp. 1	Warren 1977, Forbes & Lopez 1990
	20%	*Nephrops norvegicus*	Baden et al. 1990a
Decreased activities not related to respiration		*Metridium senile*	Wahl 1984
	0.7	*Streblospio benedicti*	Llansó 1991
Cessation of burrowing	0.8	*Capitella* sp. 1	Warren 1977
Evisceration	<0.6	*Holothuria forskali*	Astall & Jones 1991
Shallowing distribution in sediments		*Scoloplos armiger*	Schöttler & Grieshaber 1988
Mobile but with disc on bottom.	1.4, 24%	*Ophiura albida*	Baden et al. 1990a
Emergence from tubes or burrows	<2.4	*Malacoceros fuliginosus*	Tyson & Pearson 1991b
	<0.5	*Penaeus japonicus*	Egusa & Yamamoto 1961
	0.1–0.9	*Ceriantheopsis americanus*	Diaz unpublished data
	0.7	*Echinocardium cordatum*	Niermann et al. 1990, Nilsson & Rosenberg 1994
	0.7–0.8	*Amphiura filiformis*	Rosenberg et al. 1991, Nilsson & Rosenberg 1994
	0.5	*Amphiura chiaje*	Rosenberg et al. 1991
		Micropholis atra	Diaz et al. 1992
	0.7	*Pectinaria koreni*	Nilsson & Rosenberg 1994
	5%, 0.7	*Mysella bidentata*	Ockelmann & Muus 1978, Nilsson & Rosenberg 1994
	25%	*Nephrops norvegicus*	Baden et al. 1990a
	10%	*Nereis diversicolor, N. virens*	Vismann 1990

Response	Oxygen	Example	Reference
Extension into water column			
Clumping and weaving	<0.5	*Malacoceros fuliginosus*	Tyson & Pearson 1991b
Siphon stretching	0.1–0.7	*Mya arenaria*, *Abra alba*	Jørgensen 1980
	0.1–0.7	*Cerastoderma edule*	Jørgensen 1980
Taller tube construction	30%	*Corophium volutator*	Eriksson & Weeks 1994
Climbing structures	0.1–0.7	*Hydrobia ulvae*	Jørgensen 1980
Immobile standing on arm tips	0.5–0.6,7–10%	*Ophiura albida*	Dethlefsen & v. Westernhagen 1983, Baden et al. 1990a
Leg stretching	20%	*Nephrops norvegicus*	Baden et al. 1990a,b
Metabolic switching in favour of near anaerobic or anaerobic pathways			
Facultative anaerobiosis		Most polychaetes	Mangum & van Winkle 1973, Herreid 1980, Warren 1984
		Bunodosoma cavernata	Ellington 1981
		Metridium senile	Sassaman & Mangum 1972
Selective mortality of sensitive species occurs		See Table 2	
Extensive mortality of all but the most tolerant species occurs		See Table 2	
As anaerobic conditions approach the sediment surface			
RPD becomes shallower and H_2S increases			Jørgensen 1980, Vismann 1991, Ankar & Jansson 1973, Rosenberg 1977
Sulphur and anaerobic microbe populations expand			Hall et al. 1990, Rosenberg & Diaz 1993, Grant et al. 1995
Anoxic conditions extend into the water column.			Rabalais et al. 1991

1981). Similar observations were made by Taylor et al. (1985) off the northeast coast of New Zealand during a summer hypoxic/anoxic event.

The Norway lobster, *Nephrops norvegicus*, left their burrows in laboratory experiments at <25% saturation (Hagerman & Uglow 1985). At 20% saturation they extended their legs (tiptoeing) to stand higher above the sediment, and stopped feeding (Baden et al. 1990a,b). These authors have also shown that catches of Norway lobsters increased during the moderate hypoxic events of 1981 in the Kattegat, indicating that the emergence from burrows may occur in nature. Also, they found that the ratio of females to males increased from 0.07–0.38 in moderate hypoxia to 0.74–0.77 in severe hypoxia ($<1\,\mathrm{ml\,l^{-1}}$, <15% saturation). Other large crustaceans, the mantis shrimp (*Squilla empusa*) and the blue crab (*Callinectes sapidus*), have been shown to migrate from deeper hypoxic to shallower normoxic areas in Chesapeake Bay (Pihl et al. 1991). The so called "jubilees" of Mobile Bay, Alabama, which have occurred for many years, are mass migrations of fauna, from deeper to shallower water, attempting to avoid encroaching hypoxia (Loesch 1960, May 1973). Such avoidance reactions were not observed for the shrimp *Crangon crangon* or the shore crab *Carcinus maenas* in the Limfjord. These species eventually died from exposure to hypoxia (Jørgensen 1980).

The polychaetes *Nereis diversicolor* and *N. virens* left the sediment in higher numbers in hypoxia (10% saturation) + sulphide ($172\text{–}187\,\mu\mathrm{M}$) than in experiments with only hypoxia. After 10 days in these experiments 35% of the number of *N. diversicolor* and 100% of *N. virens* had left the sediment in the combined treatments, whereas the numbers in hypoxia alone were 8% and 17%, respectively (Vismann 1990). The difference in behaviour was suggested by Vismann to be a consequence of *N. diversicolor* having a significantly higher sulphide oxidation activity than *N. virens*. These experiments indicate that the addition of sulphide to the water causes a stronger behavioural reaction than hypoxia alone.

Sulphide can also act as a larval settlement cue. Larvae of *Capitella* sp. 1 was attracted by sulphidic sediment and enhanced the settlement during such circumstances (Cuomo 1985). In that experiment a sulphide concentration ranging between 0.1 mm and 1.0 mm gave higher settlements and subsequent metamorphosis and survival of settled polychaetes compared with non-sulphidic controls.

The polychaete, *Malacoceros fuliginosus*, was observed in experiments to change its behaviour in declining oxygen concentrations. Under fully oxic conditions this species lives below the sediment surface in burrows. When oxygen concentrations drop below $2.4\,\mathrm{ml\,l^{-1}}$, they emerge from their burrows and rise partly up in the water column. When oxygen concentrations fall below $0.5\,\mathrm{ml\,l^{-1}}$ *M. fuliginosus* "begin undulatory body movements and ultimately form rapidly weaving clumps of animals" (Tyson & Pearson 1991b). These authors suggest this behaviour causes water from higher up in the boundary layer (presumably with higher oxygen content) to come in contact with the worms.

The crab *Munida quadrispina* had a size distribution negatively correlated with the vertical oxygen gradient in Saanich Inlet, British Columbia (Burd 1985). *M. quadrispina* was tolerant of hypoxia as low as $0.1\,\mathrm{ml\,l^{-1}}$; however, only the largest crabs were found in the lowest oxygen. In other British Columbia fjords that do not experience severe hypoxia no size gradients were seen. This population response to hypoxia appears to be caused by a size-dependent respiration tolerance. The minimum critical oxygen concentration below which the rate of oxygen consumption declined in *M. quadrispina* is $0.14\,\mathrm{ml\,l^{-1}}$ and corresponded with the lowest oxygen levels ($0.1\text{–}0.15\,\mathrm{ml\,l^{-1}}$) at which crabs were found in Saanich Inlet (Burd 1985). Intraspecific aggression of *M. quadrispina* observed in normoxia was not seen in hypoxia, where the animals were often sitting on top of each other (Burd & Brinkhurst 1984).

Behavioural responses to predation are known to have a major influence on the distribution and activity of organisms. Relative to predation, however, behaviour appropriate for surviving or avoiding hypoxia is often inappropriate for avoiding predation. The distribution of nymphs of the mayfly *Callibaetis montanus* was influenced by both hypoxia and presence of predators. *C. montanus* endure lower oxygen concentrations when exposed to fish predators relative to conditions when fish were absent (Rahel & Kolar 1990). Complex interactions between competing species and how oxygen concentration affects these interactions needs further investigation.

A recent experimental study of such interactions with the predatory isopod *Saduria entomon* in the Baltic gave the following results. Predation on the amphipods *Corophium volutator* and *Bathyporeia pilosa* declined significantly in low oxygen saturations of 17% (compared to 95, 50 and 30% saturation) and 35% saturation (compared to 95 and 50% saturation), respectively (Sandberg 1994). These results suggest the existence of oxygen threshold saturations, where the predation efficiency of *Saduria entomon* declines depending on the behaviour of prey species.

With the intensification or persistence of hypoxia there is a metabolic switching in favour of near anaerobic or anaerobic path ways. During anoxia most polychaetes have some ability for facultative anaerobiosis (Warren 1984). As anaerobic conditions approach the sediment surface, with a shallowing of the RPD (Jørgensen 1980, Rhoads & Germano 1986), sulphur and anaerobic microbes experience population explosions (Rosenberg & Diaz 1993, Grant et al.1995). This further reduces the quality of the habitat for most metazoans (Stachowitsch 1984, 1986, Llansó 1992). With continued hypoxia, anoxic conditions and H_2S eventually reach the sediment surface and extend into the water column (Harper et al. 1991, Rabalais et al. 1991).

Once hypoxia is well developed, the magnitude of effects on infaunal community structure and energy flow are related to complex interactions of a series of biological and physical parameters. The most important of these seems to be the interaction of the duration of hypoxia and temperature. As temperature increases, the severity of hypoxia tends to increase while tolerance of hypoxia decreases. In effect this accelerates faunal change even if hypoxia decreases in duration. The successional stage of the community has an important bearing on how noticeable community changes will be and how much energy is shunted into microbial pathways.

Recovery processes

Recovery of benthic communities following hypoxic events depends primarily on the interaction between the severity and longevity of the hypoxia with the complexity of the community affected. The resilience of communities to hypoxia is dependent on the constituent species, which have different life-cycles, reproduction periods and patterns of larval dispersal (Boesch & Rosenberg 1981). The severity and longevity of the hypoxia are dependent on hydrodynamic and mixing processes. When hypoxia has reduced or eliminated benthos, initial recovery follows the Pearson & Rosenberg (1978) enrichment–disturbance model. Often habitats that experience hypoxia are affected by eutrophication driven processes, since the decay of organic matter is a primary factor in the initiation of hypoxia. In general, sediments enriched in organic matter have shallow RPD's, indicative of poor oxygen conditions within the sediments (Jørgensen & Revsbech 1985, Revsbech & Jørgensen 1986).

Hypoxia and eutrophication are often highly correlated events. One of the best examples of benthic recovery following the return to normoxic conditions can be found in the Saltkällefjord, Sweden. For decades the Saltkällefjord was a highly enriched fjordic system (Rosenberg 1976 and references therein). Following abatement of enrichment, azoic bottoms at 20–40m depth were initially recolonized by opportunists, which were followed by transitional species and the process culminated in a "mature" community. The entire recovery sequence took five to eight years. Such benthic recovery processes were later generalized by Pearson & Rosenberg (1978). One reason for the prolonged recovery time was suggested to be the long-term accumulation of organic material in the sediment, which had to be oxidized prior to the colonization of the long-lived equilibrium type species.

Recovery of "mature" equilibrium dominants eliminated by hypoxia appears to be a process requiring more than two years. In the Gullmarsfjord, the 1980/81 hypoxia, which was as low as $0.2\,\mathrm{ml\,l^{-1}}$, eliminated all macrobenthic fauna below 115m. The recovery sequence was slow and communities were not re-established one-and-a-half years after the collapse (Josefson & Widbom 1988). Nematode populations affected at the same site were restored to pre-hypoxia levels one year later (Austen & Widbom 1991). At a station below the halocline in the Kattegat, where many species died during hypoxia in 1988, little to no recovery was observed in the following two years (Table 3). If a system begins to experience seasonal hypoxia, then equilibrium communities are likely be eliminated.

Recovery of epifaunal communities in the northern Adriatic was slow after the 1983 hypoxia. In the three years following this event, Stachowitsch (1991) estimated that 15, 49, and 36% of the initial biomass had returned. These first phases of recolonization were not by the same species that characterized the earlier community.

On the inner continental shelf off New Jersey the benthic communities at 25m experienced a hypoxia-related mass mortality following an unusual combination of events. An intense phytoplankton bloom during the summer of 1976, calm winds, and current reversals combined to cause an extensive pool of severe hypoxic and anoxic water ($8000\,\mathrm{km^2}$) for about two months (Falkowski et al. 1980). Populations of *Goniadella gracilis* and *Astarte castanea* survived the hypoxia, and appeared unaffected. After this hypoxic stress, the affected area was rapidly recolonized by species with pelagic larvae. Some of these were previous community dominants (*Echinarachnius parma*, *Spisula solidissima*) that, together with other taxa (*Spiophanes bombyx*, ampharetid polychaetes), established themselves opportunistically. After one year the opportunists declined in abundance, but many previously dominant species had still not returned (Boesch & Rosenberg 1981). It was suggested by Boesch & Rosenberg (1981) that several years will be required for recovery of pre-hypoxia communities. On the inshore edge of this hypoxic water mass, however, benthic effects were not as severe. Mortality of *Echinarachnius parma* populations was about 90%, while *Spisula solidissima* and polychaetes experienced low mortality ($<10\%$). Mobile species were able to avoid the hypoxia (Garlo et al. 1979).

In the Bornholm basin of the Baltic, recolonization occurs after aperiodically hypoxic bottom water is reoxygenated. However, recovery to "mature" communities characteristic of the pre-hypoxic conditions does not seem to happen, as abundance and biomass are low. Leppäkoski (1971) describes the polychaete *Scoloplos armiger* as one of the strong colonizers of the area, and states that the recolonizing community was not similar to the original community. The ability of *S. armiger* to colonize hypoxia stressed habitats quickly may be related to its ability to maintain fully aerobic metabolism at oxygen concentrations near $0.8\,\mathrm{ml\,l^{-1}}$ and partial aerobic metabolism at $\leq 0.4\,\mathrm{ml\,l^{-1}}$ (Schöttler & Grieshaber 1988).

In Kiel Bay, southwest Baltic, Arntz (1981) found recolonization to be rapid after a return of normoxic conditions from hypoxia. Initial rapid colonizers (*Abra alba*, *Harmothoe sarsi*, *Pectinaria koreni*, *Halicryptus spinulosus*, and *Diastylis rathkei*) were fast-growing and highly fecund organisms. From the same area experiencing mass-mortality in 1981, colonization rapidly restored the former community structure (Weigelt 1987).

From 1984 to 1987 hypoxia did not occur in the German Bight, or was very short lived, and there was a rapid recovery of benthic communities following the 1981–8 severe hypoxic events. By 1986, community structure and biomass had recovered to pre-hypoxia levels (Niermann et al. 1990). The rapid recovery can be attributed to two basic factors; communities in these shallow water habitats are adapted to physically stressful environmental conditions, and a strong recruitment pulse occurred shortly after the hypoxic event.

In shallow water, colonization of post hypoxic habitats is rapid and appears to be consistently dominated by opportunistic species. In Tomoe Cove, Japan, the opportunist *Capitella capitata* rapidly colonized areas disturbed by hypoxia in high abundance following reoxygenation (Tsutsumi 1987). Similar rapid recolonization by opportunists occurred following annual summer anoxia in the subtropical Hillsborough Bay, Florida (*Streblospio benedicti*, *Paraprionospio pinnata*, *Polydora ligni*, *Gyptis vittata*, and *Mulinia lateralis*; Santos & Simon 1980) and Tolo Harbor, Hong Kong (Wu 1982). The rapid recolonization occurred through a combination of adult migration and larval recruitment. In Hillsborough Bay the timing of the stress-response was stable from one year to the next with only the magnitude of recruitment varying from year to year (Santos & Bloom 1980).

In the shallow macrotidal Bay of Somme, France, hypoxia and anoxia first became apparent in 1982 with the mass mortality of benthic populations and collapse of the cockle fishery (Desprez et al. 1992). Anoxia-associated mass mortalities were recorded in subsequent years (1983, 1985, 1989) and were attributed to phytoplankton blooms fuelled by nutrients derived from river and land runoff. The 1982 hypoxia and subsequent anoxia developed after the coincidence of high summer temperatures (2°C above average) with high river flows (50% above average). Cockle, *Cerastoderma edule*, populations did not recover from this series of events until 1987 and the fishery did not recover until 1988. Two years after the severe anoxia in 1982, the opportunist *Pygospio elegans* dominated the benthos, but declined in numbers with the return of the cockle. In addition to changing the composition of the benthos, anoxia-induced mortality of the cockle caused its principal predators, the oystercatcher (*Haematopus ostralegus*) and the common gull (*Larus canus*), to switch prey. Population fluctuations of these birds, however, could not be related to cockle mortalities as a result of this opportunistic feeding strategy.

Ecosystem energy-flow implications

Elmgren (1984), in an energy-flow model of the Baltic, described the dominance of zooplankton as consumers and ascribed a comparatively minor role to the benthic fauna. Below about 70 m the benthic fauna has been impoverished since the great drop in oxygen levels in the 1960s, but on the other hand the benthic biomass shallower than 70 m has increased (Cederwall & Elmgren 1980). Whether this increase in shallow water biomass compensates for the losses in deeper waters is not known. Large areas of hypoxic bottoms in the Baltic are probably inhabited by sulphur bacteria (*Beggiatoa* spp.) (Rumohr 1990, Rosenberg & Diaz 1993).

In separate models for the southwest Baltic, Arntz (1978, 1981) has shown how the benthic system changes in relation to episodic hypoxia. Depending on the severity and duration of hypoxia and presence of H_2S, a completely different size structure of macrobenthos occurs in different years. This in turn will affect demersal fish populations.

An energy-flow model outlined for the southeast Kattegat showed that the benthic fauna (suspension feeders) played a major role in energy transfer (Pearson & Rosenberg 1992). Below about 13m, however, the benthic faunal compartment was affected by intermittent hypoxia. Consumption of large crustaceans, shrimps and crabs, was only 23% in this zone compared with shallower water. As was described earlier, the Norway lobster was eliminated from this area in the late 1980s. The Pearson & Rosenberg (1992) model showed that during prolonged severe hypoxia or anoxia, energy flow through the macrobenthic compartments would be reduced and finally cease. This could result in enhanced accumulation of organic carbon, which could lead to development of sulphur bacterial mats and increased prominence of anaerobic pathways. Williams & Reimers (1983) found that bacterial mats are common in coastal upwelling OMZs and that they are an important source of organic matter. Gallardo (1977) recorded bacterial mats with biomass as high as 1000 $\mathrm{gWW\,m^{-2}}$ at 60m off the Chilean coast. Rosenberg & Diaz (1993) found similar mats existing in hypoxic habitats of the inner Stockholm archipelago. Thus, in areas dominated by bacterial mats, a large portion of the organic input is remineralized and utilized by prokaryotic organisms. This in effect weakens benthic–pelagic coupling, and tends to shorten the food chain (Baird & Ulanowicz 1989).

The Kattegat ecosystem seems to be vulnerable to severe hypoxia, which shifts energy from macrobenthic compartments and the commercially important Norway lobster to benthic microbes. The importance of chemoautotrophic bacteria in the energy flow of hypoxic habitats was also seen in the partly anoxic Byfjord, Sweden (Rosenberg et al. 1977). In the normoxic water above the halocline a great proportion of the energy was channelled through the suspension feeding macrobenthic compartment, as was seen in the Kattegat, but below the halocline bacteria dominated the energy flow.

Meta-analysis of global hypoxic events

We found approximately 40 systems around the world that experience oxygen stress and have benthic community response and recovery data (Table 1). There are still many other systems that report oxygen problems, such as New Zealand (Taylor et al. 1985) or Long Island Sound, New York (Welsh & Eller 1991), but conditions within the benthos relative to response and recovery are not documented. To evaluate the material in Table 1, each of the systems was treated as a replicate and cross-classified by type, level, and temporal trends of hypoxia, benthic community response and recovery, and fisheries response. Table 1 is a contemporary summary of hypoxic conditions and effects around the world. We suspect that significant changes have already occurred or will occur in the near future within these systems.

The impression that most systems experience seasonal or persistent hypoxia is due to the attention given to the recurrence of hypoxic events. A number of these systems, however, were not historically known to experience hypoxia, i.e. Kiel Bay, the Gulf of Trieste, the Kattegat, or the Baltic Sea. Others have long histories of hypoxia, i.e. Chesapeake Bay or most of the fjordic and OMZ systems.

When hypoxia does occur it tends to be severe ($<0.5\,\mathrm{ml\,l^{-1}}$). Few systems experience only moderate hypoxia, between 2 to $0.5\,\mathrm{ml\,l^{-1}}$, such as most years in the Kattegat and the York River, Virginia. Only mild hypoxia is reported from the deeper Texas shelf and the

Seto Island Sea, Japan, but this may be due to sparse temporal or spatial coverage of oxygen measurements or through failure to measure oxygen close to the bottom. In both these systems, hypoxia-related mortality is reported.

Mortality, in particular mass mortality (virtual elimination of the fauna), is the most frequent responses of benthic communities to aperiodic and seasonal hypoxia. In the case of ecosystems experiencing aperiodic hypoxia, the mortality eliminates established and usually well developed communities. For persistent and seasonally hypoxic ecosystems, the mortality primarily occurs as premature death of recent recruits. Only about a third of the persistently hypoxic systems experience mortality. The other two thirds experience a stable but reduced benthic community structure. The only system where some form of community change to hypoxia has not been reported is the York River, Virginia, where periodic moderate to severe hypoxia occurs. This is linked to the preconditioning of the benthos by years of hypoxic stress, as discussed earlier.

In about 50% of all hypoxia-stressed systems, benthic recovery is annual; that is, community structure at least returns to the previous year's level of organization. Of these, about 80% experience seasonal hypoxia. A low recovery rate is seen in about 30% of the systems and 20% show little or no signs of community change through time. Systems with low recovery rates are about evenly split between aperiodic, seasonal and persistent hypoxia. All of the systems that show little change in community structure experience persistent hypoxia, except the York River, as explained above.

Benthic fisheries stocks are often adversely affected by hypoxia, resulting from migration of fish and mobile invertebrate species out of hypoxic areas and mortality of sessile species. All aperiodic hypoxic events appear to involve at least short-term reduction in commercial catches or high mortality of sessile species. Seasonal severe hypoxia accounts for reductions in the Norway lobster in the Kattegat and the reduction of commercial catches in fjordic systems. Persistently hypoxic systems have no bottom fisheries.

Discussion and conclusions

Higher taxa and individual responses

Most species of the marine macrobenthic infauna belong to the taxonomic groups polychaetes, molluscs, echinoderms and crustaceans. From the summarized literature, it is apparent that these groups exhibit different levels of tolerance to hypoxia. Studies in coastal areas in Scandinavia (Rosenberg 1977, Gray et al. 1988), the Adriatic (Stachowitsch 1992), Japan (Tsutsumi 1987), USA (Llansó 1992, Harper et al. 1991), the Black Sea (Bacesco 1963), and in offshore upwelling areas off Peru (Rosenberg et al. 1983, Levin et al. 1991) and California (Mullins et al. 1985) show that in general, polychaetes are the most tolerant taxa, followed by bivalves. Crustaceans are less tolerant than bivalves (Stickle et al. 1989). The same general grouping of taxa related tolerance was recorded in experiments with "natural" benthic communities (Nilsson & Rosenberg 1994). Some species are found repeatedly in hypoxic-stressed areas (Table 2) such as the polychaetes *Heteromastus filiformis*, *Streblospio benedicti*, *Paraprionospio pinnata* and the bivalves *Corbula gibba* and *Arctica islandica*, but echinoderms and crustaceans are rarely described from such areas. From experiments it is known, however, that exceptions exist, for example the isopod *Saduria entomon* can survive in hypoxic water for very long periods (Hagerman & Szaniawska 1988).

In the brackish southwest Baltic, several bivalves (e.g. *Astarte borealis*) are mentioned as the most resistant species to extended hypoxic periods along with some polychaetes (Leppäkoski 1969). This was also found in experimental work with species from the same area, where Theede (1973) and Dries & Theede (1974) found bivalves to be the most tolerant group followed by polychaetes, echinoderms and crustaceans. The priapulid *Halicryptus spinulosus* was also recorded among the more tolerant species. Other taxonomic groups that have particularly tolerant species to hypoxia are anemones (*Cerianthus* sp., *Epizoanthus erinaceus*) in the Adriatic (Stachowitsch 1992) and in Danish fjords (Jørgensen 1980), and phoronids in Swedish fjords (Rosenberg 1977).

Even though some general relations are found between taxa and tolerance to hypoxia, a detailed examination of some genera demonstrate significant differences. The significantly higher tolerance to hypoxia in the presence of sulphide shown by the polychaete *Nereis diversicolor* compared with *N. virens* was related to higher sulphide oxidation activity in the blood in *N. diversicolor*, which had an impact on the distribution of these species (Vismann 1990). In another experiment without sediment it was shown that *N. diversicolor* had the highest tolerance to hypoxia followed by *N. virens* and *N. succinea* and finally *N. pelagica* (Theede et al. 1973). During successively lowered oxygen concentrations the brittle star *Amphiura filiformis* left their sedentary position and appeared at the sediment surface before *A. chiajei* (Rosenberg et al. 1991). The higher tolerance shown by *A. chiajei* was attributed to the lower respiration rate shown by this species compared to *A. filiformis*. In similar experiments the bivalve *Abra alba* was more active (number of siphons stretched out of the sediment) compared with *A. nitida* (Rosenberg et al. 1991). Thus, species of the same genera can show different mortality rates and behaviour in the same hypoxic concentration.

Subsurface-feeding fauna penetrate to various depths within the sediment and should be expected to be tolerant of low oxygen concentrations and perhaps also to rather high concentrations of H_2S. However, there is no indication that any specific infaunal functional grouping is more or less tolerant of hypoxia and its related effects. Even though some subsurface feeders (e.g. *Heteromastus filiformis*) are found in hypoxic environments, surface deposit feeders (*Paraprionospio pinnata*), filter feeders (*Astarte borealis, Corbula gibba* and *Arctica islandica*), predators (*Ophiodromus flexuosus* and *Halicryptus spinulosus*) and anthozoans (*Epizoanthus erinaceus)* are also commonly found in hypoxia. Some of the species or faunal groups mentioned above are mobile, while some are mainly stationary or even sessile. Thus, there is no clear evidence that the position in the sediment occupied by infaunal species, their motility, or their feeding mode or trophic level is related to their tolerance to hypoxia.

As another example supporting this conclusion, the decapod *Nephrops norvegicus*, inhabiting deep burrows in the sediment, resists oxygen saturation of 12% for a few days only (Baden et al. 1990b). Another decapod, *Homarus gammarus,* living in rock crevices where oxygen concentrations ought to be high can tolerate oxygen concentrations in the range of $0.5-1.0\,\mathrm{ml\,l^{-1}}$ (8–15% saturation) for several weeks (Rosenberg et al. 1991). Thus, the latter species, presumably poorly adapted to hypoxia, is slightly more tolerant to hypoxia than *N. norvegicus,* which should experience seasonally lowered oxygen concentrations in its preferred habitat: deep muddy bottoms.

We have found three studies in particular where the tolerance of meiofauna and macrofauna to hypoxia are compared in the same area. In the Gullmarsfjord, Sweden, declining oxygen concentrations had a greater impact on the macrofauna compared with the meiofauna (Josefson & Widbom 1988). In the Baltic, Elmgren (1975) found that meiofauna extends deeper into the hypoxic zone than the macrofauna. In deep, permanently hypoxic waters in the Pacific, associated with an OMZ, Levin et al. (1991) found that microbial and meiofaunal communities are more tolerant than macro- and megafaunal communities. Nematodes are generally the most tolerant group in the meiofauna whereas harpacticoids are much more sensitive to hypoxia. Thus, we suggest that this tolerance is to some extent related to taxonomic group and not to size only.

Hypoxia and community structure

The initial development of benthic hypoxia is through a combination of water column processes that involves isolation of a water mass from mixing and subsequent lowering of dissolved oxygen concentration. In estuarine and shallow coastal waters, physical forces stratify the water column, isolating the bottom water from mixing with oxygen rich surface waters. Once hypoxia is established, benthic processes respond in a synergistic way to accelerated declining oxygen levels that is dependent upon a combination of factors including temperature, and the quantity and quality of organic matter. Sedimentary biological and chemical oxygen demand cause the RPD to become shallower. As the RPD approaches the sediment surface reduced compounds are mobilized into the water column. The principal reduced compound that further stresses the fauna is H_2S. Hypoxia and anoxia may also enhance the recycling of nutrients from the sediments, which supports increased primary production which leads to increased water column and bottom oxygen demand.

Benthic habitats experiencing recurring hypoxia share a common set of features that are related to the interaction of oxygen dynamics and faunal response. Oxygen availability influences community structure and function by directly affecting metabolic processes and by indirectly affecting water column processes. Seasonal hypoxia is predominantly a summer–autumnal phenomena, so the elimination or suppression of macrobenthic activity during periods when biological activity should be peaking leads to an increase in organic matter in surface sediments and to an increased importance of microbes in energy cycling and carbon remineralization. Anaerobic metabolism is less efficient than aerobic pathways and does not utilize deposited organic matter as quickly. During hypoxic events the energy, from dead macrofauna and newly deposited organic matter, is sequestered by microfauna. This transfer of benthic energy to microbes still favours recolonization by macrobenthos if the duration of the hypoxia is short. As hypoxic events become longer and more intense, a larger proportion of the organic carbon will be remineralized by the microbes and less energy will be available to support benthic recruitment with the return of normoxic conditions.

Hypoxia is a major factor in the structuring of benthic communities and their function. The degree of tolerance to hypoxia and anoxia by species is of critical importance, particularly for maintenance of local deep-water populations which tend to experience prolonged summer–autumn hypoxia. The elimination of a functionally important species from these communities could have significant effects on geochemical and biological processes (Rosenberg & Diaz 1993, Llansó & Diaz 1994). Many times oxygen gradients are paralleled by organic gradients (Pearson & Rosenberg 1978) and when hypoxia has reduced or eliminated benthos, initial recovery typically follows the Pearson–Rosenberg enrichment–disturbance model. When exposed to long-term or severe hypoxia, macrofaunal communities experience mass mortality. Temporal variability of communities increases and energy flow through the community becomes more pulsed. Large individuals and long-lived equilibrium species are eliminated, and populations shifted toward younger individuals, and smaller and more short-lived species that possess opportunistic life histories.

The effects of seasonal hypoxia on benthic community structure are consistent between ecosystems, and depend on the frequency and severity of the hypoxia. A conceptual model of how hypoxia and community successional stage or complexity of organization interact is presented in Figure 10. Prior to hypoxic stress, communities underwent natural cycles of annual variation. In systems that begin to experience aperiodic hypoxia, communities are not conditioned to low oxygen, so mortality of individuals and elimination of species is significant, particularly at advanced successional stages. Annual variation within advanced stage communities increases significantly. While lower successional stage communities may experience some variance increase, the increase cannot be detected from the background of their high natural variability. Aperiodic hypoxic events are precursors to the development of hypoxia-resistant communities. Increased energetic costs of population maintenance under low oxygen stress eliminates sensitive species. By the time a system experiences periodic or seasonal hypoxia, communities have undergone most of their structural and organizational changes.

Communities found in systems that experience periodic hypoxia, consisting of repeated brief periods of days to weeks, are already stress-preconditioned, and show little change during or shortly after hypoxic events. With seasonal hypoxia, lasting for the order of months, despite the fact that communities are preconditioned, mass mortality often occurs with almost complete elimination of macrofauna in communities at all stages of organization. Variance of community parameters again increases significantly. Systems with persistent hypoxia are occupied only by early successional stage communities. Diversity, abundance,

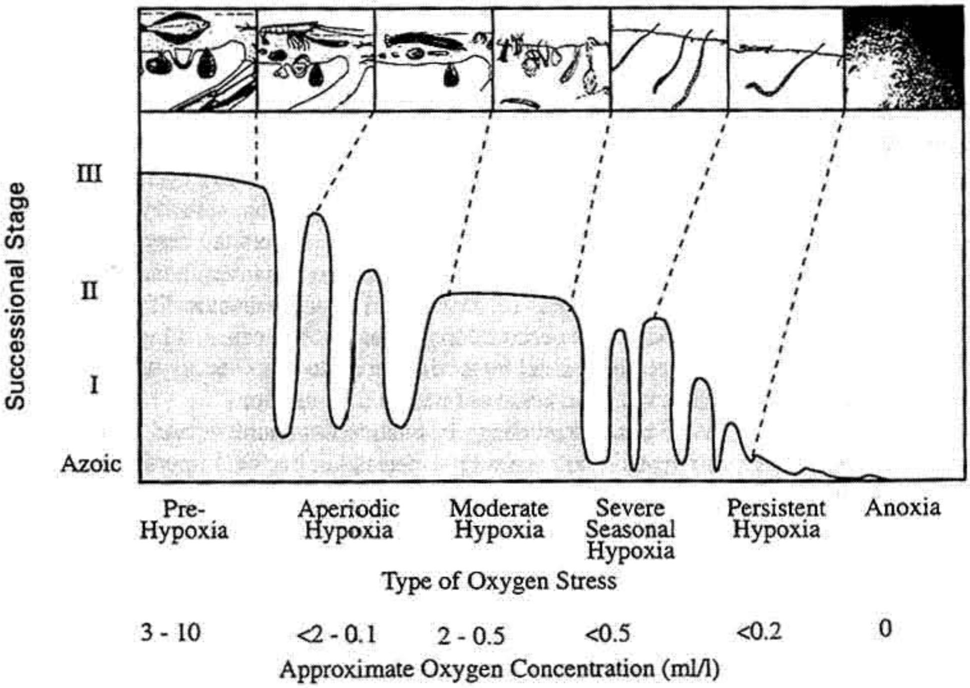

Figure 10 The general influence of progressively increasing hypoxia on benthic community succession and variability. Stage III is a mature community, stage II a transitional community and stage I a pioneering or "opportunistic" community (successional stages after Rhoads & Germano 1986). The timescale is relative, with the time interval for progressive ecosystem decline being system dependent. Systems studied to date follow this same general pattern.

and biomass of these communities decrease along stable gradients of increasing hypoxia to the point of stable persistent anoxia, which is characterized by the absence of macrofauna. Partial exceptions to this type of community decline are OMZs that contact the bottom. OMZs tend to have stable hypoxia, and are frequently associated with the production of large quantities of high quality organic matter that has allowed the development of a low diversity but stable fauna with high abundance and biomass.

Long-term or persistent severe hypoxia or anoxia induces retarded growth and poor reproductive success, resulting in failures in recolonization and in habitats that are devoid of macrofauna or possibly of all metazoan life. Exceptions to this are OMZs and highly eutrophic areas where large quantities of labile organic matter are available. This combination of hypoxia and organic matter creates a unique edge habitat in estuarine and marine habitats that supports a low diversity, high energy flux community.

No macrofauna occur in persistent anoxic environments. For severe hypoxia/anoxia there appear to be no long-term mechanisms for survival. While some species (such as *Halicryptus spinulosus* and *Metridium senile)* appear to exhibit long-term tolerance of anoxia, they do not survive to complete their life-cycles in severe hypoxic/anoxic environments. Intermediate-term adaptations do exist for survival of seasonal hypoxic events, but few macrofaunal species, except those mentioned above, possess them. Many macrobenthic species, however, possess behavioural and physiological mechanisms that allow survival of short-term aperiodic and periodic hypoxia (Table 4).

A key feature for the identification of hypoxia-related mortality is a shift in the timing of major population declines. Within most pulsed systems, increases in populations are related to recruitment events timed to take advantage of the input of new organic material. Mortality, even when rapid, can be related to a lack of resources or predation. Hypoxia shifts the timing of major mortality so that it is out of phase with resource depletion or peak predation pressure. Additional mortality peaks may occur in systems where populations are not completely adapted to seasonal hypoxia.

Hypoxia and sedimentary processes

Penetration of oxygen into muddy sediments by molecular diffusion is limited to a few millimetres (Revsbech et al. 1980). Bioturbation by infauna, such as burrowing and tube building, leads to irrigation of the sediments and is responsible for distribution of oxygen into deeper sediment layers (McCall & Tevesz 1982). The oxygenation effect of the burrowing shrimp *Callianassa subterranea* has been shown in a long-term experiment. Over a three-month period the bioturbating activity of this species increased the redox potential so that recordings of more than 300mV were obtained on over 100 occasions (Forster & Graf 1992). Most infauna cease or severely modify their bioturbational activities during hypoxia. Cessation of feeding, emergence from the sediment, and shallowing of the vertical distribution are infaunal behaviour responses to hypoxia that alter sedimentary processes (Table 4).

Bioturbation in areas characterized by low dissolved oxygen is limited or absent. Schaffner et al. (1992) attributed the absence of bioturbation in the Himmerfjärd (Swedish east coast) to hypoxia and anoxia. In Chesapeake Bay and Long Island Sound, depth gradients of declining bioturbation are consistently associated with deep water hypoxia or anoxia (Schaffner et al. 1987, 1992). Laminated sediments, a key indicator of lack of bioturbation, have accumulated in the persistent hypoxic/anoxic basin of the Baltic at some depths >75m for the past 200 to 300 years. Since the 1940s the area of laminated sediments has increased and extended into shallower waters (Schaffner et al. 1992, Jonsson et al. 1990).

By even temporarily reducing the volume of actively bioturbated sediments, hypoxia shifts the balance of benthic–pelagic coupling by altering the cycling of nitrogen and phosphorus. Nitrification–denitrification processes in sediments require a juxtaposition of oxic and anoxic habitats (Jenkins & Kemp 1984, Kristensen 1988), which burrowing organisms enhance through their bioturbation and irrigation activities (Kristensen & Blackburn 1987). When such activities stop, the oxic volume of sediment declines thus reducing the rate of denitrification and increasing the flux of nitrogen to the water column. Simultaneously, anoxic sediments release more phosphorus to the water column than do oxidized sediments. This represents a positive feedback loop that increases primary production which in turn increases the oxygen demand from the decomposition of the new organic matter. A self-accelerating system is created that perpetuates hypoxia and can lead to anoxia.

Hypoxia and energy flow

In well developed, successionally advanced communities not exposed to hypoxic stress, the cycling of energy and nutrients out of the community is minimal, usually taking the form of predation processes. This results in an overall increase in the efficiency of the trophic functioning of the system (Odum 1981). These advanced successional communities can be maintained through time, as shown by long-term benthic studies (Petersen 1915, Josefson & Jensen 1992, Rosenberg et al. 1992), if the physical environment does not experience catastrophic perturbations, such as hypoxia or anoxia. In systems that have long-term benthic data and now experience seasonal hypoxia or anoxia, such as the Kattegat, community organization has declined (Pearson et al. 1985, Josefson & Jensen 1992). Various functional processes within these oxygen stressed systems such as nutrient cycling and energy transfer have changed drastically, for the most part becoming more pulsed. Prior to the occurrence of hypoxia the principal pulsing force in these systems was seasonality, but hypoxia has increased the magnitude of the pulse and shortened the time interval over which it occurs.

In hypoxia- or anoxia-stressed habitats, community organization during periods of stress tends to decline or is returned to an earlier pioneering successional stage (*sensu* Pearson & Rosenberg 1978). If hypoxia is aperiodic and not repetitious, the systems seem to return to their previous level of organization. This was the case in the New York Bight hypoxia/anoxia event of 1978. When hypoxia becomes predictable, either periodic or seasonal, the ultimate level of community organization achieved is lower than that prior to the occurrence of hypoxia, and also lower than that expected for the system considering only physical environment parameters, as is seen in the current state of the Kattegat (Josefson & Jensen 1992, Pearson & Rosenberg 1992).

Faced with very stressful hypoxic conditions, a community with a lower level of organization would be optimally poised for capturing and processing the system's energy during the shortened time intervals when normoxia and temperature combine to allow rapid growth and reproduction. This energy utilization could either occur prior to or post hypoxia. Communities with simpler organization would then be better able to respond and to rebuild structure and functions following a catastrophic stress. This is, in principle, what happens in systems exposed to recurring hypoxic and anoxic stress. Recurring low oxygen stress not only halts successional development of a community but also keeps the communities in a perpetual pioneering state that could have mixed consequences for ecosystem energy flow (Rhoads et al. 1978). For example, the pulse of production that follows or precedes a hypoxic event can be a temporary benefit to predators, but in the long term altered productivity patterns could leave predators with little resources later in the season.

Periodic and seasonally low oxygen stressed habitats favour genotypes that maximize energy flow to growth and reproduction, limiting energy loss to maintenance or long-term stress tolerance (Odum 1971). During short-term or mild hypoxia, species exhibit plastic responses to minimize stress or sustain a temporary energy drain (Table 4). Populations using these behavioural or physiological responses cannot be sustained if their net reproduction rates are consistently less than one; instead, species replacement results. In the few systems studied that have pre- and post-hypoxia data, benthic communities have undergone major structural changes and species replacements. Systems that now experience seasonal hypoxia appear to pulse or focus their energy flow through opportunistic species prior to the onset of the hypoxia, for example the Kattegat. Systems that experience periodic hypoxia expend more energy in stress tolerance and do not pulse wildly, for example the York River, Virginia. In all cases, the increased occurrence of hypoxia leads to communities dominated by opportunists.

In all cases hypoxic stress represents an energy drain (Odum 1971) and as energy is lost the community changes. Sensitive taxa succumb to stress and are removed in order of sensitivity resulting in a reduction in species richness. Species changes are accompanied by changes in relative abundance of individual species and increase in dominance of a few tolerant species.

With the return of normoxic conditions, after a severe hypoxic or anoxic event, the organic matter fluxed into the habitat becomes available to aerobic respiration (Graf 1989). In all cases the opportunistic species come in first and utilize energy released from the previous community. This energy utilization is related to the opportunist's adaptation to quick response to stress. The anaerobic microbes take their part but a significant part returns to the macrofauna. If this was not the case then opportunistic species would not do so well. The longer and more intense the hypoxia, the more the microbes will remineralize carbon and the smaller will be the organic matter available to support recruitment with the return of normoxic conditions.

The effects of hypoxia on ecosystem energy flow are less predictable than effects on community structure or succession. Response and recovery sequences for community structure following hypoxia are similar between ecosystems and highly predictable. Effects on energy flow, however, vary from collapse of secondary production and extreme enhancement of bacterial populations, to no effect on production but pulsed transfer of benthic biomass to upper-level consumers.

Seasonal hypoxia or anoxia in bottom waters is a key factor in affecting secondary productivity, depending on the concentration of oxygen and the length of time a habitat is exposed. Habitats that are exposed to extensive periods of anoxia have low annual production (Rainer & Fitzhardinge 1981). The amount of productivity in these severely stressed habitats is a function of how quickly benthos can recruit and grow during periods of normoxia. In a near anoxic basin – Port Hacking, Australia – productivity was almost 16 times lower than at a nearby station that only experienced hypoxia (Rainer & Fitzhardinge 1981). Chesapeake Bay areas that experience anoxia do not seem to have as high a factor differentiating annual productivity of habitats. While some areas known to be affected by seasonal anoxia do have lower productivity, the trend is not consistent across habitat types. This results from a combination of duration of exposure to anoxia and rapid recovery of benthos. Annual secondary production of Chesapeake Bay habitats known to experience only seasonal hypoxia is of the same magnitude as habitats that are always normoxic (Diaz & Schaffner 1990).

In systems that have secondary production and energy flow estimates, about 50–70% of the annual secondary infaunal production is consumed by epibenthic predators (Arntz 1981, Möller et al. 1985, Holland et al. 1987). The remaining production is used for biomass maintenance or is recycled within the benthos by infaunal predators. As a system first experiences hypoxic stress (usually aperiodic) there is a temporary increase in the proportion of production transferred to epibenthic predators and at the same time an increase in the importance of microbes in recycling the secondary production. Mild periodic hypoxia also pulses a higher portion of the production to predators. Severe seasonal hypoxia, however, shifts a large proportion of the secondary production away from epifaunal predators to microbes. In the Kattegat, for example, hypoxia led to a 23% reduction in predation by crabs (Pearson & Rosenberg 1992). In persistent hypoxia and anoxia there is a drastic reduction in secondary production, and virtually all of the production goes to microbes.

Critical oxygen concentrations

In an earlier review Rosenberg (1980) suggested that benthic infaunal mortality will be initiated when the oxygen concentration drops below about 2 $\mathrm{ml\,l^{-1}}$. It appears, however, that the oxygen measurements in several of the field studies referred to in that review were made at some distance above the bottom. It is known from some studies (Jørgensen 1980, Rosenberg & Loo 1988) that a strong gradient in oxygen concentrations often occurs close to the sediment surface. The actual oxygen concentration experienced by the fauna in some of the cited works may have been lower than 2 $\mathrm{ml\,l^{-1}}$.

In the Gullmarsfjord in Sweden, benthic mortality occurred when the oxygen concentration dropped below 0.83 $\mathrm{ml\,l^{-1}}$ (Josefson & Widbom 1988). At the Texas shelf, benthic mortality was discovered at an oxygen concentration of 1.1 $\mathrm{ml\,l^{-1}}$ and mass mortality at 0.5 $\mathrm{ml\,l^{-1}}$ (Harper et al. 1991). In the Kattegat a significant mortality was recorded in oxygen concentrations of 0.9–1.0 $\mathrm{ml\,l^{-1}}$ (14–17% saturation) (Rosenberg et al. 1992). Bottom trawling in the Kattegat in 1988 demonstrated a mass mortality over large areas in oxygen concentrations below 1 $\mathrm{ml\,l^{-1}}$ (15% saturation) or slightly less (Baden et al. 1990a). In 0.5–0.6 $\mathrm{ml\,l^{-1}}$ *Ophiura albida* were seen standing on their arm tips, but in a concentration of 1.4 $\mathrm{ml\,l^{-1}}$ the behaviour appeared to be normal (Baden et al. 1990a). Thus, these studies of seasonal hypoxia suggest that mortality is initiated at oxygen concentrations close to 1 $\mathrm{ml\,l^{-1}}$ (about 15% saturation) and that mass mortality is initiated at about 0.5 $\mathrm{ml\,l^{-1}}$ (about 7% saturation).

In offshore areas with permanent oxygen deficiency the benthic communities seem to be adapted to lower oxygen concentrations. At the Volcano 7 site a high abundance community was found in stable oxygen concentrations of 0.11–0.16 $\mathrm{ml\,l^{-1}}$, but the fauna was significantly reduced below 0.1 $\mathrm{ml\,l^{-1}}$ (Levin et al. 1991). Off the Peruvian coast rather diverse benthic communities were found in oxygen concentrations to at least 0.6 $\mathrm{ml\,l^{-1}}$, but were reduced below 0.2 $\mathrm{ml\,l^{-1}}$ (Rosenberg et al. 1983). The higher tolerance shown by the benthic fauna in these offshore areas may be due to evolutionary adaptation to take advantage of increased organic production typically associated with the OMZ systems. In the Black Sea, with lower salinities and rates of organic production, however, the biomass and number of species are strongly reduced below an oxygen concentration of about 0.7 $\mathrm{ml\,l^{-1}}$ (Bacesco 1963).

Sediment quality is also important for reactions of the animals. A "sulphidic" sediment induced significant reductions in abundance and number of species in an oxygen concentration of 0.7 $\mathrm{ml\,l^{-1}}$ (12% saturation, 17–19°C), whereas in a parallel experiment with less sulphidic sediment the same effects were induced at about 0.4 $\mathrm{ml\,l^{-1}}$ (7% saturation, 11–13°C) (Nilsson

& Rosenberg 1994). Experiments with benthic animals performed with natural sediments give similar tolerance levels to hypoxia as documented in the field for seasonal hypoxia.

Concluding remarks

Hypoxia is a growing global problem. Over 35 years ago, Brongersma-Sanders (1957) documented worldwide occurrence of hypoxia and anoxia. Some of the hypoxic and anoxic systems and events she described appear to be recurring long-term situations, as in the Black Sea. Many of the European systems we currently recognize as stressed by hypoxia and anoxia, however, were not mentioned by Brongersma-Sanders even though there are data extending back to near the turn of the century, the Skagerrak and the Baltic Sea, for example.

While hypoxic and anoxic environments have existed through geological time, their occurrence in shallow coastal and estuarine areas appears to be increasing; most likely it is being accelerated by human activities. The consequence of many human activities (i.e. eutrophication) has manifested itself many times as a problem of low dissolved oxygen at the bottom. It appears that the oxygen budget of most major estuarine and coastal ecosystems has been adversely affected mainly through the process of eutrophication. The area of hypoxic and anoxic bottom water is even increasing within systems that historically are considered oxygen stressed. Over the past 20 years the area affected by hypoxia has dramatically increased over the northwest shelf of the Black Sea, the largest anoxic system on Earth. A similar shallowing of hypoxic and anoxic bottom water has occurred in the Baltic Sea and Chesapeake Bay, and in other systems around the world.

Eutrophication acts as an accelerant or enhancing factor to hypoxia and anoxia, and when coupled with adverse meteorological and hydrodynamic events, hypoxia increases in frequency and severity. Many ecosystems that are now severely stressed by hypoxia appear to be near or at a threshold (Table 5). Should oxygen concentrations get slightly lower, catastrophic events may overcome the systems and alter the productivity base that leads to species important to fisheries. Examples of such events are becoming increasingly common (see Table 1). At what point permanent damage will result is difficult to say. To date there is no large system that has recovered after development of persistent hypoxia or anoxia. The only exception may be small systems where point effluents have ceased and recovery was initiated from surrounding non-affected areas (Rosenberg 1976).

Table 5 Levels of hypoxia that initiated, or were measured during, mass mortality of benthic systems. Increased exposure time to these concentrations or further decline of oxygen may lead to permanent changes in benthic communities and the temporary, permanent collapse of fisheries stocks.

System	Critical oxygen concentration	Reference
Gullmarsfjord, Swedish West Coast	0.8–0.2 $\mathrm{ml\,l^{-1}}$	Josefson & Widbom 1988
North Sea, Danish & German Bight	0.7	Rachor & Albrecht 1983, Niermann et al. 1990
Kiel Bay, Germany	1.0	Arntz 1981
Kattegat, Sweden–Denmark	1.0–0.9	Baden et al. 1990a, Josefson & Jensen 1992, Rosenberg et al. 1992
Louisiana–Texas Continental Shelf	1.4	Harper et al. 1981, 1991, Boesch & Rabalais 1991

The expanding occurrence of hypoxia and anoxia continues to bring about significant structural changes in benthic communities and to affect benthic-pelagic coupling. Restoring ecosystem balance and reversing the trend of increasing hypoxia and anoxia will require dealing with the global problem of coastal eutrophication and determining how to reduce nutrient input to estuarine and coastal areas.

There is no other environmental parameter of such ecological importance to coastal marine ecosystems that has changed so drastically in such a short period as dissolved oxygen. Even if benthos and fish stocks can presently process and utilize the excess input of organic carbon reaching well ventilated bottoms, these areas experiencing hypoxia are spreading into shallower waters with increasing frequency, and have the potential to cause deleterious effects on fish stocks. If we do not move quickly to reduce or stop the primary cause of low oxygen, the decomposition of excess primary production associated with eutrophication, then the productivity structure of our major estuarine and coastal areas will be permanently altered. Should the input of nutrients to the sea be significantly reduced, however, and followed by increased oxygen concentrations in hypoxic/anoxic bottom water, a rapid colonization is anticipated that could restore the ecosystems within a decade.

Acknowledgments

We would like to thank Tom Pearson, Nancy Rabalais, Peter DeFur and Linda Schaffner for discussions on the topic and review of the manuscript. Additional reviews were extracted from the students Giancarlo Cicchetti, Beth Hinchey, Janet Nestlerode and Eric Wooden. This is contribution 1957 of the Virginia Institute of Marine Science.

References

Aller, R. C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In *Animal-sediment relationships*, P. L. McCall & M. J. S. Tevesz (eds), 53–102. New York: Plenum.

Andersin, A. B., Lassig, J., Parkkonen, L. & Sandler, H. 1978. The decline of macrofauna in the deeper parts of the Baltic proper and the Gulf of Finland. *Kieler Meeresforschungen* (Sonderheft 4), 23–52.

Andersin, A. B. & Sandler, H. 1991. Macrobenthic fauna and oxygen deficiency in the Gulf of Finland. *Memoranda Societatis pro Fauna et Flora Fennica* **67**, 3–10.

Ankar, S. & Jansson, B. O. 1973. Effects of an unusual natural temperature increase on a Baltic soft bottom community. *Marine Biology* **18**, 9–18.

Arntz, W. 1981. Zonation and dynamics of macrobenthos biomass in an area stressed by oxygen deficiency. In *Stress effects on natural ecosystems*, G. W. Barrett & R. Rosenberg (eds), 215–25. Chichester: John Wiley.

Arntz, W. E. 1977. Results and problems of an "unsuccessful" benthos cage predation experiment (Western Baltic). In *Biology of benthic organisms*, B. F. Keegan et al. (eds), 31–44. London: Pergamon.

— 1978. The "upper part" of the food web: the role of macrobenthos in the western Baltic. *Rapports et Procès-Verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer* **173**, 85–100.

Arntz, W. E. & Fahrbach, E. 1991. *El Niño. Klimaexperiment der Natur*. Basel: Birkhäuser.

Astall, C. M. & Jones, M. B. 1991. Respiration and biometry in the sea cucumber *Holothuria forskali*. *Journal of the Marine Biological Association of the United Kingdom* **71**, 73–81.

Austen, M. C. & Widbom, B. 1991. Changes in and slow recovery of a meiobenthic nematode assemblage following a hypoxic period in the Gullmar Fjord basin, Sweden. *Marine Biology* **111**, 139–45.

Bacesco, M. 1963. Contribution a la biocoenologie de la Mer Noire l'étage périazoique et le faciés dreissenifère leur caractéristiques. *Rapports et Procès-Verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer* **17**, 107–22.

Baden, S. P., Loo, L. O., Pihl, L. & Rosenberg, R. 1990a. Effects of eutrophication on benthic communities including fish – Swedish west coast. *Ambio* **19**, 113–22.

Baden, S. P., Pihl, L. & Rosenberg, R. 1990b. Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. *Marine Ecology Progress Series* **67**, 141–55.

Baird, D. & Ulanowicz, R. E. 1989. The seasonal dynamics of the Chesapeake bay ecosystem. *Ecological Monographs* **59**, 329–64.

Bagarinao, T. 1992. Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. *Aquatic Toxicology* **24**, 21–62.

Benson, B. B. & Krause, D. 1984. The concentration and isotopic fractionation of gases dissolved in freshwater in equilibrium with the atmosphere: 1. Oxygen. *Limnology and Oceanography* **25**, 662–71.

Bestwick, B. W., Robbins, I. J. & Warren, L. M. 1989. Metabolic adaptations of the intertidal polychaete *Cirriformia tentaculata* to life in an oxygen-sink environment. *Journal of Experimental Marine Biology and Ecology* **125**, 193–202.

Beukema, J. J. 1992. Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. *Netherlands Journal of Sea Research* **30**, 73–9.

Boesch, D. F. & Rabalais, N. N. 1991. Effects of hypoxia on continental shelf benthos: comparisons between the New York Bight and the northern Gulf of Mexico. In *Modern and ancient continental shelf anoxia*. R. V. Tyson & T. H. Pearson (eds), 27–34. London: Geological Society [Special Publication 58].

Boesch, D. F. & Rosenberg, R. 1981. Response to stress in marine benthic communities. In *Stress effects on natural ecosystems*, G. W. Barrett & R. Rosenberg (eds), 179–200. Chichester: John Wiley.

Boesch, D. F., Wass, M. L. & Virnstein, R. W. 1976. The dynamics of estuarine benthic communities. In *Estuarine processes, Vol. 1: uses, stresses, and adaptation to the estuary*, M. L. Wiley (ed.), 177–96. New York: Academic Press.

Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. *Ecological Monographs* **62**, 525–46.

Broenkow, W. & Greene, N. 1981. *Oceanographic results during VERTEX particle interceptor trap experiment 17 August to 8 September 1980*. Moss Landing Marine Laboratories Technical Publication 81-1, Moss Landing, California.

Brongersma-Sanders, M. 1957. Mass mortality in the sea. In *Treatise on marine ecology and paleoecology, Vol. 1*, J. W. Hedgpeth (ed.), 941–1010. Baltimore: Waverly Press.

Buchanan, J. B. 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. *Journal of the Marine Biological Association of the United Kingdom* **44**, 565–76.

Burd, B. J. 1985. Respiration of a low oxygen tolerant galatheid crab, *Numida quadrispina* (Benedict 1902). *Canadian Journal of Zoology* **63**, 2538–42.

Burd, B. J. & Brinkhurst, R. O. 1984. The distribution of the galatheid crab *Numida quadrispina* (Benedict 1902) in relation to oxygen concentrations in British Columbia fjords. *Journal of Experimental Marine Biology and Ecology* **81**, 1–20.

Caspers, H. 1957. Black Sea and Sea of Azov. In *Treatise on marine ecology and paleoecology, Vol. 1*, J. W. Hedgpeth (ed.), 801–90. Baltimore: Waverly Press.

Cederwall, H. & Elmgren, R. 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic sea. *Ophelia* (Suppl. 1), 287–304.

Colombo, G., Ferrari, I., Ceccherelli, U. & Rossi, R. (eds) 1992. *Marine eutrophication and population dynamics*. Fredensborg: Olsen & Olsen.

Colt, J. 1984. *Computation of dissolved gas concentrations in water as functions of temperature, salinity, and pressure*. Special Publication 14, American Fisheries Society, Bethesda, Maryland.

Cooper, S. R. & Brush, G. S. 1991. Long-term history of Chesapeake Bay anoxia. *Science* **254**, 992–6.

Coull, B. C. 1969. Hydrographic control of meiobenthos in Bermuda. *Limnology and Oceanography* **14**, 953–7.

Coull, B. C. & Chandler, G. T. 1992. Pollution and meiofauna: field, laboratory and mesocosm studies. *Oceanography and Marine Biology: an Annual Review* **30**, 191–271.

Cuomo, M. C. 1985. Sulphide as a larval settlement cue for *Capitella* sp I. *Biogeochemistry* **1**, 169–81.

Dauer, D. M., Rodi Jr, A. J. & Ranasinghe, J. A. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* **15**, 384–91.

Davis, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *Journal of the Fisheries Research Board of Canada* **32**, 2295–332.

Desprez, M., Rybarczyk, H., Wilson, J. G., Ducrotoy, J. P., Sueur, F., Olivesi R. & Elkaim, B. 1992. Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. *Netherlands Journal of Sea Research* **30**, 149–59.

Dethlefsen, V. & Westernhagen, H. von 1983. Oxygen deficiency and effects on bottom fauna in the eastern German Bight 1982. *Meeresforschung* **60**, 42–53.

Diaz, R. J. & Schaffner, L. C. 1990. The functional role of estuarine benthos. In *Perspectives in the Chesapeake Bay, 1990: Advances in estuarine sciences*, M. Haire & E. C. Krome (eds), 25–56. Report CBP/TRS 41/90, Chesapeake Research Consortium, Gloucester Pt, Virginia.

Diaz, R. J., Neubauer, R. J., Schaffner, L. C., Pihl, L. & Baden, S. P. 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. *Science of the Total Environment* (Suppl. 1992), 1055–68.

Dries, R. R. & Theede, H. 1974. Sauerstoffmangelresistenz mariner Bodenvertebraten aus der Westlichen Ostsee. *Marine Biology* **25**, 327–33.

Dyer, M. F., Pope, J. G., Fry, P. D., Law, R. J. & Portmann, J. E. 1983. Changes in fish and benthos catches off the Danish coast in September 1981. *Journal of the Marine Biological Association of the United Kingdom* **63**, 767–75.

Egusa, S. & Yamamoto, T. 1961. Studies on the respiration of the "Kumura" prawn *Penaeus japonicus* Bate. I. Burrowing behaviour with special reference to its relation to environmental oxygen concentration. *Bulletin of the Japanese Society of Scientific Fisheries* **27**, 22–7.

Ehrhardt, M. & Wenck, A. 1984. Wind pattern and hydrogen sulfide in shallow waters of the western Baltic Sea, a cause and effect relationship? *Meeresforschung* **30**, 101–10.

Ellington, R. W. 1981. Effect of anoxia on the adenylates and the energy charge in the sea anemone, *Bunodosoma cavernata* (Bosc). *Physiological Zoology* **54**, 415–22.

Elmgren, R. 1975. Benthic meiofauna as indicator of oxygen conditions in the northern Baltic proper. *Merentutkimuslaitoksen Julkaisu Havsforskningsinstitutets Skrift* **239**, 265–71.

— 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. *Rapports et Procès-Verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer* **183**, 152–69.

Eriksson, S. P. & Weeks, J. M. 1994. Effects of copper and hypoxia on two populations of the benthic amphipod *Corophium volutator* (Pallas). *Aquatic Toxicology* **29**, 73–18.

Falkowski, P. G., Hopkins, T. S. & Walsh, J. J. 1980. An analysis of factors affecting oxygen depletion in the New York Bight. *Journal of Marine Research* **38**, 479–506.

Fallesen, G. & Jørgensen, H. M. 1991. Distribution of *Nephtys hombergii* and *N. ciliata* (Polychaeta: Nephtyidae) in Århus Bay, Denmark, with emphasis on the effect of sewage oxygen deficiency. *Ophelia* (Suppl. 5), 443–50.

Fenchel, T. 1969. The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. *Ophelia* **6**, 1–182.

Fenchel, T. M. & Riedl, R. J. 1970. The sulphide system: a new biotic community underneath the oxidized layer of marine sand bottoms. *Marine Biology* **7**, 255–68.

Fonselius, S. H. 1969. Hydrography of the Baltic deep basins III. Report 23 (pp. 1-97), Series Hydrography, Fishery Board of Sweden.

Forbes, T. L. & Lopez, G. R. 1990. The effect of food concentration, body size, and environmental oxygen tension on the growth of the deposit-feeding polychaete, *Capitella* species 1. *Limnology and Oceanography* **35**, 1535–44.

Forster, S. & Graf, G. 1992. Continuously measured changes in redox potential influenced by oxygen penetrating from burrows of *Callianassa subterranea*. *Hydrobiologica* **235/236**, 527–35.

Friligos, N. 1976. Seasonal variations of nutrients around the sewage outfall in the Saronikos Gulf (1973). *Thalassia Jugoslavica* **12**, 441–53.

Friligos, N. & Zenetos, A. 1988. Elefsis Bay anoxia: nutrient conditions and benthic community structure. *Publicazioni della Stazione Zoologica di Napoli I. Marine Ecology* **9**, 273–90.

Gallardo, A. 1977. Large benthic microbial communities in sulphide biota under Peru-Chile subsurface countercurrent. *Nature* **268**, 331–2.

Garlo, E. V., Milstein, C. B. & Jahn, A. E. 1979. Impact of hypoxic conditions in the vicinity of Little Egg Inlet, New Jersey in summer 1976. *Estuarine and Coastal Marine Science* **8**, 421–32.

Gaston, G. R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. *Estuarine, Coastal and Shelf Science* **20**, 603–13.

Gnaiger, E. & Forstner, H. 1983. *Polarographic oxygen sensors: aquatic and physiological applications*. Berlin: Springer.

Gomoiu, M. T. 1983. Sur la mortalité en masse des organismes benthiques du littoral Roumain de la Mer Noir. *Rapports et Procès-Verbaux des Réunions. Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* **28**, 203–4.

Gowing, M. M. & Silver, M. W. 1983. Origins and microenvironments of bacteria mediating fecal pellet decomposition in the sea. *Marine Biology* **73**, 7–16.

Graf, G. 1989. Benthic-pelagic coupling in a deep-sea benthic community. *Nature* **341**, 437–9.

Graf, G., Bengtsson, W., Diesner, U., Schultz, R. & Theede, H. 1982. Benthic response to sedimentation of a spring phytoplankton bloom: progress and budget. *Marine Biology* **67**, 201–8.

Grant, J., Hatcher, A., Scott, D. B., Pocklington, P., Schafer, C. T., Winters, G. V. & Honig, C. 1995. A multidisciplinary approach to evaluating benthic impacts of shellfish aquaculture. *Estuaries*, **18**, 124–44.

Gray, J. S. 1979. Pollution-induced changes in populations. *Philosophical Transactions of the Royal Society of London* **B 286**, 545–61.

Gray, J. S., Aschan, M., Carr, M. R., Clarke, K. R., Green, R. H., Pearson, T. H., Rosenberg, R., Warwick, R. M. & Bayne, B. L. 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series* **46**, 151–65.

Groenendaal, M. 1980. Tolerance of the lugworm (*Arenicola marina*) to sulphide. *Netherlands Journal of Sea Research* **14**, 200–207.

Gundersen, J. K. & Jørgensen, B. B. 1990. Microstructure of diffusive boundary layers and the oxygen uptake of the sea floor. *Nature* **345**, 604–7.

Haas, L. W. 1977. The effect of spring-neap tidal cycle on the vertical salinity structure of the James, York, and Rappahannock rivers, Virginia, USA. *Estuarine and Coastal Marine Science* **5**, 485–96.

Hagerman, L. & Szaniawska, A. 1988. Respiration, ventilation and circulation under hypoxia in the glacial relict isopod *Saduria (Mesidothea) entomon*. *Marine Ecology Progress Series* **47**, 55–63.

Hagerman, L. & Uglow, R. F. 1985. Effects of hypoxia on the respiratory and circulatory regulation of *Nephrops norvegicus*. *Marine Biology* **57**, 273–8.

Hall, P., Anderson, L. G., Holby, O., Kollberg, S. & Samuelsson, M.-O. 1990. Chemical fluxes and mass balances in a marine fish cage farm. I. Carbon. *Marine Ecology Progress Series* **61**, 61–73.

Harper, D. E. & Guillen, G. 1989. Occurrence of a dinoflagellate bloom associated with an influx of low salinity water at Galveston, Texas, and coincident mortalities of demersal fish and benthic invertebrates. *Contributions in Marine Science of the University of Texas* **31**, 147–61.

Harper, D. E., McKinney, L. D., Nance, J. M. & Salzer, R. B. 1991. Recovery responses of two benthic assemblages following an acute hypoxic event on the Texas continental shelf, northwestern Gulf of Mexico. In *Modern and ancient continental shelf anoxia,*. R. V. Tyson & T. H. Pearson (eds), 49–64. London: Geological Society [Special Publication 58].

Harper, D. E., McKinney, L. D., Salzer, R. B. & Case, R. J. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contributions in Marine Science of the University of Texas* **24**, 53–79.

Hendelberg, M. & Jensen, P. 1993. Vertical distribution of the nematode fauna in a coastal sediment influenced by seasonal hypoxia in the bottom water. *Ophelia* **37**, 83–94.

Henriksson, R. 1969. Influence of pollution on the bottom fauna of the sound (Öresund). *Oikos* **20**, 507–23.

Herreid, C. F. 1980. Hypoxia in invertebrates. *Comparative Biochemistry and Physiology*, **67A**, 311–20.

Hill, A. D., Taylor, A. C. & Strang R. H. C. 1991. Physiological and metabolic responses of the shore crab *Carcinus maenas* (L.) during environmental anoxia and subsequent recovery. *Journal of Experimental Marine Biology and Ecology* **150**, 31–50.

Holland, A. F., Mountford, N. K. & Mihurski, J. A. 1977. Temporal variation in upper bay benthic communities: 1. The 9m mud habitat. *Chesapeake Science* **18**, 370–78.

Holland, A. F., Shaughnessy, A. T. & Hiegel, M. H. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. *Estuaries* **10**, 370–78.

Hyland, J., Baptiste, E., Campbell, J., Kennedy, J., Kropp, R. & Williams, S. 1991. Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. *Marine Ecology Progress Series* **78**, 147–61.

Imabayashi, H. 1986. Effect of oxygen-deficient water on the settled abundance and size composition of the bivalve *Theora lubrica*. *Bulletin of the Japanese Society of Scientific Fisheries* **5**, 391–7.

Innes, A. J. 1985. Aerobic scope for activity of the burrowing mantis shrimp *Heterosquilla tricarinata* at low environmental oxygen tensions. *Comparative Biochemistry and Physiology* **81A**, 827–32

Jenkins, M. C. & Kemp, W. M. 1984. The coupling of nitrification and denitrification in two estuarine sediments. *Limnology and Oceanography* **29**, 609–19.

Jonsson, P., Carman, R. & Wulff, F. 1990. Laminated sediments in the Baltic Sea – a tool for evaluating mass balances. *Ambio* **19**, 152–8.

Josefson, A. B. & Jensen, J. N. 1992. Effects of hypoxia on soft-sediment macrobenthos in southern Kattegat. In *Marine eutrophication and population dynamics*, G. Colombo et al. (eds), 21–8. Fredensborg: Olsen & Olsen.

Josefson, A. B. & Rosenberg, R. 1988. Long-term soft-bottom faunal changes in three shallow fjords, west Sweden. *Netherlands Journal of Sea Research* **22**, 149–59.

Josefson, A. B. & Widbom, B. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Marine Biology* **100**, 31–40.

Justic, D. 1987. Long-term eutrophication of the Northern Adriatic Sea. *Marine Pollution Bulletin* **18**, 281–4.

Justic, D., Rabalais, N. N., Turner, R. & Wiseman Jr, W. J. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. *Marine Pollution Bulletin* **26**, 184–9.

Jørgensen, B. B. 1977. Distribution of colorless sulfur bacteria (*Beggiatoa* spp.) in a coastal marine sediment. *Marine Biology* **41**, 19–28.

— 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* **34**, 68–76.

Jørgensen, N. & Revsbech, N. P. 1985. Diffusive boundary layers and the oxygen uptake of sediments and detritus. *Limnology and Oceanography* **30**, 111–22.

Kamykowski, D. & Zentara, S.-J. 1990. Hypoxia in the world ocean as recorded in the historical data set. *Deep Sea Research* **37**, 1861–74.

Kennedy, V. S. 1990. Anticipated effects of climate change on estuarine and coastal fisheries. *Fisheries* **15**, 16–25.

Kester, D. R. 1975. Dissolved gases other than CO_2. In *Chemical oceanography, Vol. 2*, 2nd edn, J. P. Riley & G. Skirrow (eds), 498–556. London: Academic Press.

Kitching, J. A., Ebling, F. J., Gable, J. C., Hoare, R., McLeod, A. A. Q. R. & Norton, T. A. 1976. The ecology of Lough Ine. XIX. Seasonal changes in the western trough. *Journal of Animal Ecology* **45**, 731–58.

Kristensen, E. 1988. Factors influencing the distribution of nereid polychaetes in Danish coastal waters. *Ophelia* **29**, 127–40.

Kristensen, E. & Blackburn, T. H. 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *Journal of Marine Research* **45**, 231–57.

Kuo, A. Y. & Neilson, B. J. 1987. Hypoxia and salinity in Virginia estuaries. *Estuaries* **10**, 277–83.

Kuo, A. Y., Park, K. & Moustafa, M. Z. 1991. Spatial and temporal variabilities of hypoxia in the Rappahannock River, Virginia. *Estuaries* **14**, 113–21.

Larsen, H. S. & Petersen, A. H. 1991. *Effekter av hypoxi på overlevelse og vaekst af juvenil marin infauna*. Helsingør: Marine Biology Laboratory (mimeo.), 1–71.

Leming, T. D. & Stuntz, W. E. 1984. Zones of coastal hypoxia revealed by satellite scanning have implications for strategic fishing. *Nature* **310**, 13–138.

Leppäkoski, E. 1968. Some effects of pollution on the benthic environment of the Gullmarsfjord. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **17**, 291–301.

— Transitory return of the benthic fauna of the Bornholm Basin, after extermination by oxygen insufficiency. *Cahiers de Biologie Marine* **10**, 163–72.

— 1971. Benthic recolonization of the Bornholm basin (Southern Baltic) in 1969–1971. *Thalassia Jugoslavica* **7**, 171–9.

Levin, L. A., Huggett, C. L. & Wishner, K. F. 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *Journal of Marine Research* **49**, 763–800.

Llansó, R. J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti* (Webster). *Journal of Experimental Marine Biology and Ecology* **153**, 165–78.

— 1992. Effects of hypoxia on estuarine benthos: the lower Rappahannock River (Chesapeake Bay), a case study. *Estuarine, Coastal and Shelf Science* **35**, 491–515.

Llansó, R. J. & Diaz, R. J. 1994. Tolerance to dissolved oxygen by the tubicolous polychaete *Loimia medusa*. *Journal of the Marine Biological Association of the United Kingdom* **74**, 143–8.

Loesch, H. 1960. Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. *Ecology* **41**, 292–8.

Mangum, C. & van Winkle, W. 1973. Responses of aquatic invertebrates to declining oxygen tensions. *American Zoologist* **13**, 529–541.

May, E. B. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. *Limnology and Oceanography* **18**, 353–66.

McCall, P. L. & Tevesz, M. J. S. (eds) 1982. *Animal–sediment relationships*. New York: Plenum.

Mee, L. D. 1992. The Black Sea in crisis: a need for concerted international action. *Ambio* **21**, 278–86.

Miron, G. & Kristensen, E. 1993. Factors influencing the distribution of nereid polychaetes – the sulfide aspect. *Marine Ecology Progress Series* **93**, 143–53.

Mirza, F. B. & Gray, J. S. 1981. The fauna of benthic sediments from the organically enriched Oslofjord, Norway. *Journal of Experimental Marine Biology and Ecology* **54**, 181–207.

Möller, P., Pihl, L. & Rosenberg, R. 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Marine Ecology Progress Series* **27**, 109–21.

Mountford, N. K., Holland, A. F. & Mihursky, J. A. 1977. Identification and description of macrobenthic communities in the Calvert Cliffs region of the Chesapeake Bay. *Chesapeake Science* **14**, 360–69.

Mullins, H. T., Thompson, J. B., McDougall, K. & Vercoutere, T. L. 1985. Oxygen-minimum zone edge effects: evidence from the central California coastal upwelling system. *Geology* **13**, 491–4.

Murrell, M. & Fleeger, J. K. 1989. Meiofaunal abundance on the Gulf of Mexico continental shelf affected by hypoxia. *Continental Shelf Research* **9**, 1049–62.

Neubauer, R. J. 1993. *The relationship between dominant macrobenthos and cyclical hypoxia in the lower York River.* Masters thesis, College of William and Mary, Williamsburg, Virginia.

Newcombe, C. L. & Horne, W. A. 1938. Oxygen poor waters of the Chesapeake Bay. *Science* **88**, 80–81.

Nichols, J. A. 1976. The effect of stable dissolved-oxygen stress on marine benthic invertebrate community diversity. *Internationale Revue des Gesamten Hydrobiologie* **61**, 747–60.

Niermann, U., Bauerfeind, E., Hickel, W. & Westernhagen, H. von 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. *Netherlands Journal of Sea Research* **25**, 215–26.

Nilsson, H. & Rosenberg, R. 1994. Hypoxic response of two marine benthic communities. *Marine Ecology Progress Series*, **115**, 209–17.

Ockelmann, K. W. & Muus, K. 1978. The biology, ecology and behaviour of the bivalve, *Mysella bidentata*. *Ophelia* **17**, 1–93.

Odum, E. P. 1981. The effects of stress on the trajectory of ecological succession. In *Stress effects on natural ecosystems*, G. W. Barrett & R. Rosenberg (eds), 43–7. Chichester: John Wiley.

Odum, H. T. 1971. *Environment, power, and society*. New York: Wiley-Interscience.

Oertzen, J. A. von & Schlungbaum, G. 1972. Experimentell – ökologische Untersuchungen über O_2-Mangel und H_2S-Resistung an marinen Evertebraten der westlichen Ostsee. *Beiträge zur Meereskunde* **29**, 79–91.

Oeschger, R. 1990. Long-term anaerobiosis in subtidal marine invertebrates from the western Baltic Sea: *Halicryptus spinulosus* (Priapulida), *Astarte borealis* and *Arctica islandica* (Bivalvia). *Marine Ecology Progress Series* **59**, 133–43.

Oeschger, R. & Janssen, H. H. 1991. Histological studies on *Halicryptus spinulosus* (Priapulida) with regard to environmental hydrogen sulfide resistance. *Hydrobiologia* **222**, 1–12.

Oeschger, R. & Storey, K. B. 1990. Regulation of glycolytic enzymes in the marine invertebrate *Halicryptus spinulosus* (Priapulida) during environmental anoxia and exposure to hydrogen sulfide. *Marine Biology* **106**, 261–6.

Officer, C. B., Biggs, R. B., Taft, J. L., Cronin, L. E., Tyler, M. A. & Boynton, W. R. 1984. Chesapeake Bay anoxia: origin, development, and significance. *Science* **223**, 22–7.

Orel, G., Fonda Umani, S. & Aleffi, F. 1993. *Ipossie e anossie di fondali marini L'Alto Adriatico e il Golfo di Trieste*. Trieste: Regione Autonomia Friuli–Venezia Giulia.

Pavela, J. S., Ross, J. L. & Chittenden Jr, M. E. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. *Northeast Gulf Science* **6**, 167–73.

Pearson, T. H. & Eleftheriou, A. 1981. The benthic ecology of Sullom Voe. *Proceedings of the Royal Society of Edinburgh* **80B**, 241–69.

Pearson, T. H., Josefson, A. B. & Rosenberg, R. 1985. Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic? *Journal of Experimental Marine Biology and Ecology* **92**, 157–206.

Pearson, T. H. & Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review* **16**, 229–311.

— 1992. Energy flow through the SE Kattegat: a comparative examination of the eutrophication of a coastal marine ecosystem. *Netherlands Journal of Sea Research* **28**, 317–34.

Petersen, C. G. J. 1915. On the animal communities of the sea bottom in the Skagerak, the Christiania Fjord and the Danish waters. *Report from the Danish Biological Station* **23**, 1–28.

Petersen, J. K. & Petersen, G. I. 1988. *Sandkutlingens respiration og vækst under hypoxi*. Masters thesis, University of Copenhagen.

Pihl, L. 1989. Effects of oxygen depletion on demersal fish in coastal areas of the south-east Kattegat.

In *Reproduction, genetics and distribution of marine organisms*, J. S. Ryland (ed.), 431–9. Fredensborg: Olsen & Olsen.

— 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Journal of the Fisheries Research Board of Canada* **51**, 321–36.

Pihl, L., Baden, S. P. & Diaz, R. J. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* **108**, 349–60.

Pihl, L., Baden, S. P., Diaz, R. J. & Schaffner, L. C. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. *Marine Biology* **112**, 349–61.

Powell, E. 1989. Oxygen, sulfide and diffusion: why thiobiotic meiofauna must be sulfide-insensitive first-order respirers. *Journal of Marine Research* **47**, 887–932.

Rabalais, N. N., Turner, R. E., Wiseman Jr, W. J. & Boesch, D. F. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985–1988. In *Modern and ancient continental shelf anoxia*, R. V. Tyson & T. H. Pearson (eds), 35–47. London: Geological Society [Special Publication 58].

Rabalais, N. N., Wiseman, W. J. & Turner, R. E. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone of Louisiana. *Estuaries* **17**, 850–61.

Rachor, E. 1985. Eutrophierung in der Nordsee - Bedrohung durch Sauerstoffmangel. *Abhandlung Naturwissenschaftlichen Verein Bremen* **40**, 283–92.

Rachor, E. & Albrecht, H. 1983. Sauerstoffmangel im Bodenwasser der Deutschen Bucht. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **19**, 209–27.

Rahel, F. J. & Kolar, C. S. 1990. Trade-offs in the response of mayflies to low oxygen and fish predation. *Oecologia (Berlin)* **84**, 39–44.

Rainer, S. F. & Fitzhardinge, R. C. 1981. Benthic communities in an estuary with periodic deoxygenation. *Australian Journal of Marine and Freshwater Research* **32**, 227–43.

Reish, D. J. 1955. The relation of polychaetous annelids to harbor pollution. *Public Health Report, Washington* **70**, 1168–74.

Reish, D. J., Soule, D. F. & Soule, J. D. 1980. The benthic biological conditions of Los Angeles -Long Beach Harbours: results of 28 years of investigations and monitoring. *Helgoländer Meeresuntersuchungen* **34**, 193–205.

Renaud, M. L. 1986a. Hypoxia in Louisiana waters during 1983: implications for fisheries. *Fishery Bulletin* **84**, 19–26.

— 1986b. Detecting and avoiding oxygen deficient sea water by brown shrimp, *Penaeus aztecus* (Ives), and white shrimp *Penaeus setiferus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **98**, 283–92.

Revsbech, N. P. & Jørgensen, B. B. 1986. Microelectrodes: their use in microbial ecology. *Advances in Microbial Ecology* **9**, 293–352.

Revsbech, N. P., Sørensen, J. & Blackburn, T. H. 1980. Distribution of oxygen in marine sediments measured with microelectrodes. *Limnology and Oceanography* **25**, 403–11.

Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanography and Marine Biology: an Annual Review* **12**, 263–300.

Rhoads, D. C. & Germano, J. D. 1982. Characterization of organism-sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remots™ system). *Marine Ecology Progress Series* **8**, 115–28.

— 1986. Interpreting long-term changes in benthic community structure: a new protocol. *Hydrobiologica* **142**, 291–308.

Rhoads, D. C., McCall, P. L. & Yingst, J. Y. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* **66**, 577–86.

Rhoads, D. C. & Morse, J. W. 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia* **4**, 413–28.

Rhoads, D. C., Mulsow, S. G., Gutschick, R., Baldwin, C. T. & Stolz, J. F. 1991. The dysaerobic zone revisited: a magnetic facies? In *Modern and ancient continental shelf anoxia*, R. V. Tyson & T. H. Pearson (eds), 187–99. London: Geological Society [Special Publication 58].

Richards, F. A. 1957. Oxygen in the ocean. In *Treatise on marine ecology and paleoecology*, Vol. 1, J. W. Hedgpeth (ed.), 185–238. Baltimore: Waverly Press.

— 1965. Dissolved gases other than carbon dioxide. In *Chemical oceanography*, Vol. 1, J. P. Riley & G. Skirrow, (eds), 197–226. New York: Academic Press.

Rochford, D. J. 1953. Estuarine hydrological investigations in eastern and south-western Australia 1951. Oceanographic Station List 12, CSIRO, Australia.

Rosenberg, R. 1972. Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. *Oikos* **23**, 92–108.

— 1976. Benthic faunal dynamics during succession following pollution abatement in a Swedish estuary. *Oikos* **27**, 414–27.

— 1977. Benthic macrofaunal dynamics, production, and dispersion in an oxygen-deficient estuary of west Sweden. *Journal of Experimental Marine Biology and Ecology* **26**, 107–33.

— 1980. Effects of oxygen deficiency on benthic macrofauna in fjords. In *Fjord oceanography*, H. J. Freeland, D. M. Farmer & C. D. Levings (eds), 499–514. New York: Plenum Press.

— 1985. Eutrophication – the future marine coastal nuisance? *Marine Pollution Bulletin* **16**, 227–31.

— 1990. Negative oxygen trends in Swedish coastal bottom waters. *Marine Pollution Bulletin* **21**, 335–9.

Rosenberg, R., Arntz, W. E., Chumán de Flores, E., Flores, L. A., Carbajal, G., Finger, I. & Tarazona, J. 1983. Benthos biomass and oxygen deficiency in the upwelling system off Peru. *Journal of Marine Research* **41**, 263–79.

Rosenberg, R. & Diaz, R. J. 1993. Sulphur bacteria (*Beggiatoa* spp.) mats indicate hypoxic conditions in the Inner Stockholm Archipelago. *Ambio* **22**, 32–6.

Rosenberg, R., Gray, J. S., Josefson, A. B. & Pearson, T. H. 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? *Journal of Experimental Marine Biology and Ecology* **105**, 219–51.

Rosenberg, R., Hellman, B. & Johansson, B. 1991. Hypoxic tolerance of marine benthic fauna. *Marine Ecology Progress Series* **79**, 127–31.

Rosenberg, R. & Loo, L. O. 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia* **29**, 213–25.

Rosenberg, R., Loo, L. O. & Möller, P. 1992. Hypoxia, salinity and temperature as structuring factors for marine benthic communities in a eutrophic area. *Netherlands Journal of Sea Research* **30**, 121–9.

Rosenberg, R., Olsson, I. & Ölundh, E. 1977. Energy flow model of an oxygen-deficient estuary on the Swedish west coast. *Marine Biology* **42**, 99–107.

Rumohr, H. 1990. Photographic evidence of changes in the sediment. *Ambio* (Special Report 7), 11–12.

Rydberg, L., Edler, L., Floderus, S. & Granéli, W. 1990. Interaction between supply of nutrients, primary production, sedimentation and oxygen consumption in SE Kattegat. *Ambio* **19**, 134–41.

Rygg, B., Bjerkeng, B. & Molvaer, J. 1985. *Grelandsfjordene of Skienselva 1985*. Overvokningsrapport 202/85, Norsk Institutt for Vannforskning, Oslo.

Sandberg, E. 1994. Does short-term oxygen depletion affect predator–prey relationships in zoobenthos? Experiments with the isopod *Saduria entomon*. *Marine Ecology Progress Series* **103**, 73–80.

Sanford, L. P., Sellner, K. G. & Breitburg, D. L. 1990. Covariability of dissolved oxygen with physical processes in the summertime Chesapeake Bay. *Journal of Marine Research* **48**, 567–90.

Santos, S. L. & Bloom, S. A. 1980. Stability in an annually defaunated estuarine soft-bottom community. *Oecologia (Berlin)* **46**, 290–94.

Santos, S. L. & Simon, J. L. 1980. Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment. *Marine Ecology Progress Series* **2**, 235–41.

Sassaman, C. & Mangum, C. P. 1972. Adaptation to environmental oxygen levels in infaunal and epifaunal sea anemones. *Biological Bulletin (Woods Hole, Massachusetts)* **143**, 657–78.

Savrda, C. E. & Bottjer, D. J. 1991. Oxygen-related biofacies in marine strata: an overview and update. In *Modern and ancient continental shelf anoxia*, R. V. Tyson & T. H. Pearson (eds), 201–19. London: Geological Society [Special Publication 58].

Schaffner, L. C. 1990. Small-scale organism distribution and patterns of species diversity: evidence for positive interactions in an estuarine benthic community. *Marine Ecology Progress Series* **61**, 107–17.

Schaffner, L. C., Diaz, R. J., Olsen, C. R. & Larsen, I. L. 1987. Faunal characteristics and sediment accumulation processes in the James River estuary, Virginia. *Estuarine, Coastal and Shelf Science* **25**, 211–26.

Schaffner, L. C., Jonsson, P., Diaz, R. J., Rosenberg, R. & Gapcynski, P. 1992. Benthic communities and bioturbation history of estuarine and coastal systems: effects of hypoxia and anoxia. *Science of the Total Environment* (Suppl. 1992), 1001–16.

Schöttler, U. & Grieshaber, V. 1988. Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. *Marine Biology* **99**, 215–22.

Seliger, H. H. & Boggs, J. A. 1988. Long-term pattern of anoxia in the Chesapeake Bay. In *Understanding the estuary: advances in Chesapeake Bay research*, M. P. Lynch & E. C. Krome (eds), 570–83. Chesapeake Research Consortium Publication 129, Solomons, Maryland.

Seliger, H. H., Boggs, J. A. & Biggley, W. H. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* **228**, 70–73.

Shumway, S. E., Scott, T. M. & Shick, J. M. 1983. The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, *Mulinia lateralis* (Say). *Journal of Experimental Marine Biology and Ecology* **71**, 135–46.

Sindermann, C. J. & Swanson, R. L. 1980. Historical and regional perspective. In *Oxygen depletion and associated benthic mortalities in New York Bight, 1976*, R. L. Swanson & C. J. Sindermann (eds), 1–16. Professional Paper 11, National Oceanic and Atmospheric Administration, Washington DC.

Stachowitsch, M. 1984. Mass mortality in the Gulf of Trieste: the source of community destruction. *Publicazioni della Stazione Zoologica di Napoli I. Marine Ecology* **5**, 243–64.

— 1986. The Gulf of Trieste: a sensitive ecosystem: *Nova Thalassia* **8** (Suppl. 3), 221–35.

— 1991. Anoxia in the Northern Adriatic Sea: rapid death, slow recovery. In *Modern and ancient continental shelf anoxia*, R. V. Tyson & T. H. Pearson (eds), 119–29. London: Geological Society [Special Publication 58].

— 1992. Benthic communities: eutrophication's "memory mode". In *Marine coastal eutrophication*, R. A. Vollenweider, R. Marchetti & R. Viviani (eds), 1017–28. Amsterdam: Elsevier.

Stefanon, A. & Boldrin, A. 1981. The oxygen crisis of the Northern Adriatic Sea waters in late fall 1977 and its effects on benthic communities. In *Proceedings of the 6th Symposium of the Confédération Mondiale des Activitiés Subaquatique*, J. Blanchard et al. (eds), 167–75. Natural Environmental Research Council.

Steimle Jr, F. W. & Radosh, D. J. 1979. Effects on the benthic invertebrate community. In *Oxygen depletion and associated benthic mortalities in New York Bight, 1976*, R. L. Swanson & C. J. Sindermann (eds), 281–93. Professional Paper 11, National Oceanic and Atmospheric Administration, Washington, DC.

Stickle, W. B., Kapper, M. A., Liu, L., Gnaiger, E. & Wang, S. Y. 1989. Metabolic adaptation of several species of crustaceans and molluscs to hypoxia: tolerance and microcalorimetric studies. *Biological Bulletin* **177**, 301–12.

Summers, J. K. & Engle, V. D. 1993. Evaluation of sampling strategies to characterize dissolved oxygen conditions in northern Gulf of Mexico estuaries. *Environmental Monitoring and Assessment* **24**, 219–29.

Taylor, F. J., Taylor, N. J. & Walsby, J. R. 1985. A bloom of the planktonic diatom, *Cerataulina pelagica*, off the coast of northeastern New Zealand in 1983, and its contribution to an associated mortality of fish and benthic fauna. *International Revue des Gesamten Hydrobiologie* **70**, 773–95.

Tenore, K. R. 1972. Macrobenthos of the Pamlico River estuary, North Carolina. *Ecological Monographs* **42**, 51–69.

Theede, H. 1973. Comparative studies on the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates. *Netherlands Journal of Sea Research* 7, 244–52.

Theede, H., Ponat, A., Hiroki, K. & Schliper, C. 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology* **2**, 325–37.

Theede, H., Schaudinn, J. & Saffé, F. 1973. Ecophysiological studies on four *Nereis* species in the Kiel Bay. *Oikos Supplementum* **15**, 246–52.

Thiel, H. 1978. Benthos in upwelling regions. In *Upwelling ecosystems*, R. Boje & M. Tomczak (eds), 124–38. Berlin: Springer.

Thompson, J. B., Mullins, H. T., Newton, H. T. & Vercoutere, T. L. 1985. Alternative biofacies model for dysaerobic communities. *Lethaia* **18**, 167–79.

Tietjen, J. H. 1969. The ecology of shallow water meiofauna in two New England estuaries. *Oecologia (Berlin)* **2**, 251–91.

Tolmazin, D. 1985. Changing coastal oceanography of the Black Sea. I: Northwestern shelf. *Progress in Oceanography* **15**, 217–76.

Torrans, E. L. & Clemens, H. P. 1982. Physiological and biochemical effects of acute exposure of fish to hydrogen sulfide. *Comparative Biochemistry and Physiology* **71C**, 183–90.

Tsutsumi, H. 1987. Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. *Marine Ecology Progress Series* **36**, 139–49.

Tsutsumi, H. & Kikuchi, T. 1983. Benthic ecology of a small cove with seasonal depletion caused by organic pollution. *Publications from the Amakusa Marine Biological Laboratory, Kyusha University* 7, 17–40.

Tulkki, P. 1965. Disappearance of the benthic fauna from the basin of the Bornholm (southern Baltic) due to oxygen deficiency. *Cahiers de Biologie Marine* **6**, 455–63.

Tunnicliffe, V. 1981. High species diversity and abundance of the epibenthic community in an oxygen-deficient basin. *Nature* **294**, 354–6.

Turner, R. E. & Rabalais, N. N. 1994. Coastal eutrophication near the Mississippi river delta. *Nature* **368**, 619–21.

Tyson, R. V. & Pearson, T. H. (eds) 1991a. *Modern and ancient continental shelf anoxia*. London: Geological Society [Special Publication 58].

Tyson, R. V. & Pearson, T. H. 1991b. Modern and ancient continental shelf anoxia: an overview. In *Modern and ancient continental shelf anoxia*, R. V. Tyson & T. H. Pearson (eds), 1–24. London: Geological Society [Special Publication 58].

Valente, R. M., Rhoads, D. C., Germano, J. D. & Cabelli, V. J. 1992. Mapping of benthic enrichment patterns in Narragansett Bay, Rhode Island. *Estuaries* **15**, 1–17.

Van Es, F. B., Van Arkel, M. A., Bouwman, L. A. & Schröder, H. G. 1980. Influence of organic pollution on bacterial, macrobenthic and meiobenthic populations in intertidal flats of the Dollard. *Netherlands Journal of Sea Research* **14**, 288–304.

Vernberg, F. J. 1972. Dissolved gases. Animals. In *Marine ecology*, Vol. 1, Part 3, O. Kinne (ed.), 1491–526. London: Wiley-Interscience.

Vismann, B. 1990. Sulfide detoxification and tolerance in *Nereis (Hediste) diversicolor* and *Nereis (Neanthes) virens* (Annelida: Polychaeta). *Marine Ecology Progress Series* **59**, 229–38.

— 1991. Sulfide tolerance: physiological mechanisms and ecological implications. *Ophelia* **34**, 1–27.

Vollenweider, R. A., Marchetti, R. & Viviani, R. (eds) 1992. *Marine coastal eutrophication*. Amsterdam: Elsevier.

Wahl M. 1984. The fluffy sea anemone *Metridium senile* in periodically oxygen depleted surroundings. *Marine Biology* **81**, 81–6.

Walsh, J. J. 1981. A carbon budget for overfishing off Peru. *Nature* **290**, 300–304.

Wang, W. X. & Widdows, J. 1991. Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia. *Marine Ecology Progress Series* **70**, 223–36.

Warren, L. M. 1977. The ecology of *Capitella capitata* in British waters. *Journal of the Marine Biological Association of the United Kingdom* **57**, 151–9.

— 1984. How intertidal polychaetes survive at low tide. In *Proceedings of the First International Polychaete Conference, Sydney*, P. A. Hutchings (ed.), 238–53. New South Wales: The Linnean Society.

Wassmann, P. 1990. Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnology and Oceanography* **35**, 464–71.

Weigelt, M. 1987. *Auswirkungen von Sauerstoffmangel auf die Bodenfauna der Kieler Bucht*. Berichte 176, Institut für Meereskunde, Christian-Albrechts-Universität Kiel.

— 1990. Oxygen conditions in the deep water of Kiel Bay and the impact of inflowing salt-rich water from the Kattegatt. *Meeresforschung* **33**, 1–22.

— 1991. Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforschung* **33**, 197–224.

Weigelt, M. & Rumohr, H. 1986. Effects of wide-range oxygen depletion on benthic fauna and demersal fish in Kiel Bay 1981–1983. *Meeresforschung* **31**, 124–36.

Weiss, R. F. 1970. The solubility of nitrogen, oxygen and argon in water and seawater. *Deep-Sea Research* **17**, 721–35.

Welsh, B. L. & Eller, F. C. 1991. Mechanisms controlling summertime oxygen depletion in Western Long Island Sound. *Estuaries* **14**, 265–78.

Westernhagen, H. von & Dethlefsen, V. 1983. North Sea oxygen deficiency 1982 and its effects on the bottom fauna. *Ambio* **12**, 264–6.

Whitledge, T. E. 1985. *Nationwide review of oxygen depletion and eutrophication in estuarine and coastal waters*. Informal Report BNL 37144, National Oceanic and Atmospheric Administration, Rockville, Maryland.

Williams, L. A. & Reimers, C. 1983. Role of bacterial mats in oxygen-deficient marine basins and coastal upwelling regimes: preliminary report. *Geology* **11**, 267–9.

Winkler, L. 1888. The determination of dissolved oxygen in water. *Berichte der Deutschen Chemischer Gesellschaft* **21**, 28–43.

Winn, R. N. & Knott, D. M. 1992. An evaluation of the survival of experimental populations exposed to hypoxia in the Savannah River estuary. *Marine Ecology Progress Series* **88**, 161–79.

Wishner, K., Levin, L., Gowing, M. & Mullineaux, L. 1990. Involvement of the oxygen minimum in benthic zonation on a deep seamount. *Nature* **346**, 57–9.

Wright, L. D. 1989. Benthic boundary layers of estuarine and coastal environments. *Reviews in Aquatic Sciences* **1**, 75–95.

Wu, R. S. S. 1982. Periodic defaunation and recovery in a subtropical epibenthic community, in relation to organic pollution. *Journal of Experimental Marine Biology and Ecology* **64**, 253–69.

Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. *Oceanography and Marine Biology: an Annual Review* **4**, 33–68.

Zaitsev, Y. P. 1991. Cultural eutrophication of the Black Sea and other south European seas. *La Mer* **29**, 1–7.

— 1993. Impacts of eutrophication on the Black Sea fauna. In *Fisheries and environment studies in the Black Sea system*. Rome: Food and Agricultural Organization of the United Nations, 64–86.

Zenkevitch, L. 1963. *Biology of the seas of the USSR*. London: Allen & Unwin.