

REVIEW

Effects of hypoxia and organic enrichment on the coastal marine environment

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ABSTRACT: Eutrophication is one of the most severe and widespread forms of disturbance affecting coastal marine systems. Whilst there are general models of effects on benthos, such as the Pearson-Rosenberg (P-R) model, the models are descriptive rather than predictive. Here we first review the process of increased organic matter production and the ensuing sedimentation to the seafloor. It is shown that there is no simple relationship between nutrient inputs and the vertical flux of particulate organic matter (POM). In particular, episodic hydrographic events are thought to be the key factor leading to high rates of sedimentation and accompanying hypoxia. We extend an earlier review of effects of hypoxia to include organisms living in the water column. In general, fishes are more sensitive to hypoxia than crustaceans and echinoderms, which in turn are more sensitive than annelids, whilst molluscs are the least sensitive. Growth is affected at oxygen concentrations between 6.0 and 4.5 mg O₂ l⁻¹, other aspects of metabolism are affected at between 4 and 2 mg O₂ l⁻¹ and mortality occurs where concentrations are below 2.0 to 0.5 mg O₂ l⁻¹. Field studies, however, show that complex behavioural changes also occur as hypoxia increases, and these are described herein. The areas where hypoxia occurs are frequently areas that are stagnant or with poor water exchange. Thus again, hydrographic factors are key processes determining whether or not hypoxia and eutrophication occur. Tolerance to ammonia and hydrogen sulphide is also reviewed, as these substances are found at near zero concentrations of oxygen and are highly toxic to most organisms. However, the effects of interactions between oxygen, ammonia and hydrogen sulphide only occur below oxygen concentrations of ca. 0.5 mg O₂ l⁻¹, since only below this concentration are hydrogen sulphide and oxygen released into the water. Models of eutrophication and the generation of hypoxia are discussed, and in particular the P-R model is analysed. Although agreement with the model is widely reported the actual predictions of the model have rarely been tested. Our review suggests that the major effects on benthic fauna result from hypoxia rather than organic enrichment per se and suggests that the P-R model is descriptive rather than predictive. Finally, a managerial tool is proposed, based on the stages of effects of hypoxia and organic enrichment suggested by the P-R model and on an earlier study. The proposed strategy involves rapid assessment tools and indicates where more detailed surveys are needed. Managers are advised that remedial action will not produce rapid results and that recovery from eutrophication will probably take decades. Thus it is essential to detect potential hypoxia and eutrophication effects at early stages of development.

KEY WORDS: Eutrophication · Hypoxia · Hydrogen sulphide · Ammonia · Effects on fauna

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INTRODUCTION

The Group of Experts on Scientific Aspects of Marine Pollution (GESAMP), in their review of the State of the Marine Environment (GESAMP 1990) concluded that marine eutrophication was 'one of the major causes of

immediate concern in the marine environment'. The GESAMP report stresses that the scale of the problem

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varies from region to region, but emphasizes that the primary causal effect is discharge of nitrate and phosphate to coastal waters. In the latest report (GESAMP 2001), eutrophication is still recorded as one of the most severe problems affecting the oceans.

Eutrophication arises from an increase in nutrient and dissolved organic matter (DOM) concentrations over natural levels, which in turn leads to a greater production of particulate organic matter (POM) in the water column or on the sea-bed, (Dugdale & Goering 1967, Cadée & Hegeman 1974, Cadée 1984, Smith 1984). The organic matter usually originates from bacteria, phytoplankton and zooplankton in the water column, and from surface-living bacteria and diatoms on sediments or/and production by algae and epiphytes on hard substrata (Chapman & Craigie 1977, Hillebrand & Sommer 1999). The amounts of organic matter produced are often too large to be grazed and sink to the seabed along with faeces and other particulate organic matter. The sedimenting organic matter is degraded largely in the water column, a process that uses up oxygen. If oxygen is not supplied by advective and vertical mixing then decreases in oxygen concentrations lead to hypoxia and, in extreme cases, to anoxia.

The major external sources of nutrients and DOM/POM to coastal waters are domestic sewage and agricultural fertilizers input, largely via rivers (Ryther & Dunstan 1971, Taslakian & Hardy 1976, Nixon & Pilson 1983, Borum & Sand-Jensen 1996). Nixon (1990) pointed out that the dramatic growth of human populations in the coastal zones, the increased agricultural production through the use of fertilizers, deforestation and the increased release of nitrogen oxides into the atmosphere have made the problem more acute. He noted that eutrophication is a problem around the rim of the Mediterranean, and in an increasing numbers of bays and estuaries along the coastlines of North and South America, Africa, India, Southeast Asia, Australia, China and Japan. Yet there are areas that naturally have high nutrient content and low oxygen content in the water, such as upwelling areas off Peru, Walvis Bay in SW Africa and the Horn of Africa. Fjords (in Canada, Chile, New Zealand, Scotland, Norway, and Sweden) also have natural periodically low oxygen concentrations.

The 3 key elements of the eutrophication process therefore are (1) increased nutrient levels leading to (2) production of particulate and dissolved organic matter and (3) degradation of the organic matter leading to lowered oxygen concentrations.

In their classic paper Pearson & Rosenberg (1978) described a general model for 1 of these processes—the effects of organic enrichment on sediment-living organisms. Since their paper was published it has been

cited many hundreds of times and the model has been shown to be valid for many coastal regions of the world. The model describes the changes in patterns of numbers of species, abundances and biomass along a 'gradient' from a normal assemblage to an assemblage in sediment containing very high amounts of organic matter with accompanying anerobiosis. However, the ordinate merely represents 'increasing organic enrichment' and is not quantitative. Pearson & Rosenberg pointed out that a number of other trends accompany changes in organic enrichment, namely changes in the oxygen concentration in the water column that may lead to changes independent of those arising from increased organic matter, and physical changes that occur in the sediment which usually becomes finer grained. Since over 20 yr have elapsed since their model was devised, it is time to re-examine the model in the light of more recent data. Since the P-R model was produced there have been a number of recent general reviews of eutrophication (Pearson 1982, Carpenter & Capone 1983, Walsh 1988, Gray 1992, Heip 1995, Nixon 1995, Jørgensen & Richardson 1996). In particular, the recent review by Cloern (2001) has covered, in an excellent way, the process of eutrophication and the development of conceptual models. We will not attempt to repeat this study, but instead move towards a goal that Cloern set (Cloern 2001, p. 241): 'the evolution of our conceptual model should produce a set of tools, reflecting a more mechanistic understanding of the problems, that can be used to guide strategies of coastal ecosystem management, rehabilitation or protection.' Here we examine the development of hypoxia and its effects on the benthos in relation to tools for management.

PRIMARY PRODUCTION AND SEDIMENTATION OF ORGANIC MATTER

Sedimentation

One assumption often made is that under normal conditions the amount of organic material generated in the water column is in equilibrium with grazing and degradation processes (Graneli et al. 1990). Grazing pressure is usually a major factor influencing phytoplankton abundance. Studies show that in the enriched plume of the New York Bight 28 to 53% of the daily production can be consumed (Dagg & Turner 1982), whereas on the open coast at George's Bank, Gulf of Maine, USA, only 5 to 10% of the summer production is consumed. This is due to the continual input of recycled nutrients on the Bank from tidal stirring. In shelf systems of the Mid-Atlantic Bight, Gulf of Mexico and Bering Sea around 50% of the phytoplankton bio-

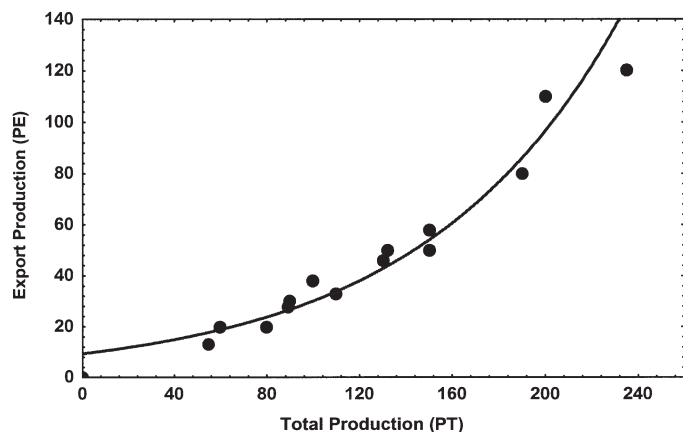


Fig. 1. Wassmann's model of export production (P_E) against total production (P_T) in gC m^{-2} , for the boreal zone of the N. Atlantic (from Wassmann 1990). Fitted regression of Export Production $P_E = 9.39^{0.012P_T}$

mass is consumed by grazers (Walsh 1988). Under eutrophic conditions, an excess of organic matter is produced which sediments out of the surface layers as exported production.

Wassmann (1990) reviewed the data and suggested a model of export production as a function of total primary production (Fig. 1). The model requires that reliable data are available for total annual primary production, which is not the case for many areas. In temperate areas, sedimentation rates are strongly seasonal, with 2 main periods of heavy sedimentation during the spring and autumn plankton blooms, and relatively little sedimentation during times of stratification. For tropical and sub-tropical areas, production is generally low and more uniform due to the oligotrophic nature of surface waters and sedimentation rates are extremely low. However, many tropical and sub-tropical areas are influenced by seasonal monsoons, when surface-water salinity drops and high amounts of organic matter enter the coastal system. It is usually following such conditions that harmful algal bloom (HAB) outbreaks occur (e.g. in Hong Kong the south-west monsoon occurs in July-August and HAB outbreaks occur in late August and September). Studies in areas subject to heavy wave action, e.g. most shallow areas, have shown that sedimentation rates increase with increasing depth (Steele & Baird 1972, Ansell 1974, Hargrave & Taguchi 1978, Smetacek 1980, Sand-Jensen et al. 1994). However, in a study of 2 fjords in Norway, which are sheltered and have little wave action, Wassmann (1985) found that sedimentation rate decreased with increasing depth. This is in keeping with data on the benthos for the outer Oslofjord which indicates that biomass decreases with increasing depth (J.S.G. unpubl. data).

Wassmann's model shows that in oligotrophic areas only 25 to 30% of the produced organic matter is exported, whereas in mesotrophic areas with primary production of $200 \text{ gC m}^{-2} \text{ yr}^{-1}$, 45% of the primary production is exported. His model predicts that under eutrophic conditions where total production is between 300 and $500 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Nixon 1995), 50% of the carbon will be exported; Borum (1996) suggested that there is a maximum rate of around $500 \text{ gC m}^{-2} \text{ yr}^{-1}$ irrespective of the amounts of nutrient inputs for most coastal areas. Measured values are in agreement with this model. For shelf areas (Mid-Atlantic Bight, the Gulf of Mexico and Bering Sea), Walsh (1988) found that 50% of primary production was exported. In the upwelling area off Peru where nutrient input levels were high before changes to the system caused by El Niño and overfishing, again 50% of the primary production was exported. (It should be kept in mind that dead and decaying phytoplankton contribute DOM to the water column that is rapidly utilised by algae and micro-organisms: Otsuki & Hanya 1972). Cloern (1982) showed that in parts of San Francisco Bay the benthos controlled phytoplankton biomass and this may well be a widespread phenomenon.

A major contributor of POM and DOM to coastal areas is discharge of sewage. In the past, dumping of raw sewage was practised in many areas, notably off the Thames estuary in UK and in New York Bight. The raw sewage dumped added much particulate and dissolved organic carbon directly to the water column. Walsh (1988) simulated a 10-fold increase in carbon and nitrogen loading to the New York Bight. He found that near the sewage dump site 1% light penetration depth occurred at 2–3 m, with a sharp increase to 7–8 m near the Hudson River plume and to 25–40 m at the outer apex. This high turbidity led to a 60–70% reduction of primary production within the Hudson River plume whereas beyond the influence of the estuary production increased slightly. Where sewage is treated, the amounts of POM are much reduced compared with raw sewage disposal, but nevertheless sewage effluents are a major source of particulate material in coastal areas. Oviatt et al. (1986, 1987, 1989) studied effects of added sewage in a mesocosm system and found that sludge particulate inputs in excess of $1 \text{ gC m}^{-2} \text{ d}^{-1}$ caused hypoxic events.

Other forms of POM added to coastal waters are paper and pulp mill effluents (Pearson & Rosenberg 1978). The POM increases turbidity, which leads to reduced primary production and reduced growth of macroalgae (Kautsky et al. 1986), and more importantly, as the organic matter is oxidised, decreases the oxygen content of the water column. Fortunately, most sewage dumping has been phased out and sewage entering coastal waters in developed countries is now treated, but the input of nutrients from this treated

sewage is a major factor influencing the state of hypoxia in coastal systems.

In estuarine and coastal areas organic matter (particulate and dissolved) can also be derived from macrophyte tissues (dead leaves, seagrasses, kelp and other algae, mangroves and terrestrial plant material: Fenchel & Blackburn 1979), but this is not thought to be a large source compared with the planktonic components. Other sources of sedimenting organic matter are faeces from zooplankton, pseudofaeces from bivalves and other encrusting species, and particulate matter where sewage sludge is dumped or paper and pulp mill waste discharged.

Wassmann's model is based on data for annual primary productivity and sedimentation, yet sedimentation is highly seasonal. In Kiel Bay diatoms in the spring bloom settle over a few days (Graf et al. 1982). This material has a high nutritional value (C:N ratio of ca. 6 to 8) and is utilised rapidly by the bacteria and micro-organisms in the sediment (Graf et al. 1982, Aubert 1990); it has also been found in mesocosm experiments in Norway (Skeie 1987). In temperate waters, sedimentation of POM occurs mainly in spring when grazing pressure by mesozooplankton is low (for an overview of processes in open oceanic water [Pacific Ocean] see Thomas 1971a,b, Knauer et al. 1979), yet the amounts that settle vary greatly from year to year (Santos & Simon 1980, Smetacek 1980, Christensen & Kanneworff 1985) depending primarily on physical conditions. It is the hydrodynamic control of 'new' inorganic nutrients from outside the system that controls the spatial and temporal variability in primary production rates.

Kjørboe et al. (1996) have recently reviewed material fluxes in the water column. They suggest that where small-sized organisms dominate the production, the microbial loop operates and sedimentation is unimportant as the particles are remineralized by micro-organisms within the surface layers. In such systems grazing control is highly efficient and the system is rarely food-limited. Light limitation however, is often important. In the Kattegat (and in most fjords) during the stratified summer period there are high concentrations of autotrophic flagellates at the pycnocline (ca. 30 % of the annual primary production in the Kattegat: Kjørboe et al. 1996). Sedimentation is proportional to the amounts of new nutrients entrained across the pycnocline. Whilst eutrophication may enhance the vertical flux of POM and potentially lead to hypoxia and anoxia below the pycnocline, the magnitude of the oxygen deficit is not related to nutrient input in a simple manner (Kjørboe 1996). With a steady input of nutrients remineralisation of the POM usually occurs within the water column and there is no flux to the seabed. If the input is episodic, however, there is considerable sedimentation and oxygen deficits can occur in deeper waters

During sedimentation (and after resuspension from the seabed) bacteria degrade POM and DOM. A key factor in the degradation process is the C:N ratio of the organic material. Phytoplankton has a C:N ratio of 6 to 7, whereas large brown algae have values of 16 to 68, seagrasses 17 to 70, rhodophytes 20 and terrestrial plant leaves including mangroves 100 to 300 (Fenchel & Blackburn 1979). Degradation and nutrient mineralisation take place when the C:N ratio, is under 10, whereas above this value net immobilization of dissolved nitrogen occurs. Thus, under eutrophic conditions with high inputs of settling dead phytoplankton cells with a low C:N ratio, mineralisation will proceed rapidly, releasing more nutrients into the water column and exacerbating eutrophication. For the Eastern seaboard of the US, Walsh et al. (1981) used C:N ratios in sediments as an indicator of the quality of material arriving at the sediment surface. Valderhaug & Gray (1984) showed that C:N ratios varied seasonally at 35 m depth in the Oslofjord, Norway, with values similar to those for plankton (8 to 10) in spring, rising to 18 in summer and winter, with a slight increase following the autumnal plankton bloom and subsequent sedimentation. Lateral advection of organic material is also highly important (Heip 1995). Many suspension-feeders utilise this material.

From the data and discussion presented here it is clear that trying to link amounts of sedimenting organic material to primary production is a difficult task (Josefson 1987, Rosenberg et al. 1987) since sedimentation rates vary with production, grazing, mineralisation, stratification and advective processes. In addition the separation of true sedimentation rates from those effected by resuspension cannot be achieved successfully with present techniques, (Dymond et al. 1981). This is an important problem as most eutrophication problems occur in shallow waters, where resuspension from wave and current action is a dominating process. Thus measurement of the amounts of organic material exported from the upper water column as a result of higher rates of production is difficult. Richardson (1996) suggests that measurements directly at the bottom of the pycnocline would resolve the problem of resuspension. In fact remarkably few studies of sedimentation rates have considered eutrophication.

Oxygen concentrations in the water column give a good indication of the state of eutrophication. For example, changes in oxygen saturation or concentrations over time have been used to show that in the inner Oslofjord conditions have worsened since the turn of the century (Mirza & Gray 1983), and in the Kattegat the average annual concentration during August, September and October decreased linearly between 1965 and 1995 (Richardson 1996).

Hydrographic conditions are extremely important in relation to whether or not hypoxia occurs. During calm

periods, with no high inputs of nutrients and no correspondingly high primary production, hypoxia can build up in summer (Richardson 1996). Conversely, even with a high nutrient input, unusually high exchange rates can also remove nutrients before production can increase, thereby preventing hypoxia conditions from evolving. Thus, the hydrography of a system is perhaps the most critical element determining whether or not hypoxia will occur, and may override the input of new inorganic nutrients; see 'Hypoxia: Areas where hypoxia has been recorded'.

Sedimenting organic matter is usually in particulate form. Under normal conditions (50 to $300 \text{ g C m}^{-2} \text{ yr}^{-1}$), it is utilised by the benthos (Graf et al. 1982). Grebmeier et al. (1988), Grebmeier & McRoy (1989), Grebmeier et al. (1989) studied 2 different water masses in the Bering and Chukchi Seas off Alaska, USA, and found that in open waters where productivity was high (250 to $300 \text{ g C m}^{-2} \text{ yr}^{-1}$) C:N ratios were low (5.8 to 7.6). In coastal waters with lower productivity (ca. $50 \text{ g C m}^{-2} \text{ yr}^{-1}$) C:N ratios were higher (7.7 to 14.0). The 2 types of benthic communities utilising this material differed, with open waters having highly productive, low (family level) diversity systems dominated by deposit-suspension-feeding amphipods, whereas inshore areas had less productive, high diversity systems. Grebmeier et al. (1989) suggested that in low productivity systems food is limiting and determines benthic diversity whereas in high-productivity systems it is largely sediment heterogeneity that determines diversity, with low diversity occurring in homogeneous sediments such as silt-clay. Such findings are highly relevant to eutrophication as primary production is often in the range of 250 to $500 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Borum & Sand-Jensen 1996). Under highly productive conditions the proportion of silt-clay may be correlated with faunal species richness provided that other factors such as hypoxia and hydrogen sulphide production play no role.

Sedimenting organic matter may also have another effect, as it can smother benthic organisms that are unable to adapt to the amounts sedimenting. Gray (1982) suggested that one of the primary effects of eutrophication was that many organisms were smothered by the sedimenting organic matter and could not survive heavy sedimentation (see also Main & Nelson 1988). The result of such effects is that species that are able continuously to colonise the newly available sediment will dominate. Examples are the polychaetes *Capitella capitata* complex and spionids such as *Polydora* spp. Gray listed a number of opportunistic species that probably had similar characteristics. Colonising ability may therefore be as important as tolerance of low oxygen concentrations in determining which species are found in the most heavily organically enriched sediments.

Hypoxia

Since sedimentation rates are difficult to obtain and are difficult to relate to nutrient inputs the simplest indication of eutrophication that can be measured is likely to be the hypoxia resulting from degradation of sedimenting POM.

Whereas under eutrophic conditions, air-sea interactions keep the surface waters above the pycnocline oxygen-saturated, increased phytoplankton production arising from increased nutrient levels often leads to super-saturation in surface waters (e.g. in the northern Adriatic: Justic 1987, Justic et al. 1987, 1988). Water above the pycnocline in the New York Bight has a slightly higher gross photosynthetic input than losses due to respiration (Walsh 1988), including losses from sewage sludge and dissolved organic carbon. Below the pycnocline, respiration losses from sedimenting phytoplankton (75%), water column (19%), faecal pellets (4%) and the benthos (5%) exceeded the oxygen available in the water column. As there was no increase in oxygen production from photosynthesis, oxygen saturation of surface water in the Hudson River plume dropped to 60 to 65% oxygen and that of bottom water to only $<1 \text{ ml O}_2 \text{ l}^{-1}$ ($<1.4 \text{ mg O}_2 \text{ l}^{-1}$), ca. 17% saturation. Walsh suggested that increases in carbon loading of ca. 50 to 100 g C m^{-2} will lead to anoxia. He calculated that with low vertical diffusive inputs anoxia will develop within ~ 30 d whereas with high diffusive input anoxia will take >600 d to develop. Thus, in addition to nutrient input, hydrographic factors largely determine the degree of hypoxia and anoxia. In the Baltic Sea, Matthäus (1998, 1999) correlated river runoff with deep water oxygen concentration. However, the influence of influxes of Atlantic water is also of major significance in determining the oxygen content of the deep basins in the Baltic (Nehring 1979). Rosenberg (1990) showed a long-term decrease in the bottom water of West coast fjords in Sweden, and relates the changes primarily to nutrient inputs from agricultural runoff. The enclosed Northern Adriatic Sea also has low oxygen concentrations in bottom water and high mortality of benthic species (Justic et al. 1987).

Effects of hypoxia

Diaz & Rosenberg (1995) reviewed the effects of hypoxia on benthic organisms. Here we have extended their review to cover species living in the water column. The data are maintained as a database available at: www.cityu.edu.hk/bch. Table 1 shows the data.

The data have obvious limitations in that often the aim was not to determine the lowest oxygen concentration that affects a species, but rather to conduct an

Table 1. Literature review of hypoxia effects on marine organisms. All data converted to mg l^{-1} and oxygen saturation based on given salinity and temperature data. LOEC: lowest observable effect concentration; NOEC: no observable effect concentration; LC: lethal concentration (50, 50% mortality); LT: lethal threshold (50, 50% mortality; 100, 100% mortality) GRR: growth rate reduction; ACT: activity; BE: behavioural effect; FEED: feeding; GRO: growth; MET: metabolism; MOR: mortality; Not: no time limit; RA: respiratory activity; REP: reproduction; F: field; L: laboratory; CAT: chloramphenicol acetyl transferase; GA: glucose reductase, PEK: protein kinase; SOD: super-oxide dismutase; ns: not specified

Species	DO level (mg l^{-1})	%	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
Algae										
<i>Gracilaria tikvahial</i>	1	14.1	1	LOEC	REP	1	21–25°C, 30%	L	Peckol & Rivers (1995)	Reduced to 23.6%
Sipunculida										
<i>Phascolosoma arcuatum</i>	0	0	48	LOEC	MET	48	ns	L	Lim & Ip (1991a)	Enzymatic activities (PEK) increased
	0	0	48	LOEC	MET	12	25°C, 15%	L	Lim & Ip (1991b)	Succinate increased from 0 to 3.62 μM , alanine by 46.7%
	0	0	48	LOEC	MET	24	25°C, 15%	L		pH decreased by 4.72% in coelomic plasma, CO_2 increased by 53.8%
	0	0	48	LOEC	MET	36	25°C, 15%	L		Aspartate decreased by 46.38% in body wall
	0	0	48	LOEC	MET	48	25°C, 15%	L	Ip et al. (1992)	Total free amino acid content decreased by 14%, aspartate by 50%, cystine increased 3.7-fold
Oligochaetes										
<i>Heterochaeta costata</i>	0.032	0.36	72	NOEC	MOR	72	16°C, 14%	L	Gamenick et al. (1996)	
<i>Paranais litoralis</i>	0.032	0.36	48	NOEC	MOR	48	16°C, 14%	L		
Polychaetes										
<i>Arenicola marina</i>	<0.2		5	LOEC	MET	5	10°C, ns	L	Abele-Oeschger & Oeschger (1995)	Haemoglobin autoxidation increased by 165%, methaemoglobin by 160%
<i>Capitella capitata</i>	1.12–1.26		ns	LT ₅₀	MOR	312	ns		Rosenberg (1972)	
	0.06–2.1	0.8–17.3	ns	GRR	GRO	0.83–1.25*	22°C, 28%	L	Forbes & Lopez (1990)	
<i>Hediste diversicolor</i>	0.032	0.36	14	LT ₅₀	MOR	14	16°C, 14%	L	Gamenick et al. (1996)	Postlarval stage
	0.032	0.36	105	LT ₅₀	MOR	105	16°C, 14%	L		Juvenile
<i>Loimia medusa</i>	0.98	13.59	ns	LT ₁₀₀	MOR	336	ns		Llansó & Diaz (1994)	
	<1	<13.87	348	LOEC	FEED	<20	26°C, 17%	L		Reduced to 0%
	0.5	6.93	348	LOEC	ACT	348	26°C, 17%	L		Reduced overall activities
<i>Polyphysia crassa</i>	1.12–1.26		ns	LT ₅₀	MOR	192	ns		Rosenberg (1972)	

Table 1 (continued)

Species	DO level (mg l ⁻¹)	%	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
<i>Riftia pachyptila</i>	0		ns	LOEC	MET	6	15°C, ns	L	Arndt et al. (1998)	Succinate level in body fluid increased by 243%
	0		ns	LOEC	MET	60	15°C, ns	L		Succinate level in tissue increased by 443%
	0		ns	LOEC	MET	6-48	15°C, ns	L		Succinate level in plume tissue increased by 133%
	0		ns	LOEC	MET	6	15°C, ns	L		Malate decreased by 90% in blood, 50% in tissue, 60% in body
	0		ns	LOEC	MET	48	15°C, ns	L		Glycogen in trophosome reduced by 60%, glutamate reduced by 70%
	0		ns	LOEC	MET	60	15°C, ns	L		Glycogen reduced by 60% in body wall, 50% in tissue
<i>Streblospio benedicti</i>	0	0	56	LT ₅₀	MOR	43			Llanso (1991)	
	0-0.56		336-Not	LT ₁₀₀	MOR	55-336				
Molluscs										
<i>Hydrobia ventrosa</i>	0.032	0.36	168	LT ₅₀	MOR	168	16°C, 14%	L	Gamenick et al. (1996)	
<i>Stramonita haemastoma</i>	0	0	528	LT ₁₀₀	MOR	528			Das & Stickle (1993)	
	0	0	672	LT ₀	MOR	20, 27, 20,	10°C, 10, 20, 30%	L	Stickle et al. (1989)	
	0	0	672	LT ₀	MOR	18, 19, 20	20°C, 10, 20, 30%	L		
	0	0	672	LT ₀	MOR	>28, 10, 15	30°C, 10, 20, 30%			
<i>Arctica islandica</i>	0	0	240	LOEC	MET	240	9.5 + 0.5°C, 22%	L	Oeschger & Storey (1993)	Total glycogen phosphorylase in adductor decreased by 34%, in foot by 27%, in mantle by 30% GR in gills increased by 500%
<i>Astarte borealis</i>	<0.2		48	LOEC	MET	48	10°C, ns	L	Abele-Oeschger & Oeschger (1995)	Methaemoglobin increased by 260%, CAT in gills decreased by 70%
	<0.2		240	LOEC	MET	240	10°C, ns	L		
<i>Crassostrea virginica</i>	0	0	672	LT ₅₀	MOR	>28, >28,	10°C, 10, 20, 30%	L	Stickle et al. (1989)	
	0	0	672	LT ₅₀	MOR	20, 18, 20	20°C, 10, 20, 30%	L		
	0	0	672	LT ₅₀	MOR	8, 4, 3	30°C, 10, 20, 30%	L		
	0-1.5	0-20	336-Not	LT ₅₀	MOR	84-336			Baker & Mann (1994)	Post-settlement phase
	<0.07	<1	24	LT ₁₀₀	MOR	24	25°C, 21%	L		
	<0.07	<1	24	LT ₁₀₀	MOR	24	25°C, 21%	L		Dissoconch post-larvae
	1.5	20	96	LOEC	GRO	96	25°C, 21%	L		Reduced from 40 to 22%

(Table continued on next page)

Table 1 (continued)

Species	DO level (mg l ⁻¹)	%	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
<i>Macoma balthica</i>	0	0	ns	LT ₅₀	MOR	432			Henniksson (1990)	
<i>Mytilus edulis</i>	0.61	6.7	>96	LT ₁₀₀	MOR	60	10°C, 31%	L	Wang & Widdows (1991)	Fertilized eggs can develop to gastrula stage only
	0.61	6.7	96		GRO	96	10°C, 31%	L		Eye-spot development delayed by <6 d
	0.6	7.3	ns	-	GRO	ns	15°C, 31%	L		Delayed development from embryos to prodissoconch stage
	1.3	15.7	60	-	GRO	60	15°C, 31%	L		Eye-spot development delayed by 2 d
	1.3	15.7	ns	-	GRO	ns	15°C, 31%	L		Eye-spot development delayed by 1 d
	2.4	29.1	ns	-	GRO	ns	15°C, 31%	L		
<i>Perna perna</i>	1	-	720	LT ₅₀	MOR	156			Marshall & Mcquaid (1993)	
<i>Scaphareia inaequalis</i>	0	0	ns	LC ₅₀	MOR	468	20°C, 36.4%	L	de Zwaan et al. (1993)	Tolerance experiments: part of a metabolic study
<i>Venus gallina</i>	0	0	ns	LC ₅₀	MOR	125	20°C, 36.4%	L		
<i>Mytilus galloprovincialis</i>	0	0	ns	LC ₅₀	MOR	360	20°C, 36.4%	L		
Crustaceans										
<i>Acartia tonsa</i>	0.06	-	288	LT ₅₀	MOR	288	ns		Marcus & Lutz (1994)	
<i>Centropages hamatus</i>	0.06	-	288	LT ₅₀	MOR	288	ns			
<i>Labidocera aestiva</i>	0.06	-	288	LT ₅₀	MOR	768	ns			
<i>Cyprideis torosa</i>	0.032	0.36	660	LT ₅₀	MOR	660	16°C, 14%	L	Gamenick et al. (1996)	
<i>Monoporeia affinis</i>	4	33	24	LOEC	RA	20	5°C, 6.5%	L	Johansson (1997)	
<i>Pontoporeia femorata</i>	0.5	4.2	24	LOEC	RA	24	5°C, 6.5%	L		55% amphipods lying on the sediment
<i>Corophium volutator</i>	0.032	0.36	4	LT ₅₀	MOR	4	16°C, 14%	L	Gamenick et al. (1996)	
<i>Idotea baltica</i>	0	0	ns	LT ₅₀	MOR	1.5	15°C, 32%	L	Vetter et al. (1999)	Mancas (stage before juvenile)
	0	0	ns	LT ₅₀	MOR	1.9	15°C, 32%	L		Juvenile
	0	0	ns	LT ₅₀	MOR	3.8	15°C, 32%	L		Adult female
	0	0	ns	LT ₅₀	MOR	6.2	15°C, 32%	L		Adult male
<i>Idotea emarginata</i>	0	0	ns	LT ₅₀	MOR	1.9	15°C, 32%	L		Mancas
	0	0	ns	LT ₅₀	MOR	2.6	15°C, 32%	L		Juvenile
	0	0	ns	LT ₅₀	MOR	6.8	15°C, 32%	L		Adult female
	0	0	ns	LT ₅₀	MOR	9.7	15°C, 32%	L		Adult male
<i>Saduria entomon</i>	0.044	0.43	8	LT ₅₀	REP	8	11°C, 10%	L	Vismann & Hagerman (1996)	Normal respiration rate re-established after 8h
	0.044	0.43	8	LOEC	MET	8	11°C, 10%	L		Metabolism reduced by 70%, oxygen debt was 0.57 mg O ₂ l ⁻¹
<i>Crangon crangon</i>	1	8.3	24	LOEC	RA	24	5°C, 6.5%	L	Johansson (1997)	Remained immobile on the sediment
	0.044	0.57	2.5	LT ₅₀	MOR	2.5	18°C, 30%	L	Hagerman & Vismann (1995)	
	0.45	5.79	30	LT ₅₀	MOR	30	18°C, 30%	L		
	0.91	11.71	ns	-	BE	ns	18°C, 30%	L		Only very sporadic movement occurred
<i>Calocaris macandreae</i>	0.7		ns	LT ₅₀	MOR	43	ns		Anderson et al. (1994)	

Table 1 (continued)

Species	DO level (mg l ⁻¹)	%	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
<i>Penaeus setiferus</i>	2	28.3	1440	-	MET	1440	28°C, 15‰	L	Rosas et al. (1999)	Unfed, ammonia excretion reduced by 76.9%
	2	28.3	1440	-	MET	1440	28°C, 15‰	L		Fed, ammonia excretion reduced by 51.1%
	2	28.3	1440	-	REP	1440	28°C, 15‰	L		Unfed, oxygen uptake reduced by 80.4%
	2	28.3	1440	-	REP	1440	28°C, 15‰	L		Fed, oxygen uptake reduced by 50.3%
	2	31.7	1440	-	REP	1440	28°C, 35‰	L		Unfed, oxygen uptake reduced by 71.8%
	3	42.4	1440	-	REP	1440	28°C, 15‰	L		Unfed, oxygen uptake reduced by 58.7%
	3	47.6	1440	-	REP	1440	28°C, 35‰	L		Unfed, oxygen uptake reduced by 47.2%
	3	47.6	1440	-	REP	1440	28°C, 35‰	L		Fed, oxygen uptake reduced by 35.5%
	3	47.6	1440	-	MET	1440	28°C, 35‰	L		Metabolic substrate changed from proteins + lipids to proteins
<i>Palaemon adspersus</i>	0	0	672	LT ₅₀	MOR	<1, <1,	20°C, 20, 30‰	L	Stickle et al. (1989)	Critical level of DO: 3.4 + 0.48 mg l ⁻¹
<i>Palaemonetes varians</i>	3.4	38.9	ns	ns	REP	ns	24°C, 14‰	L	Nielsen & Hagerman (1998)	Critical level of DO: 2.89+ 0.26 mg l ⁻¹
<i>P. pugio</i>	0	0	672	LT ₅₀	MOR	1	24°C, 14‰	L		
<i>Callinectes sapidus</i>	0	0	144	LT ₁₀₀	MOR	144	30°C, 10‰	L	Stickle et al. (1989)	
	0	0	672	LT ₅₀	MOR	<1, <1,	24°C, 30‰	L	Das & Stickle (1993)	
	0	0	672	LT ₅₀	MOR	<1, <1,	20°C, 10, 20, 30‰	L	Stickle et al. (1989)	
	0	0	672	LT ₅₀	MOR	<1, <1,	30°C, 10, 20, 30‰	L		
<i>C. similis</i>	2.22	32	672	LOEC	FEED	672	24°C, 30‰	L	Das & Stickle (1993)	Feeding reduced by 20%
<i>Carcinus maenas</i>	0	0	12	LOEC	MET	12	10°C, 30‰	L	Hill et al. (1991)	Metabolism reduced to <20%
<i>C. maenas</i>	0.04	0.4	8	LOEC	MET	8	11°C, 10‰	L	Vismann & Hagerman (1996)	Metabolism reduced by 30%
<i>Eurypanopeus depressus</i>	0	0	672	LT ₅₀	MOR	1	30°C, 10‰	L	Sickle et al. (1989)	-
<i>Rhithropanopeus harrisi</i>	0	0	672	LT ₅₀	MOR	<1	30°C, 10‰	L		-
<i>Homarus gammarus</i>	0.88		ns	LT ₁₀₀	MOR	984			Rosenberg et al. (1991)	-
<i>Nephrops norvegicus</i>	<2.8	<30	504	LOEC	FEED	504	8-10°C, 32-34‰	L	Baden et al. (1990)	Mortality reduced to 0%
	2.5	30.5	ns	ns	ACT	1	15°C, 34‰	L	Eriksson & Baden (1997)	Activity reduced to 0%
	<2		ns	ns	MET	1	ns	F	Eriksson et al. (1998)	Manganese concentration in gill increased over 20-fold
Echinoderms										
<i>Amphitura filiformis</i>	<0.1	<1.1	168	LT ₅₀	MOR	168	8.5 + 1.5°C, 29.5 + 1.4‰	L	Vistisen & Vismann (1997)	
	0.3	3.27	348	LT ₅₀	MOR	348	8.5 + 1.5°C, 29.5 + 1.4‰	L		
	0.5	5.45	780	LT ₅₀	MOR	780	8.5 + 1.5°C, 29.5 + 1.4‰	L		

(Table continued on next page)

Table 1 (continued)

Species	DO level (mg l ⁻¹)	%	DO level	Expt duration (h)	Expt Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
	0.1–1	1.1–11		ns	LOEC	BE	29.5 + 1.4 ^{ns}	8.5 + 1.5°C,	L		All rose to the sediment surface and lifted the disc into the water column
	1.8	20		1440		GRO	1440	10°C, 33%	L	Nilsson & Skold (1996)	Arm regeneration rate slowed by 65%, Length reduced by 25% and area by 36%
	2.7	30		1440		GRO	1440	10°C, 33%	L		Length reduced by 14%, area by 21%
	1.8–2.2	20–24.4		1488		GRO	1488	10°C, 34%	L	Nilsson (1999)	Arm regeneration rate decreased by 20%
<i>Ophiura albida</i>	<0.1	<1.1		60	LT ₅₀	MOR	60	8.5 + 1.5°C,	L	Vistisen & Vismann (1997)	Quickly became inactive & moribund
	0.3	3.27		144	LT ₅₀	MOR	144	29.5 + 1.4 ^{ns}	L		
	0.5	5.45		336	LT ₅₀	MOR	336	8.5 + 1.5°C,	L		
	0.1–1.1	1.1–11		ns	LOEC	BE	ns	29.5 + 1.4 ^{ns}	L		Initially showed increased mobility (escape response for 2 to 4 dl); lifted disc into water column
<i>A. filiformis</i>	1.8	20		1440		GRO	1440	10°C, 33%	L	Nilsson & Skold (1996)	Arm regeneration rate slower to 65% length reduced by 25% area by 36%
	2.7	30		1440		GRO	1440	10°C, 33%	L		Length reduced by 14%, area reduced by 21%
	1.8–2.2	20–24.4		1488		GRO	1488	10°C, 34%	L	Nilsson (1999)	Arm regeneration rate decreased by 20%
<i>Ophiura albida</i>	<0.1	<1.1		60	LT ₅₀	MOR	60	8.5 + 1.5°C,	L	Vistisen & Vismann (1997)	Quickly became inactive and moribund
	0.3	3.27		144	LT ₅₀	MOR	144	29.5 + 1.4 ^{ns}	L		
	0.5	5.45		336	LT ₅₀	MOR	336	8.5 + 1.5°C,	L		
	0.1–1.1	1.1–11		ns	LOEC	BE	ns	29.5 + 1.4 ^{ns}	L		Initially showed increased mobility (escape response for 2–4 dl), lifted discs into water column
<i>Psammochinus miliaris</i>	8	92.9		5		REP	5	12°C, 34%	L	Spicer (1995)	Reproduction decreased progressively as oxygen declined from 8 to 1.8 mg l ⁻¹
Fish											
<i>Anchoa mitchilli</i>	1	13.5		24	LT ₁₀₀	MOR	24	24–26°C,	L	Breitbart et al. (1994)	
								13–17 ^{ns}			
<i>Boleophthalmus boddarti</i>	0.8	10.8		6	LOEC	MET	6	25°C, 15%	L	Chew & Ip (1992a)	ADP in muscle reduced by 36%
	0.8	10.8		6	LOEC	REP	0.083	25°C, 15%	L		Oxygen consumption reduced by 58.3%
	0	0		0.67	LOEC	MET	0.67	25°C, 15%	L		In muscle, CrP reduced by 24%, ATP reduced by 27%.

Table 1 (continued)

Species	DO level (mg l ⁻¹)	%	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	F/L	Source	Remarks
<i>A. filiformis</i>	0	0	0.36	LOEC	ACT	0.36	25°C, 15‰	L	Chew & Ip (1992b)	Completely inert
	0	0	1	LOEC	MET	1	25°C, 15‰	L	Low et al. (1993)	Lactate in the gills increased 12-fold Glycogen decreased by 36%
	1.12	15.1	1	LOEC	MET	1	25°C, 15‰	L	Nilsson & Skold (1996)	Arm regeneration rate slowed by 65%, Length reduced by 25% and area by 36%
	1.8	20	1440		GRO	1440	10°C, 33‰	L		Total lactate produced increased 2-fold, lactate in blood 4-fold
<i>B. boddaerti</i>	1.12	15.1	6	LOEC	MET	6	25°C, 15‰	L	Low et al. (1993)	
<i>Gadus morhua</i>	<4	<36.2–50.1	ns	LOEC	ACT	7.5	5, 10, 15°C, 19–21‰	L	Schurmann & Steffensen (1994)	Reduced swimming activity by 60%
	4.19	45	2016	LOEC	FEED	2016	10°C, 28‰	L	Chabot & Dutil (1999)	Reduced feeding by 54.3%
	4.19	45	2016	LOEC	MET	2016	10°C, 28‰	L		Lactate decreased by 21.7%, K ion increased by 8.5%
	5.21	56	2016	LOEC	MET	2016	10°C, 28‰	L		Liver glucose decreased by 26.2%
<i>Gobiosoma bosc</i>	6.05	65	2016	NOEC	GRO	2016	10°C, 28‰	L		Reduction in length
	6.8	73	2016	NOEC	GRO	2016	10°C, 28‰	L		Reduction in mass
	1	13.5	24	LT ₁₀₀	MOR	24	24–26°C, 13–17‰	L	Breitbart et al. (1994)	
	1	13.5	4	LOEC	REP	4	24–26°C, 13–17‰	L		Reproduction increased by 200%
<i>Solea solea</i>	0	0	12	LOEC	MET	12	20–24°C, 37‰	L	Dalla Via et al. (1997)	In muscle ATP decreased by 40%, in liver glucose increased 8-fold
	0.45	6.5	12	LOEC	MET	12	20–24°C, 37‰	L		Glycerol-3-P increased by 200%
	0.9	13	12	LOEC	MET	12	20–24°C, 37‰	L		In muscle lactate increased 3-fold, glucose by 114%
<i>Periophthalmus chrysospilos</i>	0.9	13	12	LOEC	MET	12	20–24°C, 37‰	L	Dalla Via et al. (1994)	Metabolism decreased by 27%
	0.75		6	LOEC	ACT	2.04	ns	L	Chew et al. (1990)	Completely inert
<i>Periophthalmodon schlosseri</i>	0.8		6	LOEC	REP	6	ns	L		Respiratory rate reduced by 70%
	0.8		6	LOEC	MET	6	ns	L		Plasma lactate increased 5-fold
	0.8	10.8	6	LOEC	MET	6	25°C, 15‰	L	Ip & Low (1990)	Lactate in gills increased by 98%, in blood by 80%
<i>Platichthys flesus</i>	0	0	1	LOEC	MET	1	25°C, 15‰	L	Low et al. (1993)	Lactate in the gills increased by 115%
	1.12	15.1	1	LOEC	MET	1	25°C, 15‰	L		Glycogen decreased by 36%
	1.12	15.1	6	LOEC	MET	6	25°C, 15‰	L		Total lactate produced increased 3.2-fold, lactate in blood by 124%, gills by 115%
	<0.4	<5.8–6.3	6	LOEC	MET	3	30°C, 15–27‰	L	Ishimatsu et al. (1999)	Heart rate increased by 29%
<i>Zoarces viviparus</i>	0.5	4.96	0.38 + 0.03	LT ₅₀	MOR	0.38 + 0.03	13°C, 5‰	L	Tallqvist et al. (1999)	
	1	9.92	2.48 + 0.13	LT ₅₀	MOR	2.48 + 0.13	13°C, 5‰	L		
	2	19.84	30.58 + 1.45	LT ₅₀	MOR	30.58 + 1.45	13°C, 5‰	L		
	3	29.76	22	LOEC	REP	22	13°C, 5‰	L		
<i>Zoarces viviparus</i>	3	29.76	24	LT ₅₀	FEED	24	13°C, 5‰	L		Ventilation rate increased by 26%
	0	0	1	LT ₁₀₀	MOR	1	15°C, 34‰	L	Fischer et al. (1992)	Predation efficiency reduced by 64%
	<2.9	<35.4	ns	LOEC	ACT	ns				Motionless

experiment at a specific concentration and exposure time. For example there are many studies on mortality rates at 0 mg O₂ l⁻¹. This concentration does lead to mortalities, but there may well be stronger effects at higher concentrations that have not been studied. Thus, in the present study more significance is given to non-lethal effects such as effects on growth, feeding and metabolic rates rather than mortality.

Diaz & Rosenberg (1995) defined hypoxia as beginning at 2.0 ml O₂ l⁻¹ and reaching the point of anoxia at 0.0 ml l⁻¹. (At 20 psu, 1 ml O₂ l⁻¹ is equivalent to 1.4 mg l⁻¹, or 4.3% O₂ and 14% saturation.) In general, prolonged exposure to 4 mg O₂ l⁻¹ causes acute mortality in many invertebrates and non-salmonid fish embryos; while 3 mg O₂ l⁻¹ causes acute mortality in most non-salmonid fishes (USEPA 1986, 1989). It is also generally accepted that larval fishes and crustaceans are more sensitive than the adults (Miller et al. 1995).

The literature data show that fishes are more sensitive to reduced oxygen concentrations than crustaceans, followed by annelids, and that bivalves are the most tolerant (Rosenberg et al. 1992, Nilsson & Rosenberg 1994, Reish 1970). There are few studies of growth reductions caused by reduced oxygen concentrations, but see Strzyewska (1978), Strzyewska & Popiel (1974) and Wrezinski (1983) for indirect evidence. Severe production impairment of early-life non-salmonid species occurred when oxygen falls below 4.5 mg l⁻¹ (USEPA 1986). An oxygen concentration of 4.7 mg l⁻¹ impairs larval growth (Miller et al. 1995), and adult fishes reduce food intake and growth when oxygen falls to 60–70% of saturation (Jobling 1993, Pichavant et al. 1999). The relatively active cod *Gadus morhua* shows reductions in growth at 6.5 mg O₂ l⁻¹, a high oxygen concentration. Whereas metabolic effects appear in *G. morhua* at concentrations of 4.5 mg O₂ l⁻¹ mudskippers (*Boleophthalmus boddarti*, *Periophthalmus chrysoplis*, *P. schlosseri*), which inhabit burrows in fine muddy sediments in tropical and sub-tropical areas, show metabolic effects only at concentrations of around 1 mg O₂ l⁻¹. The boreal *Solea solea*, a bottom-living flatfish shows levels of metabolic response similar to those of Mudskippers. Keckeis et al. (1996) showed that reduced oxygen (10% air saturation) increased mortality and decreased hatching success in nase *Chondrostoma nasus*. Most fishes show mortality at oxygen concentrations between 1 and 2 mg O₂ l⁻¹, but mudskippers are not affected until values fall to around 0.5 mg O₂ l⁻¹. Thus the behavioural habits of a species are a good indication of its probable hypoxic tolerance level.

In crustaceans, the blue crab *Callinectes sapidus*, the Norway lobster *Nephrops norvegicus* and the shrimps *Penaeus setiferus* and *Palaemon adspersus* and *P. varians* show hypoxic effects on feeding at between 2 and

3 mg O₂ l⁻¹. A decrease in growth rates at oxygen concentrations below 3.5 mg O₂ l⁻¹ has been shown for the marine amphipod *Melitta longidactyla* (Y.Y.O. unpubl. data). Abundances are reduced and mortalities occur below 1 mg O₂ l⁻¹ in the sediment-living isopod *Saduria entomon*. For *M. longidactyla* the 48 h LC₅₀ value is 1.6 mg O₂ l⁻¹.

Reductions in growth occur in the ophiuroid echinoderm *Amphiura filiformis* between 2.7 and 1.8 mg O₂ l⁻¹ and in the bivalve molluscs *Crassostrea virginica* and *Mytilus edulis* between 1.5 and 0.6 mg O₂ l⁻¹ oxygen, whereas the opportunistic polychaete *Capitella capitata* shows growth reductions between 2.1 and 0.06 mg O₂ l⁻¹, but can survive for >24 d at 2.1 mg O₂ l⁻¹ (Rosenberg 1972).

In tolerance experiments conducted without sediments, Dries & Theede (1974) found that at 17 psu, 10°C and <0.15 ml O₂ l⁻¹ the bivalves *Astarte borealis*, *A. elliptica*, *A. monatgui*, *Arctica islandica* and *Mytilus edulis* survived more than 1000 h, whereas the polychaetes *Nephtys ciliata* and *Nereis diversicolor* survived for ca. 200 h and the crustaceans *Carcinus maenas*, *Gammarus oceanicus*, *Idotea balthica* and *Crangon crangon* survived for less than 100 h. Similarly, Henriksson (1969) reported the ranking of anoxic tolerance from greatest to least as: bivalves *Macoma balthica* > *Cardium lamarkii* > polychaetes *N. diversicolor* > *Scoloplos armiger* > *Ampharete grubei* > *Terebellides stroemi*. De Zwaan et al. (1993) found that bivalves from the Mediterranean were highly tolerant of anoxia, with *Scapharea inaequalis* surviving 48 h of anoxia. Table 2 summarises these effects. Crustaceans show the least tolerance (Theede 1973, Dries & Theede 1974). Although growth and metabolic effects occur at concentrations above 2 mg O₂ l⁻¹ below this value mortality will occur if the organisms cannot escape from hypoxic conditions. Whilst fishes and some crustaceans may be able to move away from the areas affected, most benthic organisms suffer mortality. This will occur first in crustaceans and echinoids followed

Table 2. Summary of effects of reduced oxygen concentrations on marine organisms

Type of organism	Effect	Conc. (mg l ⁻¹)
Actively swimming fish	Growth	6
Actively swimming fish	Metabolism	4.5
Bottom-living fish	Metabolism	4
Most fishes	Mortality	2
Crabs, shrimps, lobsters, isopods	Growth	2–3.5
Bottom-living isopods	Mortality	1–1.6
Bivalve molluscs	Growth	1–1.5
Annelids	Growth	1–2
Mudskippers	Mortality	1

by the more sensitive annelids and finally the bivalve molluscs.

The present review clearly reveals that the secondary effects of eutrophication on benthos and fishes are largely the result of reduced oxygen saturation caused by the decay and sedimentation of organic material. Some field studies illustrate that there are behavioural responses in addition to effects on growth and metabolism (Renaud 1986). The Kattegat has undergone regular seasonal hypoxic events for many decades (Jørgensen & Richardson 1996, Richardson & Heilmann 1995). During these events, biomass reductions in benthic assemblages were recorded at stations that were subject to lowered oxygen concentrations (Pearson et al. 1985). Pihl (1989), Pihl et al. (1992, 1994) and Baden et al. (1990) reported changes in the behaviour of benthic species, whereby fishes such as cod and whiting left the area at oxygen saturation levels below 25%, whereas dabs and flounders were more resistant, leaving the area only when oxygen saturation dropped below 15%. In hypoxic water, some fish species moved to the surface and ventilated their gills in the top oxygenated layer (Val et al. 1998). One of the more unusual aspects of hypoxic events is increased catches of fishes. Fishes migrate away from areas with low oxygen saturation and concentrated in shallower areas where catches increase (Hildén et al. 1982, Pihl 1989, Hagström et al. 1989, Baden et al. 1990, Hansson & Rudstam 1990). Dyer et al. (1983) caught much higher numbers of benthic animals in trawls off the Danish coast in an area of low bottom-water oxygen concentrations; however, when low oxygen concentrations persisted, the catches of fishes were reduced. The decapod *Nephrops norvegicus* left its burrow and appeared on the sediment surface at oxygen saturation below 15%. Of the organisms commonly found in sand–mud bottoms, the bivalve *Abra* sp. and the burrowing urchins *Echinocardium* spp. are particularly sensitive to reduced oxygen concentration (Baden et al. 1990). In the Gullmarfjord, Sweden, Josefson & Widbom (1988) found that at oxygen concentrations below 1.4 mg l⁻¹ all the macrofauna was eliminated, but that no meiofaunal taxa showed significant declines in abundance. (See also Gowen & Bradbury 1987, Hargrave 1994 and Hevia et al. 1996, who examined the effects of direct organic matter input from fish farms on the benthos.) Levin & Gage (1998) found that depth and organic matter, rather than oxygen concentration, limited faunal richness and biomass.

A consequence of these behavioural changes is that predator-prey dynamics can also be altered. Although there are few studies on the effects of hypoxia on predator-prey relationships, Sandberg (1994) showed that the predatory isopod *Saduria entomon* was inhibited in its predatory activities on the Baltic Sea benthos

by low hypoxia. In laboratory experiments Taylor & Eggleston (2000) showed, that the blue crab *Callinectes sapidus* altered its predatory behaviour in response to hypoxia. Low oxygen concentrations inhibited the crab from foraging, but increased prey (the clam *Mya arenaria*) vulnerability by altering the siphon extension and depth distribution within the sediment (see also Breitburg et al. 1994, Nestlerode & Diaz 1998).

Under conditions of extreme amounts of nutrient input, mass growth occurs in opportunistic algae such as *Ulva* sp. in the Lagoon of Venice (Sfriso et al. 1987, 1988) and *Cladophora* sp. in Laholm Bay, Sweden (Baden et al. 1990). These species form huge mats and smother the sediment, which becomes anaerobic as a consequence. Large phytoplankton blooms resulting from excess nutrient addition may be toxic, the so-called 'red tides'. Examples of such toxic blooms are too numerous to mention but see Smayda (1990) for recent references.

Areas where hypoxia has been recorded

In their review Diaz & Rosenberg (1995) provide a comprehensive list of areas where hypoxia has occurred. Here we take a slightly different approach and classify the types of hypoxia and areas in which hypoxia/anoxia have been recorded (see Table 3). Upwelling areas are not included since although such areas do experience hypoxic events (e.g. the coast of Peru, Walvis Bay, South Africa and the Horn of South Arabia) these are not usually driven by anthropogenic activities, but man-induced climate change may influence these systems. Additional anoxic events not recorded in the Diaz & Rosenberg (1995) review are: in coastal waters in New South Wales (Rainer & Fitzhardinghe 1981), Northern Adriatic (Degobbis et al. 1979), Tokyo Bay (Tsuji et al. 1973), Mobile Bay (May 1973), Bay of Vilaine (Rossignol-Stick 1985) and Chesapeake Bay Seliger et al. (1985). Additional references to the New York Bight incident are found in Falkowski et al. (1980).

Table 3 shows that hypoxia occurs most commonly as a seasonal phenomenon in many areas, notably fjords, estuaries, coastal embayments, and occurs on the shelf adjacent to the Mississippi River and the anoxic basin in the central Black Sea. Hydrographic and climatic forcing processes drive these seasonal events. For example exchange of the deep (often anoxic) water in the inner Oslofjord is driven primarily by northerly winds, which move less-saline surface waters out of the fjord to be replaced by more-saline deep water from the Skagerrak. This water sinks when it flows over the 2 major sills and the anoxic water, which is

Table 3. Marine areas subjected to hypoxia. 1: seasonal; 2: periodic; 3: irregular; 4: permanent

Fjords	Estuaries	Bays	Shelf	Enclosed seas
Saanich Inlet, Canada (1)	Port Hacking, Australia (1)	Chesapeake Bay (1)	Louisiana shelf (1)	Seto Inland Sea, Japan (1)
Inner Oslofjord, Norway (1)	Pamlico River, USA (1)	Tome Cove, Japan (1)	Black Sea shelf (1)	Bornholm Basin, Baltic Sea(1)
Gullmarsfjord, Sweden (1)	46% of US estuaries (1)	Laholm Bay, Sweden (1)	Texas Shelf (3)	Kattegat, Denmark (1)
Swedish west coast fjords (1)	Rappahannock R USA (2)	Kiel Bay, Germany (1)	German Bight (3)	Northern Adriatic (3)
Limfjord, Denmark (1)	York River, USA (2)	Hillsborough Bay, Florida (1)	New York Bight (3)	Central Black Sea (4)
Lough Ine, Ireland (1)		Gulf of Trieste, Adriatic (1)	Danish-German coast (3)	Central Baltic Sea (4)
Sullom Voe, Scotland (1)		Elefsis Bay, Aegean Sea (1)	New South Wales (3)	Central Caspian Sea (4)
Byfjord, Sweden (4)		Aarhus Bay, Denmark (1)		
Idefjord, Sweden-Norway (4)		Tolo Harbour, Hong Kong (1)		
		Bay of Vilaine, France (3)		
		Somm(1) Bay, France (3)		
		German Bight, North Sea (3)		
		Mobile Bay, USA (3)		
		Tokyo Bay, Japan (3)		
		Fosa da Cariaco, Venezuela (4)		
		Gulf of Finland (4)		

less saline, is lifted and disperses and moves out of the fjord. Whilst such events are natural and have occurred over long periods of time, there is no doubt that their extent in time and space has increased in recent years with the addition of nutrients and/or organic matter from anthropogenic sources. The inner Oslofjord, Norway (Mirza & Gray 1983, Paasche & Erga 1988), Swedish fjords and coasts (Söderström 1971, Rosenberg 1977, Svane & Gröndal 1988, Diaz & Rosenberg 1995), the Kattegat (Jørgensen 1980, Andersson & Rydberg 1988, Rydberg et al. 1990, Steffensen 1990), the Baltic Sea (Wulff et al. 1986, 1990, Rosenberg et al. 1990), Dutch and German coastal waters (Bennekoum et al. 1975, Cadée 1984, Beukema & Cadée 1986, Reise et al. 1989), the German Bight (Rachor 1990), Kiel Bay (Rumohr 1986), Black Sea (Zaitsev 1992) and Chesapeake Bay (Cooper & Brush 1991) are good examples. There are only 2 examples of periodic, but non-seasonal hypoxia, both from rivers entering Chesapeake Bay. These events last from days to weeks and occur irregularly throughout a year. In the York River, tidal mixing controls the periodicity, whereas in the Rappahannock River a combination of tidal mixing and proximity to the hypoxic waters of Chesapeake Bay (Kuo & Neilson 1987) plays the key role.

Irregular events are also usually driven by unusual hydrographic and/or climatic factors. For example the New York Bight event in 1981 has been particularly well studied. Whilst this event was initially attributed

to increased anthropogenic carbon input (mainly sewage) simulation models showed that the event was most probably the result of unusual climatic conditions. These were: a warm winter with large terrestrial runoff; a low frequency of spring storm events resulting in a deep spring thermocline; persistent southerly summer winds; a large autochthonous carbon load of the dinoflagellate *Ceratium triops*; and low grazing pressure (Walsh 1988 gives a full account of this event). A simulation study (Stoddard & Walsh 1986) showed that the anoxic event would have occurred without any allochthonous input of organic carbon from anthropogenic sources. What is clear from that study is that climatic conditions were extremely important in triggering the event. The anoxic event off the Danish-German coasts in September 1981 (Dyer et al. 1983) was also probably caused by unusual hydrographic conditions.

The areas with permanent anoxia (Idefjord, Byfjord, Fosa da Cariaco, Gulf of Finland and the central areas of the Baltic, Black and Caspian Seas) are all areas with extremely limited water exchange so that replenishment of the oxygen in the deep basins is not possible. However, in all these areas there is little doubt that conditions have worsened during this century as a result of anthropogenic inputs of nutrients.

A common factor concerning all the examples shown in Table 3 is that hypoxia and anoxia occur in areas that have poor water exchange. Yet these

marine coastal environments encompass a wide variety of systems: from stratified and non-stratified estuaries, fjords with and without sills, areas with temporary and permanent frontal systems, gyres which entrain nutrients and production, areas that are constantly mixed and areas that are periodically stratified. No simple model will encompass all these forms of variability, and it is probable that each area will have to be considered per se. Waves, tides and currents are also of great significance to the large areas of intertidal and shallow subtidal zones in the marine environment. Physical factors such as wave action can limit biomass despite a rich supply of nutrients. Hypoxia in freshwater lakes has been controlled using a simple relationship established by Vollenweider (1976). If one knows the phosphorus input and output, the area and the average depth of the lake, and its mean phosphorus concentration, one can predict by how much nutrient input needs to be reduced to restore the lake to oxic conditions. Vollenweider's model has been applied successfully to many lakes. However, no simple relationship of the Vollenweider type (Vollenweider 1975, 1976) is likely to apply to coastal marine areas subjected to high nutrient loadings. Vollenweider (1992) acknowledged this by commenting on coastal eutrophication that '...difficulties rest not only with the assessment of load and nutrient budgets, but with the interpretation of such figures...their trophodynamic significance...unless further morphometric, hydrological and other parameters of the system are also taken into consideration.'

Examination of the areas where eutrophication effects have been observed reveals that hypoxia is the critical factor affecting marine life and where anoxic events occur these are most often associated with unusual climatic conditions. Likewise, high organic matter content in the sediment will not lead to negative effects if the material is difficult to breakdown (high C:N ratios) and does not enhance aerobic microbial activity and lead to hypoxia. However, where the material is of high quality (C:N < 10) and oxygen is present, microbial action will lead to mineralisation of the organic matter and lowering of the oxygen concentration and may lead to hypoxia. Thus it is important that coastal zone managers realise that discharges of nutrients either directly as sewage or indirectly from agricultural and forestry runoff will lead to problems in areas that are stagnant or that have limited water exchange.

Ammonia

Ammonia is acutely toxic to fishes and marine organisms at low concentrations, and unionized ammonia is considered the major toxic form in the aquatic environ-

ment. In the environment, ammonia is in equilibrium with ammonium. The threshold concentration of total ammonia ($[\text{NH}_3] + [\text{NH}_4^+]$) resulting in unacceptable biological effects promulgated by the USEPA (1989) was 3.48 mg N l^{-1} at pH 6.5 and 0.25 mg N l^{-1} at pH 9.0. The updated criteria (USEPA 1989) sets the acute-chronic ratio at (14.4 mg N l^{-1} , pH 8) and (1.27 mg N l^{-1} , pH 11.3). Most of our knowledge on ammonia toxicity in the aquatic environment is based on freshwater animals, and there is a paucity of data on marine animals (Handy & Poxton 1993).

Table 4 shows the effects of unionized ammonia on marine organisms. Here the mortality studies were aimed at determining the LC_{50} values. For the flounder *Paralichthys orbignyanus*, adults showed effects at between 50 and $66 \text{ mg NH}_3 \text{ l}^{-1}$ whereas 1 d old larvae were affected at concentrations of only $0.27 \text{ mg NH}_3 \text{ l}^{-1}$ and 23 d old larvae at $1.02 \text{ mg NH}_3 \text{ l}^{-1}$ (Kim et al. 1997). Penaeid shrimps varied in their LC_{50} response, from $11.5 \text{ mg NH}_3 \text{ l}^{-1}$ in *P. penicillatus* to ca. $50 \text{ mg NH}_3 \text{ l}^{-1}$ in *P. chinensis*. The burrowing amphipod *Ampelisca abdita* had a LC_{50} of ca. $50 \text{ mg NH}_3 \text{ l}^{-1}$.

The LC_{50} responses to unionised ammonia are remarkably uniform across species with the minnow *Cyprinodon variegatus*, the turbot *Scophthalmus maximus* and the lobster *Homarus americanus* being most sensitive at 2.1 to $3.8 \text{ mg NH}_3 \text{ l}^{-1}$, whereas nearly all other species studied ranging from mysids, shrimps, bivalves and fish (seabass, seabream, inland silverside, planehead pipefish, winter flounder) were affected at concentrations of $< 2 \text{ mg NH}_3 \text{ l}^{-1}$.

Hydrogen sulphide

There are considerable data on the effects of hydrogen sulphide (H_2S) on freshwater fish species, but relatively little on marine species (Tables 5 & 6). Again there appears to be a marked difference between mortality effects in active fishes (e.g. pike *Esox lucius*) with a range of 16 to $76 \text{ } \mu\text{g H}_2\text{S l}^{-1}$ (geometric mean 35) and those in benthic species (e.g. lake whitefish *Coregonus clupeaformis*), with a range of 2 to 13 (geometric mean 4.14) $\mu\text{g H}_2\text{S l}^{-1}$. Crayfish (*Cambarus diogenes* and *Procambarus clarki*) were far more tolerant with LC_{50} values of 146 and $115 \text{ } \mu\text{g H}_2\text{S l}^{-1}$ respectively.

Of the marine species for which there are data the shrimp *Palaemon pugio* had an LC_{50} of 114 and marine bottom-living foraminiferans an LC_{50} between 200 and $400 \text{ } \mu\text{g H}_2\text{S l}^{-1}$.

The polychaete *Capitella capitata*, which occurs in high numbers in organically highly rich sediments, has a requirement for hydrogen sulphide as a settlement clue (Cuomo 1985) and thus newly settled larvae are found in hydrogen sulphide-rich sediments.

Table 4. Effects of unionised ammonia (as LC₅₀ values) on marine organisms under various environmental conditions. ns: not specified

Species	LC ₅₀ conc. (mg NH ₃ l ⁻¹)	Expt duration (h)	Temp. (°C)	Salinity (‰)	pH	Source
Crustaceans						
<i>Eucalamus elongatus</i>	0.87	24–48	20.3	34	8	USEPA (1989)
<i>E. pileatus</i>	0.79	24–48	20.5	34	8.2	
<i>Latreutes fucorum</i>	0.77	24–48	23.4	28	8.07	
<i>Metapenaeus ensis</i>	0.87–1.76	48–96	25	25	7.7	Nan & Chen (1991)
<i>Mysidopsis bahia</i>	0.50	96	25	31	7	Miller et al. (1990)
	1.70	96	25	31	8	
	2.87	96	25	31	9	
	0.048	672	25	31	ns	
	0.163	672	25	31	ns	
	0.331	672	25	31	ns	
	1.02	24–48	23.2	21.4	6.8–9.2	USEPA (1989)
<i>Palamonetes pugio</i>	1.65	24–48	19.9	19.2	8	
<i>Homarus americanus</i>	2.21	24–48	21.9	33.4	8.1	
<i>Penaeus chinensis</i>	1.53–2.10	48–96	26	33	7.94	Chen et al. (1990)
	3.88	24	25	30	8.12	Chen & Lin (1992)
Molluscs						
<i>Crassostrea virginica</i>	19.10	24–48	20	27	7.7–8.0	USEPA (1989)
<i>Mercenaria mercenaria</i>	5.36	24–48	20	27	7.7–8.2	
<i>Placopecten magellanicus</i>	1.80	96	4	ns	ns	Abraham et al. (1996)
	1.00	96	10	ns	ns	
Fishes						
<i>Cyprinodon variegatus</i>	2.10	96	13	30–32.5	8.05	Miller et al. (1990)
	2.80	96	25	30–32.5	7.25	
	3.51	96	32.5	30–32.5	7.75	
<i>Dicentrarchus labrax</i>	1.70	96	17.5	34	8.15	Person et al. (1995)
<i>Menidia beryllina</i>	0.98	96	18	30–32.5	8	Miller et al. (1990)
	1.77	96	25	30–32.5	8	
	1.70	96	32.5	30–32.5	8	
	0.93–0.97	96	25	30–32.5	7	
	0.75	96	25	30–32.5	9	
	0.074	672	23.5–25	30–33	ns	
	0.38	672	23.5–25	30–33	ns	
<i>Monocanthus hispidus</i>	0.83	24–48	23.4	28	8.07	USEPA (1989)
<i>Pseudopleuronectes americanus</i>	0.49	24–48	7.5	31	8	
<i>Sciaenops ocellatus</i>	0.55	24–48	25.5	29	8.1	
<i>Scophthalmus maximus</i>	2.96	24–48	17.9	34.3	8.15	
	2.55	96	17.5	34	8.15	Person et al. (1995)
<i>Sparus aurata</i>	1.93	24–48	27	40.5	8.1	Wajsbroet et al. 1991)
	2.55	96	17.5	34	8.15	Person le Ruyet et al. (1995)

Once anaerobic conditions ensue and H₂S is present, mass mortalities of nearly all organisms occur (Stachowitsch 1984). In the innermost Oslofjord (Bunnenfjord) at depths greater than 50 m, H₂S is found in the water column and no macrobenthic fauna exists (J.S.G. unpubl.). Such conditions occur naturally under the thermocline in upwelling areas off Peru, where mats of the bacterium *Thiopluca* sp. can attain wet weight biomass of 2 kg m⁻² (Rosenberg et al. 1983, Tarazona et al. 1986).

Interactions among factors

The data on reduced oxygen concentrations, ammonia and hydrogen sulphide show that there are some general responses. In general, the sensitivity of major marine taxa is: fish > echinoderms and crustaceans > annelids > molluscs. However, within each taxon there is considerable variability, dependent on the habits of the species considered. Actively swimming fishes are more sensitive than bottom-living fishes, which in turn

Table 6. Effects of hydrogen sulphide on marine organisms under varying environmental conditions. Terms as in Table 1; TS: total sulphide.

Species	DO level (mg l ⁻¹)	H ₂ S level (µg l ⁻¹)	Expt duration (h)	Conc.	Endpoint Effect	Time (h)	Conditions	pH	Source	Remarks
Annelids										
<i>Arenicola marina</i>	<0.2	0	5	LOEC	MET	5	10°C		Abele-Oeschger & Oeschger (1995)	Haemoglobin autooxidation increased by 165%, methaemoglobin by 160%; CAT in chloragogen decreased by 40%, GR in chloragogen by 50%
<i>Hediste diversicolor</i>	1 µmol ⁻¹	980 µmol ⁻¹	60	LT ₅₀	MORT	60	16°C, 14‰	7.8	Gamenick et al. (1996)	Juvenile
	1 µmol ⁻¹	0	105	LT ₅₀	MORT	105	16°C, 14‰	7.8		
	1 µmol ⁻¹	1 mmol ⁻¹	72	LT ₅₀	MORT	72				Juvenile
	1 µmol ⁻¹	0	14	LT ₅₀	MORT	14	16°C, 14‰	7.8		Postlarval stage
	1 µmol ⁻¹	270 µmol ⁻¹	10	LT ₅₀	MORT	10	16°C, 14‰	7.8		Postlarval stage
<i>Heterochaeta costata</i>	1 µmol ⁻¹	0	72	NOEC	MORT	72	16°C, 14‰			
	1 µmol ⁻¹	1.96 mmol ⁻¹	360	LT ₅₀	MORT	360	16°C, 14‰			
	1 µmol ⁻¹	550 µmol ⁻¹	54	LT ₅₀	MORT	54	16°C, 14‰			
	1 µmol ⁻¹	0	48	NOEC	MORT	48	16°C, 14‰	7.8		
<i>Paranais litoralis</i>	1 µmol ⁻¹	50 µmol ⁻¹	7	LT ₅₀	MORT	7				
<i>Tubificoides benedii</i>	0.05	200 µM	24	LOEC	MET	12			Dubilier et al. (1997)	Succinate increased 3-fold
<i>Hydrobia ventrosa</i>	1 µmol ⁻¹	0	168	LT ₅₀	MORT	168	16°C, 14‰	7.8	Gamenick et al. (1996)	
	1 µmol ⁻¹	570 µmol ⁻¹	75	LT ₅₀	MORT	75				
Crustaceans										
<i>Cyprideis torosa</i>	1 µmol ⁻¹	0	660	LT ₅₀	MORT	660	16°C, 14‰	7.8	Gamenick et al. (1996)	
	1 µmol ⁻¹	1.8 mmol ⁻¹	528	LT ₅₀	MORT	528				
<i>Saduria entomon</i>	0.044	0	8	LOEC	REP	8	11°C, 10‰		Vismann & Hagerman (1996)	Normal respiration rate re-established after 8 h recovery
	0.308	41 µM	8	LOEC	REP	8	11°C, 10‰			Normal respiration rate re-established after 28 h recovery
<i>Corophium volutator</i>	0.04	0	8	LOEC	MET	8	11°C, 10‰		Gamenick et al. (1996)	Metabolism reduced by 70%, oxygen debt was 0.57 mg O ₂ g ⁻¹
	0.308	41 µM	8	LOEC	MET	8	11°C, 10‰			Metabolism reduced by 38%, oxygen debt was 2.74 mg O ₂ g ⁻¹
	1 µmol ⁻¹	0	4	LT ₅₀	MORT	4	16°C, 14‰	7.8	Gamenick et al. (1996)	
	1 µmol ⁻¹	90 µmol ⁻¹	2	NOEC	MORT	2	18°C, 30‰			
<i>Crangon crangon</i>	0.044	0	2.5	LT ₅₀	MORT	2.5	18°C, 30‰		Hagerman & Vismann (1995)	
	0.45	0	30	LT ₅₀	MORT	30				
	0.91	0	ns	ns	BE	ns	18°C, 30‰			Only very sporadic movements occurred, activity decreased as oxygen decreased
Molluscs										
<i>Arctica islandica</i>	0.45	0	1.33	LOEC	MET	1.33	18°C, 30‰		Oeschger & Storey (1993)	Lactate increased by 4.6–7-fold
	1.82	5 µM	1.33	LOEC	MET	1.33	18°C, 30‰			Lactate increased by 16–25-fold
<i>Arctica islandica</i>	0	0	240	LOEC	MET	240	9.5 + 0.5°C, 22‰	7.6	Oeschger & Storey (1993)	Total glycogen phosphorylase in adductor decreased by 34%, in foot by 27%
	0	200 µM	240	LOEC	MET	240	9.5 + 0.5°C, 22‰	7.6		Total glycogen phosphorylase in adductor decreased by 30.3%, in foot by 15.9%

Table 6 (continued)

Species	DO level (mg l ⁻¹)	H ₂ S level (µg l ⁻¹)	Expt duration (h)	Endpoint		Conditions	pH	Source	Remarks	
				Conc.	Effect Time (h)					
<i>Astarte borealis</i>	<0.2	0	48	LOEC	MET	48	10°C	Abele-Oeschger & Oeschger (1995)	GR in gills increased by 500 %	
	<0.2	200 µM	48	LOEC	MET	48	10°C		Hydrogen peroxide increased by 200 %	
	<0.2	0	240	LOEC	MET	240	10°C		Methaemoglobin increased by 260 %. CAT in gills decreased by 70 %	
	<0.2	200 µM	240	LOEC	MET	240	10°C		CAT in gills decreased by 40 % SOD increased by 50 % and GR increased by 860 %	
Echinoderms										
<i>Amphiura filiformis</i>	<0.1	0	168	LT ₅₀	MORT	168	8.5 + 1.5°C, 29.5 + 1.4 ‰	Vistisen & Vismann (1997)	All rose to sediment surface, lifted disc into the water column, and survived at surface for several days	
	0.3	0	348	LT ₅₀	MORT	348	8.5 + 1.5°C, 29.5 + 1.4 ‰		93 % came to sediment surface within 2 to 5 d, quickly became inactive and changed from pale red to white	
	0.5	0	780	LT ₅₀	MORT	780	8.5 + 1.5°C, 29.5 + 1.4 ‰		84 % came to sediment surface within 2 to 5 d, quickly became inactive and changed from pale red to white	
	0.1–1	0	ns	LOEC	BE	ns	8.5 + 1.5°C, 29.5 + 1.4 ‰		51 % came to sediment surface within 2 to 5 d, quickly became inactive and changed from pale red to white	
	<0.1	0	180	LT ₅₀	MORT	180	8.5 + 1.5°C, 29.5 + 1.4 ‰		Quickly became inactive and moribund	
	<0.1	2 µM	129.6	LT ₅₀	MORT	129.6	8.5 + 1.5°C, 29.5 + 1.4 ‰		Initially showed increased mobility (escape response) for 2 to 4 d, then came to rest with disc raised into water column	
	<0.1	20 µM	74.4	LT ₅₀	MORT	74.4	8.5 + 1.5°C, 29.5 + 1.4 ‰		Initially lifted disc into water column, then became paralysed	
	<0.1	200 µM (TS)	40.8	LOEC	BE	40.8	8.5 + 1.5°C, 29.5 + 1.4 ‰		Became paralysed	
	<i>Ophiura albida</i>	<0.1	0	60	LT ₅₀	MORT	60	8.5 + 1.5°C, 29.5 + 1.4 ‰		Became paralysed
		0.3	0	144	LT ₅₀	MORT	144	8.5 + 1.5°C, 29.5 + 1.4 ‰		Became paralysed
0.5		0	336	LT ₅₀	MORT	336	8.5 + 1.5°C, 29.5 + 1.4 ‰		Became paralysed	
0.1–1		0	ns	LOEC	BE	ns	8.5 + 1.5°C, 29.5 + 1.4 ‰		Became paralysed	

are more sensitive than burrowing species such as mudskippers. Similar trends occur within the other taxa, with species that inhabit sediments being the most tolerant to low oxygen and high ammonia and hydrogen sulphide concentrations.

Interactions between hypoxia, ammonia and hydrogen sulphide are poorly known. Reduced oxygen levels increase ammonia toxicity in the marine fish *Sparus auratus* and the prawn *Penaeus semisulcatus* (Wajsbrodt et al. 1990, 1991). Ammonia toxicity to the prawn was doubled when dissolved oxygen decreased from 55 to 27% saturation (Wajsbrodt et al. 1990). Thurston et al. (1983), however, found no correlation between oxygen level and ammonia toxicity to fathead minnows *Pimephales promelas*. Hiroki (1978) demonstrated that hypoxic tolerance in 3 species of marine gastropods (*Littorina ziczac*, *Neritina vorgeina* and *Olivella verreuxii*) decreased in the presence of H₂S. Similarly, Kang et al. (1993) showed that H₂S decreased the hypoxic tolerance of the crab *Portunus trituberculatus*. The isopod *Saduria entomon* is able to synthesize haemocyanin to enhance oxygen uptake during hypoxia (1.8 to 2.9 mg O₂ l⁻¹), but haemocyanin synthesis is inhibited when the isopod is exposed to hypoxia in the presence of H₂S (150 µM l⁻¹) (Hagerman & Visman 1993). Magaud et al. (1997) found that mortality of the rainbow trout *Oncorhynchus mykiss* exposed simultaneously to 0.5 mg NH₃ l⁻¹ un-ionized ammonia and hypoxia (1.7 mg O₂ l⁻¹) was significantly higher than that of trout *Salmo trutta* exposed to ammonia or hypoxia alone, suggesting a synergistic effect.

Yet to what extent do interactions among oxygen, hydrogen sulphide and ammonia affect the fauna? Hydrogen sulphide is readily oxidised in the presence of oxygen. Only in sulphide-rich coastal sediments or salt marshes overlaid by shallow water can sulphide escape to the atmosphere (Fenchel & Blackburn 1979). In marine sediments sulphate reduction is the dominant microbiological process, and results in ammonia accumulation within anoxic sediments and a concentration gradient towards the sediment surface. If the water above the sediment surface is anoxic then ammonia can be released, otherwise the ammonia is rapidly oxidised. Thus it is only under extremely poor conditions with almost no oxygen that high amounts of ammonia and hydrogen sulphide occur in bottom waters. From these considerations it is clear that hypoxia is the main contributor to faunal changes. Field studies showed that in southeastern USA all species tested (fishes and shrimp) could detect and avoid 1 mg l⁻¹ oxygen (Wannamaker & Rice 2000). The final extreme stages of eutrophication occur when the concentration drops below 0.5 mg l⁻¹ and hydrogen sulphide and ammonia are released into the water. In an interesting study of deep-sea fauna, Levin & Gage

(1998) found that depth and organic matter rather than oxygen concentration limited faunal richness and biomass.

From the foregoing it is clear that the effects that are produced are not caused by a single factor but are the interaction of a number of different factors. It is not just 'organic enrichment' that leads to the effects, but the interaction of sedimenting organic matter with reduced oxygen concentrations, and the presence of hydrogen sulphide and possibly ammonia.

The role of modelling

Visser & Kamp-Nielsen (1996) state that empirical modeling of coastal eutrophication is rare, largely due to the fact that coastal systems have complex dynamics. Walsh (1988) pointed out that the major advance in plankton modeling in the 1970s was the development of models that took into account physical variables such as the spatial resolution of velocity fields and turbulence. These models produce predictions of the spatio-temporal distribution of primary production.

Walsh (1975) made an early attempt to model the phytoplankton-nutrient-oxygen system. Using a 2-layered system model he then analysed the causes of the 1976 anoxic event in the New York Bight (Walsh 1988). As state variables the model included dissolved nitrogen (ammonium and nitrate), dissolved silicon, and dissolved and particulate organic carbon (DOC and POC) phytoplankton (nanoplankton and *Ceratium tripos*) and zooplankton (copepods and chaetognaths) above and below the pycnocline. The sources of ammonium included microbial remineralization of organic nitrogen and macrobenthic regeneration of ammonium, waste inputs and zooplankton excretion. Urea is also important (Lomstein et al. 1989). Sources of POC included photosynthetic excretion and waste discharges. Loss terms of nitrogen included nitrification and nutrient uptake by the 2 groups of phytoplankton. Sinks of DOC and POC included consumption by bacterial decomposition and settling POC. The forcing functions were water temperature, solar radiation and photoperiod, pycnocline depth, seasonal stratification, advection and eddy dispersion both horizontally and vertically. The model was able to produce spatial predictions of oxygen concentrations, which gave reasonable approximations of the 1976 event. Walsh was further able to simulate the effects of a 10-fold increase in carbon and nitrogen loading. This led to anoxia below the pycnocline. Further he was able to show that an increase of 50 to 100 gC m⁻² would induce an anoxia event.

Gowen et al. (1988, 1994) using a similar modelling approach to that of Vollenweider (1968, 1976) applied

to fjords (specifically 21 Scottish sea lochs) were able to estimate the yield of chlorophyll from nitrate. However, this was not an ecosystem model. Such models have been developed by Tett et al. (1986), Aksnes & Lie (1990) and Ross et al. (1993, 1994). Ross et al.'s model is discussed in some detail by Visser & Kamp-Nielsen (1996). The model showed that the key nutrient loading came not from riverine inputs but from the open sea and internal cycling was relatively unimportant. However, the size of the spring bloom was controlled entirely by grazing so that nutrients were never limiting for phytoplankton growth. Silvert (1994) and Doering et al. (1989) have modelled effects of organic enrichment on benthos. (See also GESAMP [1991] for an overview of general models for coastal systems.)

In reviewing the different types of models appropriate for managing coastal eutrophication, Visser & Kamp-Nielsen (1996) stated that 'fully interactive physical and biological models of such *coastal* systems are as yet not forthcoming'. Thus we are not at the stage where we have predictive models for coastal eutrophication. This is mainly because most marine systems are unbounded (Visser & Kamp-Nielsen 1996) and describing the sources and cycling of nutrients and how turbulence and mixing control production, sedimentation and oxygen concentrations is a major challenge (Mann 1982, Platt et al. 1989) and a fact acknowledged by Vollenweider (1992). Visser & Kamp-Nielsen (1996) concluded by giving the sound advice that in the development of coastal eutrophication models managers should carefully define the questions being posed of scientists, establish adequate monitoring programs, and apply risk assessments to establish model validation criteria *a priori*.

Pearson-Rosenberg (P-R) model of organic enrichment

As mentioned in the 'Introduction' the P-R model is one of the most cited marine papers (over 400 citations in the Institute for Scientific Information's list 2000). The P-R model predicts the numbers of species, the total abundance of all species, and the biomass of all species along a gradient of increasing organic enrichment of the sediment. Fig. 2 shows the model. The model suggests that the total biomass of organisms initially increases gradually as organic matter load increases above background levels, and then rises sharply to a maximum. The biomass then falls, and often shows a secondary peak near to, but lower than, that of maximal abundance. The maximum number of species coincides with the biomass peak. Abundance on the other hand rises slowly at first but then increases rapidly to a maximum (the 'peak of oppor-

tunists'), before falling sharply as oxygen concentration drops.

Pearson & Rosenberg (1978) pointed out that there are considerable difficulties in comparing biomass between studies and between areas, and thus that the suggested double peak needs to be studied in more detail. In fact, due to the difficulties of defining the biomass of, for example, an echinoderm or a bivalve (compared that of a polychaete), biomass is not often measured (but see Cedrwall & Elmgren 1980). Pearson & Rosenberg (1978) suggested that the secondary peak in biomass occurs when there are large amounts of organic matter but oxygen concentrations have not yet started to decrease. They documented the generality of the model by showing stylised figures (but with no quantitative axes) compiled from data from Sweden (Rosenberg 1976), Scotland (Pearson & Stanley 1979), Canada, France and Germany (Anger 1975).

Most papers that cite the model claim that their data 'agree' with the model. But what does 'agreement' mean? At the most extreme ends of the scale an area with low organic matter input has fairly high species numbers, low abundance and moderate biomass, whereas an area with high organic matter has low or no oxygen content in the overlying water and almost no species and low biomass and abundance. Between these extremes abundance, species number and biomass are usually higher. Thus almost any gradient of disturbance will show a similar pattern, in accord with the intermediate disturbance hypothesis (Connell & Slatyer 1977). In most cases where the P-R model is cited there are usually no tests as to whether or not the double peak of biomass, the slight increase in species

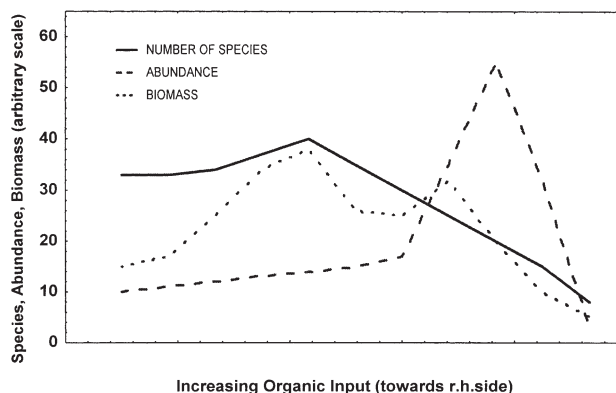


Fig. 2. The Pearson-Rosenberg model showing Species (S), Abundance (A) and Biomass (B) – SAB curves of the effects of organic enrichment on sediment-living organisms. In the original model Pearson and Rosenberg have on the ordinate a point source of organic enrichment and a decreasing gradient from the source. We prefer an increasing gradient from the origin and so have reversed the ordinate scale to one of increasing organic enrichment from left to right

number with slight enrichment, and the 'peak of opportunists' at late stages of enrichment occurs.

In fact there are remarkable few actual tests of the model compared with studies claiming that their data fit the model. The P-R model is highly descriptive and describes the stages of change as 'organic enrichment' increases. But what is meant by 'organic enrichment'? How much organic input/deposition is required to elicit biological changes? Does this refer to organic enrichment in the sediment or is it the general process of organic enrichment that occurs in the water-column? Or are the effects that are observed in fact due to other factors such as hypoxia?

In a limited test of the P-R model, Weston (1990) examined the benthic fauna under and at distances up to 450 m from a fish farm and did not find the 'peak of opportunists', predicted by the model. Heip's (1995) review likewise questions the generality of the response of opportunist species to organic enrichment and urges caution, as data on food quality and quantity and requirements is often lacking for most species. In a more extensive study, Maurer et al. (1993) tested the P-R model in an open-shelf environment off the coast of California and found that the fast long-shore currents from mixed and semi-diurnal tides and storms led to high flushing rates of organic material. Thus, although input rates of organic matter were high, the characteristic P-R model did not hold for the benthic assemblages if dispersion was good and POM did not settle on the bottom.

The P-R model was developed from studies in fjords (Saltkällefjord, Sweden, Loch Creran, Scotland), the Fraser River Estuary, Canada, and enclosed embayments off Marseille and Kiel Bay (Pearson & Rosenberg 1978). All these areas are characterised by limited water exchanges in their bottom waters and with predominantly silt-clay sediments, typical of sedimentation basins. Maurer et al. (1993) concluded that the model accurately predicts effects only in semi-enclosed waters with reduced flushing rates and net increase in sedimentation compared with open shelf areas. From the results presented by Maurer et al. (1993) and in the present analysis, it is obvious that high amounts of organic material can be produced in the water column, but if the dispersive characteristics lead to a lack of accumulation of organic matter in the sediment, then one cannot expect effects on the sediment-living fauna. Thus 'increased organic input' is probably only a very indirect measure of the effects on the benthic fauna.

The analysis presented here shows that organic enrichment and hypoxia lead to a wide range of changes in the water column and in sediments. Increased turbidity can cause changes in depth distributions of algae and lead to changes in species com-

position (Ramus et al. 1976a,b). The process of sedimentation itself may lead to direct effects on the benthos. The intermediate disturbance hypothesis predicts that any disturbance of a system will initially lead to an increase in the number of species. If the disturbance persists or increases, then the species number falls. Sedimentation alone may lead to an increase, whether this is accompanied by an increase in organic matter loading to the sediment or not. The P-R model does not separate disturbance from organic enrichment. Pearson & Rosenberg (1978) suggested that there is a secondary peak of increased biomass, where there are large amounts of organic matter but where oxygen concentrations have not started to fall. Whether such a peak occurs or not has rarely been tested. Following the initial 'disturbance effect', if organic enrichment proceeds then reduced oxygen concentrations (between 4 and 2 mg l⁻¹) can cause changes in trophodynamics, which in turn alter the species composition and the abundance of benthic organisms. We suggest that the main effects are caused by hypoxia in the water column rather than effects of organic matter on the benthos. When oxygen falls to below 0.5 mg O₂ l⁻¹ sediments often become anoxic with the redox-discontinuity layer near the surface. Ammonia and hydrogen sulphide can be released from the sediments, and would add to the effects of hypoxia and lead to catastrophic effects on the fauna in the water column and sediment. Thus, the P-R model does not properly reflect the causes of the changes observed, and therefore cannot be used as a predictive tool.

Detecting effects of hypoxia and organic enrichment

Gray's (1992) review presents a series of steps that indicate the progress of eutrophication. Here we combine data on physico-chemical variables, such as C:N ratios of POM, and oxygen concentrations, to derive a general scheme for coastal zone managers to evaluate the presence of or state of eutrophication in a given area. In this approach we include the P-R model (Pearson & Rosenberg 1978) for benthic assemblages, as the model is perhaps best used in the context of assessing the stages of eutrophication rather than as a predictive tool.

The assessment process begins with observations that may indicate eutrophication. These are discoloured water, changed species composition in the phytoplankton (McCormick & Quinn 1975, Kimor 1992) and zooplankton (Regner 1991), bottom-living algae, sea-grasses or salt marshes covered in epiphytes (Patriquin & Knowles 1972, McRoy & Goering 1974, Valiela et al. 1978, Valiela 1984), or tidal flats with large patches of *Ulva*, *Enteromorpha* or *Cladophora*. Discoloured water

from algal blooms may be a perfectly natural phenomenon so at this stage eutrophication is just 1 possible hypothesis for the observation. Often, however, early signs of eutrophication are changes in fish-catches during bottom trawling e.g. suddenly increased catches resulting from hypoxia in the bottom water-masses (Aneer 1985). Another often extremely sensitive sign is changes in species composition and/or biomass of the benthic fauna. Benthic assemblages are so sensitive because often up to 50 or more species of macrofauna (retained on a 1 mm pore-diameter sieve) occur per 1 m² seabed. Some of these species will respond to changes in food supply, and/or sedimentation rates and/or lowered oxygen concentrations. Changes in the benthos may arise from factors other than eutrophication, such as altered fishing intensity or methods, and further evidence is needed before eutrophication can be confirmed. Fig. 3 shows the assessment scheme.

Following the detection of unusual events the oxygen content of the bottom water should be investigated. If this is above 4 mg l⁻¹, it is unlikely that eutrophication effects will be observed in the area. Further monitoring is recommended to ensure that the concentration remains above 4. If it falls below 4 then assessment of the degree of eutrophication and its spatial extent should be made. Here 2 strategies are recommended, a rapid assessment or a more detailed study, with the use of multivariate statistics (see below). The rapid assessment builds on the P-R model and its modification using Sediment Profiling Imaging (SPI) cameras (Rhoads & Germano 1982, 1986, Rumohr & Schomann 1992, Nilsson & Rosenberg 2000).

Pearson & Rosenberg (1998) suggested 4 major stages of change in response to organic enrichment of the benthos: normal, transitory, polluted and grossly polluted, along a gradient of organic enrichment (or, as we have argued, more probably a gradient of hypoxia). In reality there is a smooth transition from one stage to the next and classification into 4 stages is simply a convenient abstraction of the data. These stages can be used to assess the state of eutrophication in benthic systems, and are based on the species composition determined from grab samples and species identifications: (1) Normal: characterised by the presence of large, deep-burrowing species such as decapods and echinoids, with a deep redox-potential discontinuity (RPD) layer. (2) Transitory: characterised by the presence of smaller organisms usually deposit-feeding bivalves, which replace the large deep-burrowing species. The RPD level is shallower than in (1). (3) Polluted: characterised by a very shallow RPD layer and dominance of small tube-building polychaetes; indicates severe eutrophication. (4) Grossly Polluted: characterised by sulphide patches at the sediment surface and no macrofauna, only nematodes survive. It should

be noted that the latter are marked changes, so in the RPD layer values in the range of -100 to -150 mV indicate long term, heavy organic pollution (Pearson & Stanley 1979).

Nilsson & Rosenberg (2000) have recently quantified 4 stages in a 'Benthic Habitat Quality (BHQ) index' classifying the normal conditions as Stage 3, transitory as Stage 2, polluted as Stage 1 and grossly polluted as Stage 0. They used a series of observations made with an SPI camera system. From our experience, it is quite possible to make similar observations using transparent core samples of the sediment. The scheme in our Fig. 3 is based on Nilsson & Rosenberg's BHQ index, but we have not calculated the index, as its utility has not been tested in many areas. In both a rapid and a full assessment, it is important that samples are taken over a large area including undisturbed control sediments and their assemblages. A pilot study is recommended to give a rough overview, followed by more detailed sampling to assess the extent and degree of eutrophication, if any.

We believe that a full assessment is preferable, rather than classification into subjective classes (even the P-R model shows a continuum of change). In a full-assessment approach samples should be taken with a grab or multicorer covering the area where eutrophication is suspected. Data should be collected on both fauna and sediment properties (grain size variables, redox measurements, C:N at 1 cm intervals down to 10 cm, observations on tubes and tube size). Multivariate statistical methods should then be applied to both fauna and sediments separately, since such methods have been shown to be highly sensitive (Gray et al. 1990). The PRIMER package (Clarke & Warwick 1994) and the CANOCO package (ter Braak 1987) have been widely used with data from such surveys and both have the advantage over other methods that they can relate sediment properties to fauna. Both these packages are able to integrate the physico-chemical measurements with the biological measurements to provide a correlative explanation for possible causes of changes observed in the fauna. Multivariate techniques have been shown to be highly sensitive in detecting the changes in species composition that are the earliest signs of eutrophication (Gray et al. 1990).

The emphasis here is on the detection of the earliest signs of eutrophication so that action may be taken to mitigate more severe effects. One reviewer of this paper suggested that 'as unpolluted control coasts are rarely available nearby, the only way is to analyse long-term or historical data sets'. We reject this suggestion on 2 accounts. Firstly, the scheme does not rely on there being pristine conditions, as few coastal environments anywhere in the world can today be called pristine. It is based on observations

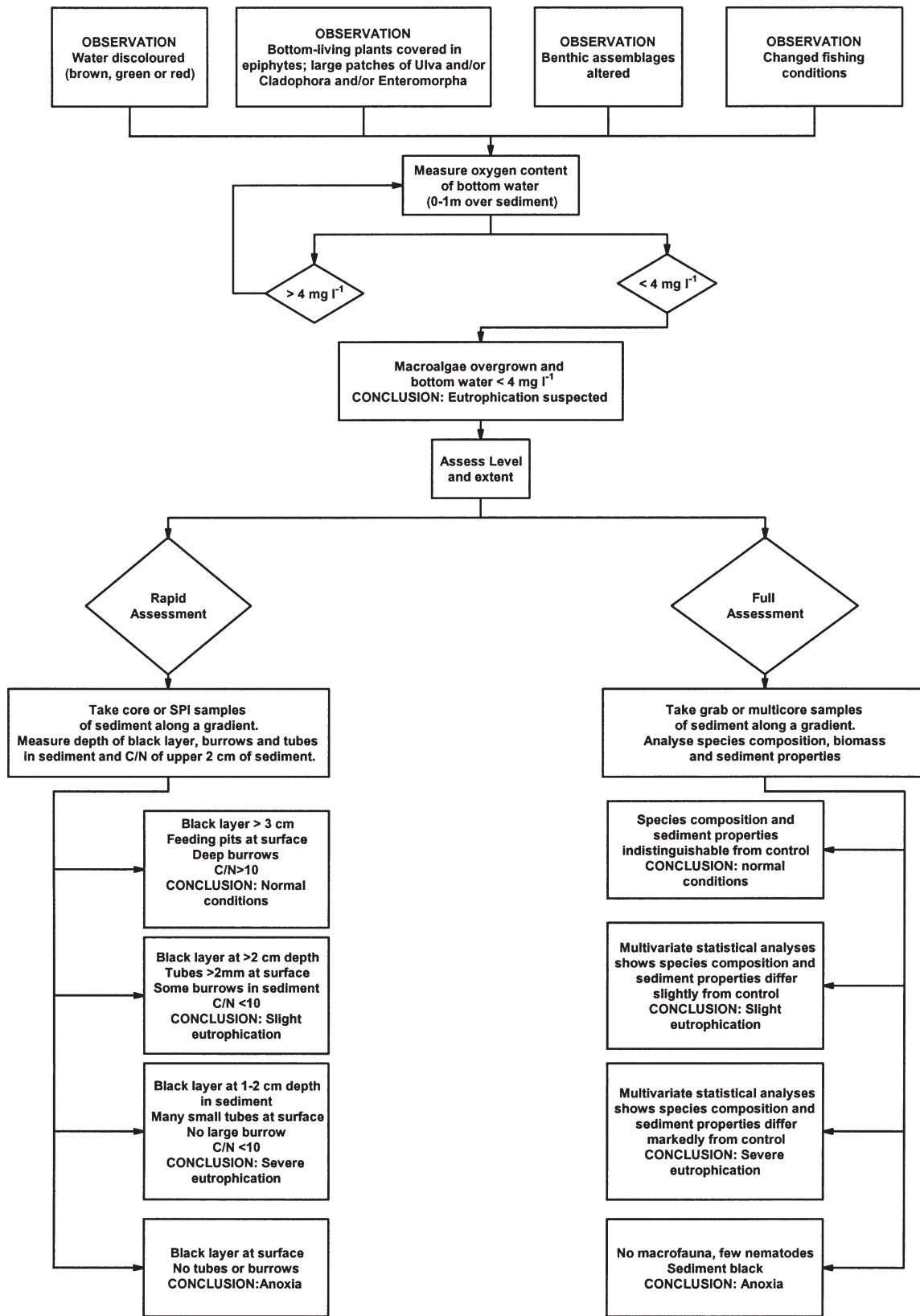


Fig. 3. Assessment scheme for suspected eutrophication

of changes occurring along gradients in systems that are being monitored. In areas with natural periodic anoxia, managers may be interested in monitoring the development of anoxia and the extent of the effects, and the proposed scheme will provide a basis for monitoring of areas covered by such effects. Secondly, analyzing historical data is fraught with the enormous problem of detecting the eutrophication signal from the noise of natural change. It is now well known that marine systems respond to large-scale oceanographic signals such as the North Atlantic Oscillation or ENSO, whose time span varies over many years if not decades. Testing for effects against such signals is not cost-effective, as it may take a decade to detect that an unwanted effect has occurred. It is far better, and statistically more sound, to monitor multiple sites along a gradient (or gradients) of a suspected effect.

Should eutrophication be diagnosed, then the managers of the coastal zone are faced with problems of remedial action. This will involve analysis of historical data for the area, preparations of mass balance budgets for nitrogen and phosphorus, analyses of climatic conditions over the period of the event, assessment of hydrographic conditions, and development of realistic dynamical models that take into account the key physical, chemical and biological processes covered in this review. Cloern (2001) discussed these aspects in some detail. From such analyses it should be possible to devise cost-effective treatments to mitigate and hopefully remediate the system. In this context managers of coastal zones should read Richardson's (1996) analyses of the time perspective over which remedial action is likely to have an effect. For the Kattegat, a statistically significant detectable improvement in oxygen conditions, given the variability present in the system, will take 18 yr. Eutrophication is a problem of global significance which, once it has occurred, is extremely difficult to reverse.

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