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Critical oxygen levels for demersal fishes and invertebrates

Norwegian Institute for Water Research

REPORT

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Abstract

The literature has been reviewed for information on hypoxic responses in marine bottom-living invertebrates and fishes, as a basis to define safe oxygen conditions for marine bottom communities in the North Sea and adjacent waters.

Hypoxic sublethal and lethal levels are tabulated according to systematic and functional groups of fauna. There is need for concern when the oxygen level drops below 65 % of air saturation, and levels below 20 % (1,2 ml/l) are considered as serious. Controlled experiments in basins with sediments are proposed in future work.

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1. Bunnfauna	1. Bottom fauna
2. Fisk	2. Fish
3. Hypoksi	3. Hypoxia
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Preface

This report was partly financed by the Nordic Council of Ministers as part of a research project to develop a concept for calculating critical loads and levels of nutrients on marine environments, and partly by a strategic institute program (TRANSFJO) at Norwegian institute for water research.

One of the main problems with eutrofication is the effect of different hypoxic states on the marine environment. Apart from a work by Diaz and Rosenberg (1995), there are few reviews in the field. In this report the literature has been reviewed regarding the effect of hypoxic responses in marine bottom-living invertebrates and fishes, mainly to define safe oxygen levels for bottom communities in the North Sea and adjacent waters. The literature review was ended in august 1997.

Oslo, August 1998

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SUMMARY

The literature has been reviewed for information on hypoxic responses in marine bottom-living invertebrates and fishes, as a basis to define safe oxygen conditions for marine bottom communities in the North Sea and adjacent waters.

Hypoxic threshold levels are tabulated for different sublethal responses like escape reactions, increased ventilation of gils, reduced resting respiration, reduced heart rate and reduced growth, together with lethal or asphyxic levels. The results are grouped according to systematic and functional animal groups.

The interval of about 65-50 % saturation (sat) is characterised by minor sublethal changes, e.g. reduced resting respiration in some species. In the interval of about 50-35 % sat more severe sublethal changes take place, like reduced growth in fishes. From about 35-20 % sat lethality may occur in the fish fauna in addition to severe sublethal responses in other hyper- and epifauna. Below about 20 % sat (1,2 ml/l) lethality also take place in epifauna, and severe sublethal responses and finally lethality take place in infauna, depending on duration. Such water may cause fish kills.

In order to quantify the metabolism of organic matter at the sea-floor in relation to hypoxia and organic load, controlled experiments in basins would be highly profitable. Such experiments would also facilitate the study of benthic in-, epi- and hyperfauna, their population dynamics and behaviour, which should be included.

Seasonal phases of hypoxia should be related to seasonal phases of vulnerable stages in the life cycles of animals to identify possible temporal and spatial coincidence. Such cases are known for some important fish stocks, e.g. Baltic cod eggs and larvae, but more information is needed.

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1. INTRODUCTION

Water bodies or zones with low levels of dissolved oxygen, or completely anoxic and sulphidic seawater exist many places around the world as a result of topographic, geophysical and biological conditions. Where the hypoxic conditions are stable and not serious, the community of organisms may have responded by adaptation, usually resulting in reduced diversity, but increased biomass of the species able to adapt.

When ambient oxygen tension for a marine bottom community is reduced over a season or shorter time scale, the different organisms will sooner or later show special behaviour like escaping, emerging from the sediment or stretching up into better water, at the cost of normal activity and feeding, sheltering from predators or choice of habitat. Physiological responses are initiated in order to maintain basic body functions Typical to most organisms is increased ventilation of gills or other respiratory surfaces as a response to rapid oxygen reduction, and increased oxygen affinity and carrying capacity of the blood in enduring hypoxia. At a certain hypoxic level, different from species to species, metabolism at rest is reduced, and usually end products from anaerobic metabolism start to accumulate in the tissues. On further reduction immobilisation and death occur. Serious mass kills of marine fauna have resulted.

In many coastal areas oxygen problems have increased seriously during the last century due to anthropogenic eutrophication (see Diaz & Rosenberg 1995 for a resent review). The runoff areas draining to the North Sea are in part densely populated, and coastal eutrophication has become a most serious problem for marine life in many areas including the Baltic Sea (Andersin *et al.* 1978, Cederwall & Elmgren 1990, Rosenberg *et al.* 1990), Kiel Bay (Weigelt & Rumohr 1986), Danish fjords and coastal waters (Dahl *et al.* 1995, Jørgensen 1980), the Kattegat (Baden *et al.* 1990A, Rosenberg *et al.* 1990, Pihl 1989), the German Bight (Dethlefsen & Westernhagen 1982, Niermann *et al.* 1990), fjords in the Skagerrak area (Josefson & Widbom 1988, Rosenberg 1980, Beyer & Indrehus 1995, Mirza & Gray 1981, Nash 1985, Rygg *et al.*1985, Magnusson & Johansen 1994). Also along the Norwegian Skagerrak coast, a conspicuous decline in midwater degree of oxygen saturation has been found (Johannessen & Dahl 1996a,b).

When the amount of organic matter increase, either due to direct supply or due to an increased production in the upper euphotic zone, and it is transported down the water column, it gives rise to increased metabolism and oxygen consumption. In stable water layers from the pycnocline and downwards, this seasonally enhance the reduction of the oxygen content of these water bodies. This will expand both the areas where hypoxic and anoxic water and sediments are encountered, and also lengthen the periods of hypoxic or anoxic conditions.

The above processes make bottom sediments and overlying water the most vulnerable habitats during oxygen reduction (see Tyson & Pearson 1991, Diaz & Rosenberg 1995). The oxygen requirements of the benthic and hyperbenthic communities, therefore, will determine the critical level of eutrophication in many areas. In order to set critical loads (Hessen *et al.* 1992) of nutrients to marine areas, information on hypoxic responses of benthic and demersal organisms is required.

The literature on the effects of low oxygen levels on aquatic life - mostly freshwater fishes - was reviewed some years ago by Davis (1975), who expressed the opinion that water quality criteria should be based on ‘no-effect’ levels to assure the long-time survival of aquatic organisms. Sufficient oxygen for fish

was supposed to give protection also for invertebrates. This is not obvious, though, and general differenses in hypoxic tolerance between animal groups is a topic for the present study.

The recent review of Diaz & Rosenberg (1995) covers marine, macrobenthic invertebrates with an emphasis on field investigations of soft bottom communities. In field studies, the presence/absence of the species are usually reported, and occasionally their condition or position relative to the bottom. But too coarse coverage by oxygen data and overlooking a sometimes significant near-bottom gradient, strongly reduce the number of field studies that can be used to asess hypoxic tolerance. The authors classify hypoxic environments into aperiodic, periodic, seasonal and persistent hypoxic environments, graded as moderate (2 - 0.5 ml/l) or severe (<0.5 ml/l) hypoxic. Within the infauna - animals digging in or burrowing most of the time - the main differences in hypoxic tolerance was found between taxonomic groups and not so much between functional groups, with crustaceans as the most vulnerable. Critical oxygen concentrations to prevent mortality of macrobenthic infauna in seasonally hypoxic environments was found to be about 1 ml/l (measured close to the sediment surface) or about 15 % air saturation.

The purpose of the present review was to cover bottom-dependent (demersal) fish species in addition to macrobenthic invertebrates, and also hard-bottom and hyperbenthic invertebrates, but with an emphasis on species found in the North Sea and adjacent waters. The aim has been to describe hypoxic threshold levels for sublethal effects in addition to mortality. Most of this information is based on laboratory tests, because it requires both careful control of the oxygen regime and close observation or measurement of the physiological process studied. The relevance of lab-tests to a given field situation depends on the similarity in environmental conditions and the keeping and handling of test organisms.

The information presented below is just a small part of the total information supplied by the literature referred to. Information on the biochemical mechanisms involved in hypoxic tolerance or anoxic resistance have been the objective of many studies, from which I have only extracted a minor part (see Taylor 1982, for a review on crustaceans). Field studies may contain much valuable information, but have largely been difficult to incorporate since the data mostly would need further elaboration for the present purpose (see the review by Diaz & Rosenberg 1995).

2. TERMINOLOGY AND PARAMETERS

Oxygen

The term 'hypoxic' is used in a broad sense in this review to describe water of low oxygen concentration that is limiting to some life process, or result in some specific physiological response or condition, sometimes also to characterise the physiological response or condition itself. A more precisely formulated definition was adopted by Diaz & Rosenberg (1995) as an oxygen concentration interval of 2 to >0 ml/l, covering the intervals 'dysoxic' and 'suboxic' in geological terminology (c.f. the recommendations of Tyson & Pearson 1991). But since in this review I want to elucidate responses to low oxygen content unlimited by linguistic restrictions, its broad sense is justified.

Theoretically, 'anoxic' means zero oxygen content. In practice such a limit has been difficult to control with traditional methods of analysis, and with the common modifications of the Winkler method one should allow for 0.15 ml/l (2.3 % sat) of oxygen (c.f. Tyson & Pearson 1991). In geological terminology these authors recommend the use of 'suboxic' for the oxygen regime 0.2 - 0.0 ml/l (3.1 - 0.0 % sat).

In physiological work, the level of oxygen in the experimental water is usually expressed in tension units (mmHg, torr, kPa) or as % of air saturation. Gradients in oxygen tension is the actual driving force of oxygen through biological membranes, and as % air saturation (usually around 100 at the sea surface) is closely related to the tension scales, readily apprehended also among non-physiologists, and give sufficient precision with 2 digits, I have listed all data with this unit.

At 10 ^{o}C and salinity 34, seawater in equilibrium with a water vapour saturated normal atmosphere (760 mmHg) contains the following level of oxygen expressed in the most common units:

100 % saturation
157.3 mmHg (= torr)
21.0 kPa (kilopascal)
9.09 mg/l
6.36 ml/l (= cm^3/dm^3)

The calculation of % saturation from other units is given in detail below to clarify the relationships with temperature and salinity. The tension units (mmHg and kPa) are proportional to % saturation when temperature is constant. But when it differs, the saturation pressure of water vapour at the given temperature must be taken into account. This may be obtained from tables (e.g. in the CRC handbook of physics and chemistry) or from the fitted exponential relation (between -1 and 25 ^{o}C):

$$P_{vap(T)} = e^{(1.5465+0.06588\ T)} \quad (1)$$

The dependence on salinity is negligible. The corresponding oxygen tension at 100 % saturation is:

$$P_{sat(T)} = (760 - P_{vap(T)}) \cdot 0.2095 \text{ (mmHg)} \quad (2)$$

or:

$$P_{sat(T)} \text{ (kPa)} = P_{sat(T)} \text{ (mmHg)} \cdot 101.325/760 \quad (3)$$

% saturation for a given oxygen tension P_T is then:

$$\%\ sat_T = 100 \cdot P_T/P_{sat(T)} \quad (4)$$

100% oxygen saturation given in concentration units, $C_{sat(S,T)}$ (mg/l, ml/l, mM or µgat/l), is a complex function of temperature and salinity. $C_{sat(S,T)}$ in mg/l and ml/l is simulated mathematically by UNESCO (1973) among others. Tabulated values are given. There is linearity between % saturation and the concentration units when both salinity and temperature are kept constant. % saturation for a given oxygen concentration, C, is:

$$\%\ sat_{S,T} = 100 \cdot C/C_{sat(S,T)} \quad (5)$$

Lethality

Death caused by hypoxic or anoxic conditions may be defined in different ways for different types of organisms, e.g. immobility, stop of ventilation, cease of heart beat, loss of response to touching combined with shell gaping of lamellibranchs and loss of balance of fish. Sometimes the casualties are controlled by inability to recover in well-oxygenated water. Lethality as % dead of the test population, preferably at certain pre-set oxygen levels, is usually reported as a function of exposure time. Mean survival (lethal) time may then be estimated for each experimental condition. Acute lethal or asphyxic level is sometimes found by gradually lowering the oxygen level until death or asphyxia is observed for the first individual, or usually 50 % of the individuals.

Different taxa of organisms vary greatly with respect to the exposure time they may survive under finally lethal hypoxic conditions. The mean lethal concentration after 4 days (4 day LC50), used as a standard in toxicology, therefore, is not paid so much interest in comparative work on hypoxic tolerance. Experimental periods range from hours to weeks, and the results must be compared in two-way plots with time and concentration as axes, rather than on single scales. Exceptions to this are anoxic resistance (mean survival time in anoxic water) and asphyxic (acute lethal) low oxygen level.

In the data tables (1 - 3) the hypoxic levels corresponding to start lethality (L1) and 50 % lethality (L50) are listed together with their respective exposure times (T1 and T50). In cases where L1 and L50 are zero, it means that the test water is anoxic. The exposure time (T50), then, is anoxic resistance. Asphyxic levels are usually found by observation of the ventilation of the animals and therefore listed in the data tables as V3 (mean threshold level for cease of ventilation)

Sublethal responses

Oxygen uptake (respiration, aerobe metabolism) is a key process for most organisms. Many vital processes require a metabolic surplus above the resting level in starvation, such as feeding (e.g. Saunders 1963) and locomotion (Thillart *et al.* 1994, Fisher *et al.* 1992). The resting level for an organism thus may be considered as a floor in its space of natural life and activity, and when the oxygen requirement even for this is no longer met, growth and activity are naturally arrested or greatly reduced. At community level, oxygen tensions below the critical level for its populations will induce functional and eventually structural changes.

As already suggested by Henze (1910) and confirmed by many later investigators (see Ultsch *et al.* 1981) aquatic animals with inner circulation and branchial oxygen acquisition are able to keep their resting respiration level about constant over an appreciable range of environmental oxygen levels. There is usually a gradual change from independent (not limited) to oxygen dependent (oxygen limited) oxygen uptake, at least when a number of individuals are averaged. For protection of the entire population, the critical level should be the point where the "curving down" start, but this is hard to define with some precision, and traditionally the point is determined by fitting straight lines to the oxygen independent and oxygen dependent part of the observations (Fig. 1).

A number of studies also have resulted in other shapes of the graph of oxygen uptake *versus* environmental oxygen tension, with apparent lack of respiratory homeostasis. Different studies on the same species reveal that departure from the condition of true rest is the most probable explanation in many cases (McMahon & Wilkens 1975, Ultsch *et al.* 1981). True rest may be difficult to assure for strange organisms and may require special facilities in the respiratory chamber, like artificial burrows or sediment, together with careful observation.

Another problem is the distinction between a curve resulting from active respiratory regulation and one resulting from passive uptake and metabolic saturation. The latter were analysed by Tang (1933), who applied hyperbolic saturation curves for the respiration of plant material and the most simple

heterotrophic organisms. Some later authors fit similar curves to their data on macrobenthic species (*e.g.* Bayne 1971 and Taylor & Brand 1975 on bivalves), but interpret the curve parameters obtained in terms of regulation. Because of their unquestionable ability to regulate oxygen uptake, the reviewer has interpreted such results for macrobenthos as respiratory homeostasis and, if necessary, estimated the critical oxygen level in the traditional way.

Anaerobiosis (anaerobic metabolism) occurs when oxygen supply is insufficient for an organism, organ or tissue, due to e.g. exercise, hibernation during tidal emersion or environmental oxygen deficiency. As a response to environmental hypoxia, anaerobiosis is usually detected as build-up of anaerobic end products in blood or tissue samples. The most common are lactate, succinate and propionate. Excess heat production compared to respiration is also used sometimes. Unfortunately, there are only a few studies that estimate the hypoxic threshold level (C1 in Tab. 2) for anaerobiosis and build-up of its end products.

Ventilation (water movement across the gills or other respiratory surface) usually increase as the ambient oxygen level is reduced. Increased ventilation is an active, energy consuming way to maintain the respiratory level required (Edwards 1971, Kramer 1983). Increased water flow improves oxygen uptake by offering a higher mean water oxygen tension near to the gill surfaces, and by reducing the thickness of the laminar water layer at the surfaces. The oxygen dependence of ventilation for an individual animal, therefore, is closely related to that of respiration. The hypoxic level giving maximum ventilation is often reported, and referred here as V2, and sometimes the point of suffocation (V3) is also given. Tentatively, I have also listed the point giving half saturation of the hypoxic maximum ventilation response (V1) where it could be obtained from the published data (Fig. 1).

Change in blood perfusion of the gills and the tissue is another way to regulate oxygen supply to the tissues. Increased perfusion is a general hypoxic response, usually obtained by increased cardiac stroke volume in fishes (Randall 1982). Heart beat frequency usually is kept constant over a certain range of proceeding hypoxia, but eventually, at a certain critical oxygen level (H1), start to reduce. Exceptions are found among the anomuran crayfishes (Anderson *et al.* 1991) where *Calocaris macandreae* is found to increase its heart rate to a maximum at about 15-20 % sat, before reduction take place.

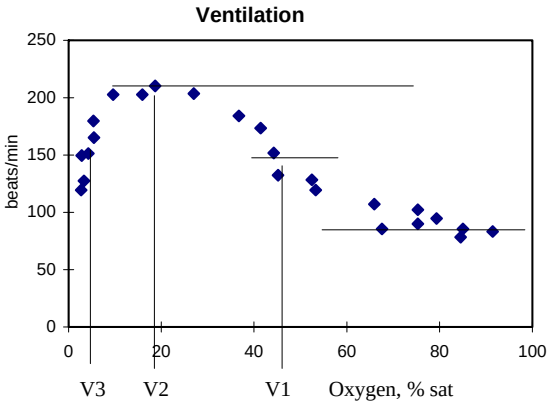
Behaviour

Many invertebrates and fishes hide in the upper part of the bottom sediment. Some, like the flounders dig themselves in during daylight, while others are permanent infaunal. Some of these construct more or less sophisticated burrows, where they spend most of their life. To dig out or leave the burrow poses the animal at risk of being eaten (or fished), and the degree of hypoxia at which this starts to occur (B1) is therefore of ecological significance.

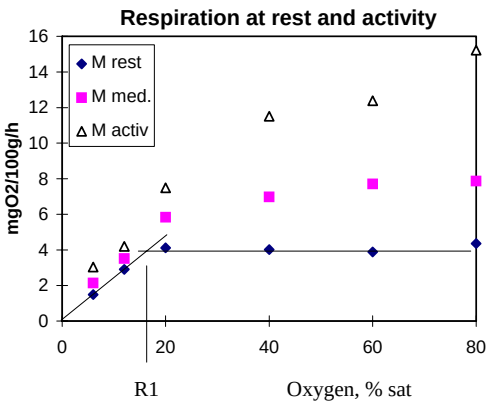
Escape reactions from the ambient water may be surfacing of fish, increased arbitrary swimming of shrimps, or even emerge from water to air by the shore crab (*Carcinus maenas*). The choice of colder water by cod in hypoxia is also listed as an escape response in table 1. This makes the oxygen levels of category B1 somewhat heterogenic. But nevertheless it indicates what the organisms themselves prefer.

Growth

This is a sparsely studied parameter in relation to hypoxia, although it is ultimately useful in predicting effects. Hypoxic levels about to delimit growth in long term aquarium experiments are listed as G1 in Tab 3.



Scaphognatite beat rate of young lobsters having come to rest after handling (from Hagerman 1982). Determination of V1, V2, and V3



Respiration of sole at different activity levels (from Thillart *et al.* 1994). Determination of critical level for respiration, R1. At higher activity level, a break point may also be found, but at higher oxygen levels.

Fig. 1. Examples of the effects of hypoxia on ventilation and respiration, and how the critical levels are estimated.

Tab. 1. Critical O_2 levels (% sat) for escape reactions (B1), ventilation half saturation, maximum and shut-down (V1, V2, V3), respiration (R1), heart rate (H1), and start and 50% lethality (L1, L50) after exposure hours T1 and T50. S $^{o}/_{oo}$, T ^{o}C.

Species	B1	V1	V2	V3	R1	H1	L1	T1	L50	T50	S	T	Source
WORMS													
Polychaetes:													
Nereis virens							0	72			34	12	Schöttler-79
N. diversicolor							0	72			34	12	Schöttler-79
-			15		20						15	15	Nielsen et al-95
N. pelagica									0	36	15	12	Schöttler-79
CRUSTACEANS													
Copepods:													
Calanus finmarchicus V					32				17	4	34	15	Marshall et al-35
- female					70						34	15	
Mysids:													
Archaeomysis grebnitzkii					32		13	1			30	10	Jawed -73
Neomysis awatschensis					19		11	1			30	10	-
Isopods:													
Cirolana borealis 0.5-1		19	12		13		0	18	0	42	32	10	Taylor & Moore-95
-							0	18	0	65	32	5	-
-					30						33	7.5	Skjoldal & Bakke-78
Saduria entomon	10				10						7	8	Hagerman & Szaniawska -88
Cymodoce emarginata		41	24								34	14	Walshe-Maetz-52
Idotea basteri		53	21	13							17	14	-
Amphipods:													
Melita palmata		45	24	20							34	14	-
Gammarus locusta		37	12	11							17	14	-
G. duebeni, estuarine							0	2	0	2.7	34	20	Agnew & Jones-86
- , sewage plant							0	3	0	6.5	34	20	-
Echinogammarus pirloti		19	16	6	9	15					32	15	Agnew & Taylor-85
E. obtusatus		35	32	6	8	21					32	15	-
Decapods:													
Palaemon adspersus									6	4.4	28	19	Berglund & Bengtsson -81
P. squilla									6	12	28	19	-
P. elegans, 1g		62	13	10	13	10					32	10	Morris & Taylor-85
Pandalus borealis		44									34	18	Johnson -36
Crangon crangon					20				15	6		21	Huddart & Arthur-71
-									8	0.3		21	-
-									0	0.5		5	- (5min-3h)
-	16											21	Huddart & Arthur-71
-	35											14	-
-	12											5	-
-									10	6	20	20	Hagerman & Szaniawska -86
-									10	4.5	10	20	-
-	45								17	96	20	20	-
-	20										20	9	-
-									0	2.5	30	18	Hagerman & Visman-95
-									5	30	30	18	-
Homarus gammarus, juv.		45	18	8							27	20	Hagerman -82
, male 550-765g		54	24		25				9	72	34	15	Spoek -74
Nephrops norwegicus	25	37	18								31	10	Hagerman & Uglow -85
-									14	96	34	9	Baden *et al.* -90b
-									10	48	30	10	Hagerman *et al.* -90

Tab. 1. cont.....

Species	B1	V1	V2	V3	R1	H	L1	T1	L50	T50	S	T	Source
Galathea strigosa 7-47g					30						34	10	Bridges & Brand-80
Corystes cassivelanus					25						34	10	-
Munida sarsi		52	38	13	35				0	4	32	10	Zainal et al-92
Munida rugosa									0	8	32	10	-
Calocaris macandreae							0	24	0	43	32	10	Anderson et al-94
Cancer pagurus,250-450g			32	25	38	18					32	10	Bradford & Taylor-82
(*Cancer magister*)					32							10	Johansen et al-70
(*Cancer irroratus*,													
larvae,zoea1-4)									10	4	30	10	Vargo & Sastry-77
larvae,zoea 5)									20	4	30	10	-
larvae,megalops)									26	4	30	10	-
Carcinus maenas, 60-80g			28		45	45					34	15	Taylor-76
- , 35-79g	34										34	6	Taylor et al-77
-	39										34	11	-
-	41	42			38						34	18	-
-					25	29					34	10	-
-					38	29					17	10	-
MOLLUSCS													
Bivalves:													
Mytilus edulis					38						34	15	Bayne-71
-					38						33	16	Bayne & Livingst.-77
Ostrea edulis, age 3-4yr					63						32	22	Gaarder & Eliassen-54
Laevicardium crassum					38						34	15	Bayne-71
Arctica islandica					25						34	10	Taylor & Brand-75
Abra tenuis, 4-6mm		41	24	11	24						25	15	Wang & Widdows-93
Pecten maximus					44								Brand & Roberts-73
Nucula sulcata					10		0	10	0	360	32	10	Taylor et al-95
Cephalopods:													
Sepia officinalis. juv.					54						34	20	Wolf et al-85
Octopus vulgaris		50			45						35	22	Wells & Wells-85
ECHINODERMS													
Echinoides:													
Psammechinus miliaris					40						34	12	Spicer-95
Strongylocentrotus droeb.					28						34	16	Steen-65
-					37						34	10	Johansen & Vadas-67
(*S. purpuratus*)					38						34	10	-
Holothurians:													
Holothuria forscali		66	63	60							34	17	Newell & Courtney-65
FISHES													
Gadus morhua, baltic cod, eggs, 3-5d									35	48	11	7	Nissling -94
- eggs, 3-5d									26	48	15	7	-
- eggs, 2-7d									20	48	15	7	-
- larv. 0-4d									24	48	11	7	-
- larv. 0-4d									25	48	15	7	-
- eggs									30		11		Wieland & Zuzarte-91
Gadus morhua, atlantic cod				12	42						34	10	Sundnes -57
- 18-45 cm							60	24	40	24	35	8	Scholz & Waller-92
- 1.1-2.3kg		52			33						34	10	Saunders-63

Tab. 1. cont.....

Species	B1	V1	V2	V3	R1	H	L1	T1	L50	T50	S	T	Source
Gadus morhua, 80-200g	25											13	Schurmann & Steffensen -92
-									5			5	-
-									14			10	-
-									17			15	-
-									29			17	-
Pollachius virens, saithe				11	28						34	10	Sundnes -57
Solea solea, sole, 80±21g					17						31	20	Thillart et al-94
Platichthys flesus, flounder,	19						19	24			19	9	Kerstens et al-79
-					35						16	10	Jørgensen & Mustafa-80
-,241-830 g		64	38		53						20	10	Steffensen et al-82
-							9				17	16	-field obs.
Pleuronectes platessa, plaice							17				33	15	-quote unpubl. data
-,16-33 cm							29	24	19	24	35	8	Scholz & Waller-92
-,200-300g		16	13		25						25	10	Weber -93
Limanda limanda, dab, 17-25 cm							31	24	21	24	35	8	Scholz & Waller-92
-,200-300g		25	16		26						25	10	Weber -93
Anguilla anguilla, eel,185-725g		51	23		42						0	18	Le Moigne et al-86
-,14-18cm	17										0	25	Itazawa -71
Anarhichas lupus, wolf fish, 3.8-4.4kg		50	26								34	7.2	Steinarsson -92
-,3.8-4.4kg		59	21								34	8.5	-
-,1-2kg					49		18	3	16	5.5	34	7.5	-
Scyliorhinus canicula, dogfish, eggs, 32-308d				10	40							15	Diez & Davenport-87
-,eggs, hatched				10	65								-
(*Torpedo marmorata*, electric ray)		50	19	18								16	Hughes -78
Zoarces viviparus, eelpout,					50						14	12	Fischer et al-92
Pomatoschistus minutus, sand goby	40										20	16	Petersen & Petersen -90
-							10	2	10	4	18	15	-
-							15	7	15	24	18	15	-
Callionymus lyra, dragonet,		76	43			76						11	Hughes & Umezawa-68
NO OF RECORDS:	14	26	25	16	49	8	19	17	41	36	93	10	

Tab. 2. Critical levels (% sat) for build-up of anaerobic end products (C1) estimated after TC hours exposure time. S $^{o}/_{oo}$, T ^{o}C.

Species	R1	C1	TC	L1	T1	L50	T50	S	T	Source
Saduria entomon	10	3						7	8	Hagerman & Szaniawska-88
G. duebeni, - estuarine		10	2	0	2	0	2.7	34	20	Agnew & Jones-86
-sewage plant		1	2	0	3	0	6.5	34	20	-
Echinogammarus pirloti	13	13						32	15	Agnew & Taylor-85
E. obtusatus	13	13						32	15	-
Nephrops norwegicus		15				10	2	30	10	Hagerman et al-90 *)
Calocaris macandreae		3		0	24	0	43	32	10	Anderson et al-94
(*Scapharca inaequivalvis*)	34	34						35	20	Thillart et al-92
Solea solea 80±21g	17	16	12					31	20	Thillart et al-94
- mean 19 cm		20	12					30	20	Dalla Via et al-94

*) Range C: 10-20%

Tab. 3. Critical levels (% sat) for growth or embryonic development (G1) and inactivation (B2). S $^{o}/_{oo}$, T^{o}C.

Species	G1	B1	B2	L1	T1	L50	T50	S	T	Source
Gadus morhua, Baltic cod eggs, 3-5d			34			26	2	15	7	Nissling -94
- eggs, 2-7d			32			20	2	15	7	-
- larvae, 0-4d			34			24	2	11	7	-
- larvae, 0-4d			32			25	2	15	7	-
Gadus morhua, Atl. cod, 80-200g		30				14	0.1	33	10	Schurmann & Steffensen-92
P. platessa, juv	52		30					32	15	Petersen & Pihl-95
Limanda limanda, dab, juv	50							32	15	Petersen & Pihl-95
Hippoglossus hippoglossus,halibut, hatching	41							34	6	Helvik & Walther-93
Clupea harengus, Baltic herring, eggs	50			20	15			15	8	Braum -73
Pomatoschistus minutus		40	16					20	16	Petersen & Pet.-90
-			24					35	11	Berge et al-83
Zoarces viviparus			75					14	12	Fisher et al-92
Saduria entomon		10						7	8	Hagerman & Szaniawska -88
S. entomon preying: - *Bathyporeia*	42							5	14	Sandberg -94
- *Corophium*	32							5	13	-

The species listed in Tab. 1-3 above represent most of the animal groups found among macrobenthos in the North sea and adjacent waters. Sponges, bryozoans, brachiopods, snails, ascidians, and the crustacean orders Ostracoda, Cumacea and Euphausiacea, however are absent. At species level, 11 out of 76 fish species found in trawl catches from the Oslofjord (Lid 1967) are listed in Tab. 1-3, but only 2 of the ca 170 hyper- and epibenthic species found by Beyer and Indrehus (1995) in the Oslofjord. Of Rosenbergs (1977) 36 recorded soft-bottom species from the Byfjord, 5 are represented above.

Tab. 4 and 5 give an overview of the sublethal hypoxic levels averaged for systematic groups subdivided into depth zones (Tab. 4) or subdivided into habitat strata (Tab. 5). Tab. 4 shows that most of the lab experiments are concerned with sublitoral species. Only crustaceans and R1 of molluscs have sufficient cover to make comparisons across zones. The mean values show no clear differences between the different zones. When means of all the results (column Total) are compared across systematic groups, there seems to be no clear differences between the groups except for the echinoderms. As an example, the threshold level for asphyxia (V3) is 12% sat for crustaceans, 11 for molluscs and 14 for fishes, but 60% for the echinoderm *Holothuria forscali*. The critical level for resting respiration (R1) is 29% sat for the worms, 28 for crustaceans, 38 for molluscs, 39 for fishes, and 47 for the echinoderms (in this case sea urchins).

When grouped according to a simple habitat classification (Tab. 5), the crustaceans still show the best cover, followed by molluscs and fishes. If we compare means of more than one observation, there are, without exception, increasing oxygen threshold levels when moving from in- to epi- to hyperfauna. This classification, therefore, seems appropriate when physiological parameters are concerned.

Tab. 4. Number of species investigated, and mean values (% oxygen saturation) of the hypoxic parameters distributed on systematic groups and habitat depths.

		Number of species				Mean % sat			
Group	Data	littoral	sublitoral	abyssal	Total	littoral	sublitoral	abyssal	All
COELENTERATES	B1	-	-	-	-	-	-	-	-
	V1	-	-	-	-	-	-	-	-
	V2	-	-	-	-	-	-	-	-
	V3	-	-	-	-	-	-	-	-
	R1	-	1	-	1	-	15	-	15
	H1	-	-	-	-	-	-	-	-
WORMS	B1	1	1	-	2	10	10	-	10
	V1	-	-	-	-	-	-	-	-
	V2	1	-	-	1	15	-	-	15
	V3	-	-	-	-	-	-	-	-
	R1	1	1	-	2	20	38	-	29
	H1	-	-	-	-	-	-	-	-
CRUSTACEANS	B1	1	1	2	4	38	26	18	25
	V1	3	7	4	14	32	48	38	42
	V2	3	8	3	14	25	21	23	22
	V3	2	6	1	9	6	14	13	12
	R1	3	7	7	17	18	26	33	27
	H1	3	2	-	5	23	14	-	20
MOLLUSCS	B1	-	-	-	-	-	-	-	-
	V1	1	1	-	2	41	50	-	46
	V2	1	-	-	1	24	-	-	24
	V3	1	-	-	1	11	-	-	11
	R1	2	4	3	9	31	50	26	38
	H1	-	-	-	-	-	-	-	-
ECHINODERMS	B1	-	-	3	3	-	-	15	15
	V1	-	-	1	1	-	-	66	66
	V2	-	-	1	1	-	-	63	63
	V3	-	-	1	1	-	-	60	60
	R1	1	2	-	3	40	35	-	37
	H1	-	-	-	-	-	-	-	-
FISHES	B1	-	4	-	4	-	25	-	25
	V1	-	8	-	8	-	49	-	49
	V2	-	7	-	7	-	25	-	25
	V3	-	5	-	5	-	13	-	13
	R1	-	11	-	11	-	39	-	39
	H1	-	1	-	1	-	76	-	76
Total B1		2	6	5	13	24	23	16	20
Total V1		4	16	5	25	34	48	44	45
Total V2		5	15	4	24	23	23	33	25
Total V3		3	11	2	16	8	13	37	15
Total R1		7	26	10	43	25	36	31	33
Total H1		3	3	-	6	23	35	-	29

Definitions:

B1= Hypoxic threshold level for escape responses
V1= Hypoxic level giving increased ventilation half-way to maximum
V2= Hypoxic level giving maximum ventilation
V3= Hypoxic threshold level for shut-down of ventilation (asphyxia)
R1= Hypoxic threshold level for reduced respiration
H1= Hypoxic threshold level for reduced heart rate (bradycardia)

Tab. 5. Number of species investigated, and mean values (% oxygen saturation) of the hypoxic parameters distributed on systematic groups and habitats.

		Number of species				Mean % sat			
Group	Data	infauna	epi-	hyper-	Total	infauna	epi-	hyper-	All
COELENTERATES	B1	-	-	-	-	-	-	-	-
	V1	-	-	-	-	-	-	-	-
	V2	-	-	-	-	-	-	-	-
	V3	-	-	-	-	-	-	-	-
	R1	-	1	-	1	-	15	-	15
	H1	-	-	-	-	-	-	-	-
WORMS	B1	2	-	-	2	10	-	-	10
	V1	-	-	-	-	-	-	-	-
	V2	1	-	-	1	15	-	-	15
	V3	-	-	-	-	-	-	-	-
	R1	1	1	-	2	20	38	-	29
	H1	-	-	-	-	-	-	-	-
CRUSTACEANS	B1	3	1	-	4	20	38	-	25
	V1	2	10	2	14	28	42	53	42
	V2	2	11	1	14	15	24	13	22
	V3	-	8	1	9	-	12	10	12
	R1	3	10	4	17	20	27	34	27
	H1	-	4	1	5	-	22	10	20
MOLLUSCS	B1	-	-	-	-	-	-	-	-
	V1	1	-	1	2	41	-	50	46
	V2	1	-	-	1	24	-	-	24
	V3	1	-	-	1	11	-	-	11
	R1	3	4	2	9	20	46	50	38
	H1	-	-	-	-	-	-	-	-
ECHINODERMS	B1	-	3	-	3	-	15	-	15
	V1	-	1	-	1	-	66	-	66
	V2	-	1	-	1	-	63	-	63
	V3	-	1	-	1	-	60	-	60
	R1	-	3	-	3	-	37	-	37
	H1	-	-	-	-	-	-	-	-
FISHES	B1	-	1	3	4	-	19	27	25
	V1	-	3	5	8	-	35	57	49
	V2	-	3	4	7	-	22	27	25
	V3	-	2	3	5	-	10	15	13
	R1	-	6	5	11	-	36	41	39
	H1	-	-	1	1	-	-	76	76
Total B1		5	5	3	13	16	20	27	20
Total V1		3	14	8	25	32	42	55	45
Total V2		4	15	5	24	17	27	24	25
Total V3		1	11	4	16	11	16	14	15
Total R1		7	25	11	43	20	33	40	33
Total H1		-	4	2	6	-	22	43	29

Definitions:

B1= Hypoxic threshold level for escape responses
V1= Hypoxic level giving increased ventilation half-way to maximum
V2= Hypoxic level giving maximum ventilation
V3= Hypoxic threshold level for shut-down of ventilation (asphyxia)
R1= Hypoxic threshold level for reduced respiration
H1= Hypoxic threshold level for reduced heart rate (bradycardia)

Tab. 6. Correlations between the different threshold levels. Lacking number means that there are observations on less than three species.

	V1	V2	V3	R1	H1	L1
V2	0.64					
V3	0.59	0.83				
R1	0.46	0.43	0.40			
H1	0.64	0.79	0.11	0.57		
L1	0.25	0.11		0.40		
L50	0.04	-0.33	0.75	-0.06		0.99

Table 6 shows the correlation coefficients between the threshold levels. The threshold levels within sublethal (V1 - H1) and lethal responses (L1 - L50) are all positively correlated (Tab. 6). Naturally, L1 and L50 are highly correlated.

Asphyxic levels (V3) and lethal levels (L50) for more than a day are plotted against critical level for resting respiration (R1) in Fig. 2. The lines represent a 1:1 relationship. In Fig. 2a, the asphyxic levels are mostly far below the critical levels for resting respiration. In Fig. 2b, there is a closer relationship between the lethal and respiratory levels. This suggests that as exposure time increases, the hypoxic level that cause death approach that giving reduced resting respiration.

The various nonlethal hypoxic levels are sorted in descending order in Table 7. They show higher hypoxic tolerance of infauna compared to epi- and hyperfauna. Fishes and echinoderms cover the upper part of the list, with ventilatory or metabolic response levels. B2 for fish at 75% sat is threshold level for oxygen limitation of swimming activity. Threshold levels for normal growth or development are in the range 37 - 52 % with fish in the upper position. Fish are also more sensitive when considering emerge/escape responses (B1).

The lethal levels of hypoxia are not easily compared, since exposure duration is an integrate part of the total amount of stress. There are few studies of sufficient duration to ensure threshold levels for sustaining survival. Lethality of each species/stage, either start or 50 %, are therefore presented as a function of both oxygen and exposure time in Table 8, where the species investigated are represented by their habitat stratum (upper end) or systematic group (lower end). In the upper end, infauna is found in the left and lower part of the area, showing their higher tolerance of hypoxia compared to epi- and hyperfauna. In the lower end, fishes are found in the right and upper part of the area, showing limited tolerance of hypoxia compared to crustaceans that are spread on the whole area.

The experimental work of Rosenberg *et al*. (1991) showed the lobster (*Homarus gammarus*) to be rather tolerant to hypoxia, and comparable to the infaunal decapod *Nephrops norwegicus* and other infauna. The tolerance limit (probable L50) after several days to weeks was in the range of 8-15 % sat.

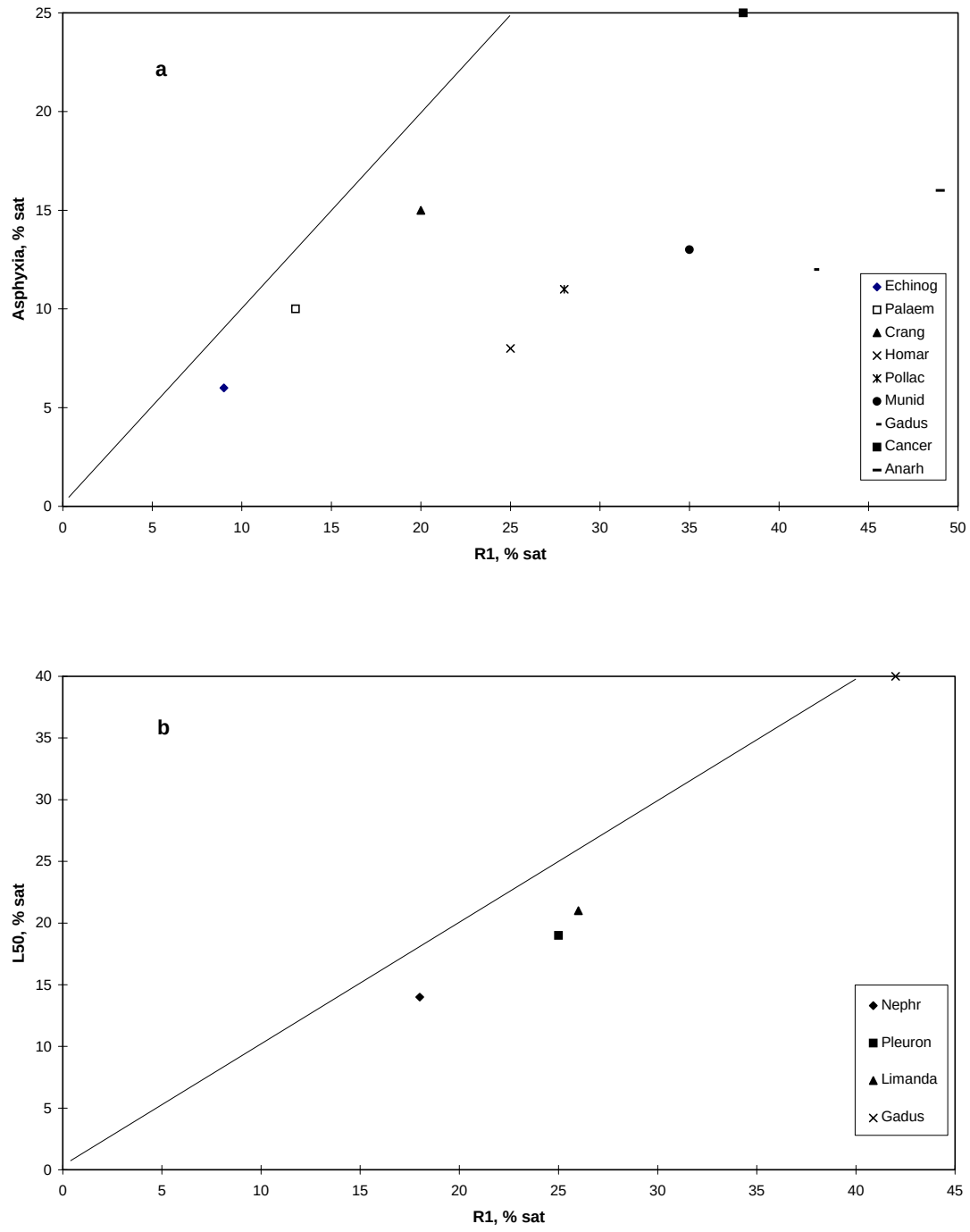


Fig. 2. Critical levels for asphyxiation (a) **and >24 h L50** (b) **plotted against critical level for resting respiration. The lines represent equality.**

Tab. 7. Hypoxic levels for species represented by systematic group and distributed on habitats.

O_2 %sat	hyperfauna	epifauna	infauna
76	H1 FISH		
76	V1 FISH		
75	B2 FISH		
70	R1 CRUST.		
66		V1 ECHINO.	
65		R1 FISH larvae	
64		V1 FISH	
63		V2 ECHINO.	
63		R1 MOLLUSC	
62	V1 CRUST.		
60		V3 ECHINO.	
55	V1 FISH		
54		V1 CRUST.	
54	R1 MOLLUSC		
53		V1 CRUST.	
52		V1 CRUST.	
52	V1 FISH		
52		G1 FISH juv	
51	V1 FISH		
50	R1 FISH		
50	V1 FISH		
50		G1 FISH egg	
50		G1 FISH juv	
50	V1 MOLLUSC		
49	R1 FISH		
45		V1 CRUST.	
45		V1 CRUST. juv	
45	R1 MOLLUSC		
44	V1 CRUST.		
44		R1 FISH	
44		R1 MOLLUSC	
43	V2 FISH		
42		V1 CRUST.	
42	R1 FISH		
41		V1 CRUST.	
41	G1 FISH egg		
41			V1 MOLLUSC
40		R1 ECHINO.	
40		B1 FISH	
40		R1 FISH egg	
38		B1 CRUST.	
38		R1 CRUST.	
38		V2 CRUST.	
38		R1 ECHINO.	
38	R1 FISH		
38		V2 FISH	
38		R1 MOLLUSC	
38		R1 MOLLUSC	
38		R1 WORM	
37			G1 CRUST.
37		R1 CRUST.	
37		V1 CRUST.	V1 CRUST.
35		R1 CRUST.	
35		V1 CRUST.	
34		H1 CRUST.	
33		R1 ECHINO.	
33	B2 FISH egg		
33	B2 FISH larvae		
32		R1 CRUST.	
32		R1 CRUST.	
32		V2 CRUST.	
32		V2 CRUST.	
32	R1 CRUST. juv		
30		R1 CRUST.	R1 CRUST.
30		B2 FISH juv	
28		V2 CRUST.	

O_2 %sat	hyperfauna	epifauna	infauna
28	B1 FISH		
28	R1 FISH		
26			B1 CRUST.
26		R1 FISH	
25			B1 CRUST.
25		R1 CRUST.	
25		V3 CRUST.	
25		R1 CRUST.	
25		R1 FISH	
25		V1 FISH	
25			R1 MOLLUSC
24		V2 CRUST.	
24		V2 CRUST.	
24		V2 CRUST.	
24		B1 ECHINO.	
24	V2 FISH		
24			R1 MOLLUSC
24			V2 MOLLUSC
23	V2 FISH		
21		H1 CRUST.	
21		V2 CRUST.	
20			R1 CRUST.
20		V3 CRUST.	
20			R1 WORM
19	R1 CRUST.		
19		V1 CRUST.	V1 CRUST.
19		B1 FISH	
19	V2 FISH		
18		H1 CRUST.	
18			V2 CRUST.
18		V2 CRUST. juv	
18	V3 FISH		
17		R1 FISH	
17	B1 FISH juv		
16		V2 CRUST.	
16		B2 FISH	
16		V1 FISH	
16		V2 FISH	
15		R1 COELENT.	
15		H1 CRUST.	
15	V3 FISH		
15			V2 WORM
13	R1 CRUST.		
13	V2 CRUST.		
13		V3 CRUST.	
13		V3 CRUST.	
13		B1 ECHINO.	
13		V2 FISH	
12		V2 CRUST.	V2 CRUST.
11		V3 CRUST.	
11	V3 FISH		
11			V3 MOLLUSC
10			B1 CRUST.
10	H1 CRUST.		
10			R1 CRUST.
10	V3 CRUST.		
10		V3 FISH egg	
10		V3 FISH larvae	
10			R1 MOLLUSC
10			B1 WORM
10			B1 WORM
9		R1 CRUST.	
8		R1 CRUST.	
8		B1 ECHINO.	
6		V3 CRUST.	
6		V3 CRUST.	
5		V3 CRUST. juv	

Tab. 8. Hypoxic tolerance (L1 or L50) **of demersal fauna according to habitat stratum** (upper end) **and systematic group** (lower end).

	Duration of exposure, hours									
Oxygen,%sat	0 - 1	1 - 2	2 - 4	4 - 8	8 - 16	16 - 32	32 - 64	64 - 128	128 - 256	256 - 512
60						hyper				
40						hyper				
35							hyper			
31						epi				
29						epi				
26							hyper			
25							hyper			
24							hyper			
21						epi				
20			epi							
20			epi							
20							hyper			
19						epi				
19						epi				
18			hyper							
17			hyper							
17								in		
16				hyper						
15				in						
15				hyper						
15						hyper				
14								in		
13	epi									
11	hyper									
10		hyper								
10			epi							
10			hyper							
10				in						
10				in						
10							in			
8	in									
6				hyper						
6					hyper					
5						in				
60						FISHES				
40						FISHES				
35							FISHES			
31						FISHES				
29						FISHES				
26							FISHES			
25							FISHES			
24							FISHES			
21						FISHES				
20			CRUSTACEANS							
20			CRUSTACEANS							
20							FISHES			
19						FISHES				
19						FISHES				
18			FISHES							
17			CRUSTACEANS							
17								CRUSTACEANS		
16				FISHES						
15				CRUSTACEANS						
15				FISHES						
15						FISHES				
14								CRUSTACEANS		
13	CRUSTACEANS									
11	CRUSTACEANS									
10		FISHES								
10			CRUSTACEANS							
10			FISHES							
10				CRUSTACEANS						
10				CRUSTACEANS						
10							CRUSTACEANS			
8	CRUSTACEANS									
6				CRUSTACEANS						
6					CRUSTACEANS					
5						CRUSTACEANS				

Anoxic resistance is high in some infaunal lamellibranch species (Tab. 9). Also the epifaunal littoral mussel *Mytilus edulis*, endure extreme hypoxia/anoxia for several weeks. And the littoral gastropod *Littorina littorea* is quite resistant (about 2 weeks). Except for the molluscs, the macrobenthic species tested resist anoxia for 5 days or less, crustaceans and fishes being the most vulnerable. About half the species listed in Tab. 9 succumb after a couple of hours to 3 days. These are mostly species that may encounter small-scale hypoxia in their natural habitats.

Tab. 9. Anoxic resistance sorted in descending order (* tested at less than 2.3 % sat, Theede 1973, Dries & Theede 1974).

Species	**Hours**
Astarte borealis *	2040
Astarte elliptica *	1536
Cyprina islandica *	1400
Astarte montagui *	912
Mytilus edulis *	900
Scrobicularia plana *	600
Macoma baltica *	528
Mya arenaria *	500
Littorina littorea *	350
Nucula sulcata	240
Littorina saxatilis *	140
Abra alba *	139
Nereis diversicolor *	120
Cardium edule *	100
Macoma calcarea *	96
Asterias rubens *	90
Terebellides stroemi *	72
Ophiura albida *	72
Nereis diversicolor	72
Nereis virens	72
Carcinus maenas *	45
Ophiura albida *	35
Limanda limanda	24
Pleuronectes platessa	24
Calocaris macandreae	24
Cirolana borealis	18
Gammarus oceanicus *	16
Pomatoschistus minutus	7
Idotea baltica *	6
Gammarus duebeni	3
Crangon crangon *	2
Neomysis awatschensis	1
Archaeomysis grebnizkii	1

3. DISCUSSION

Environmental fluctuation

Oxygen levels available to marine organisms may show considerable variation. Intertidal organisms, and subtidal organisms in the euphotic zone may experience great diurnal variation, while deeper water in bays and estuaries offer oxygen levels governed by seasonal and often erratic events overlying the balance between diffusive input and organic consumption. Deep basins in fjords often get their water exchanged annually, but also at shorter or longer intervals. Diaz & Rosenberg (1995) found that long or erratic intervals make hypoxia more harmful to the fauna, compared to predictable annual hypoxia, to which the community will easier adapt. Brett (1979) refers to growth experiments with fish in water of fluctuating oxygen concentration, and concludes that growth is markedly impaired compared to that of the mean level. Thus oxygen surplus in one period does not outweigh oxygen lack in another.

Tolerance and resistance

The coarse habitat classification used above revealed that infauna tolerates lower ambient oxygen levels than hyper- and epifauna before hypoxic responses and lethality are seen. This is not due to uneven representation of the different systematic groups, since it also holds for each systematic group taken separately. Hyper- and epifauna, on the other hand, can not be separated, neither on sublethal responses nor lethality. Although Diaz & Rosenberg (1995) suggest that functional groups are inferior to taxonomic groups in explaining differences in hypoxic tolerance, this does not mean that the former should be ignored.

The difference between infaunal and epi-/hyperfaunal tolerance pertains to absolute oxygen levels, and not necessarily to the relative drop in ambient oxygen in any of these two habitats. Thus, increased organic load may affect infauna as much as hyperfauna because of the initially lower oxygen level in the infaunal habitat.

The difference in hypoxic tolerance between infauna and epi-/hyperfauna may account for some stability of the benthic community, since swimming or walking predators will tend to leave or stop feeding before the infauna emerge from their shelter (c.f. Baden *et al.* 1990 a).

Anoxic resistance (Tab. 9) show a vast difference between molluscs - especially lamellibranchs - and other taxa. From field studies, Weigelt & Rumohr (1986) report that only a few macrofauna species survived several weeks of anoxia (*Halicryptus* of the order Priapulidae, which is not a mollusc, and 3 bivalve genuses: *Arctica*, *Astarte* and *Corbula*). This is due to their special hibernation response, which is highly developed also in the littoral, epifaunal mussel *Mytilus edulis*. Next to the outstanding ability of molluscs (and some specialists of other taxa) to resist anoxia, come some worms and echinoderms (35-120 hours) and then flatfishes and crustaceans (1-45 h) as the most vulnerable.

The matter of long-time survival and population dynamics is complicated by the existence of vulnerable phases, some frequent like the moulting (ecdysis - change of exoskeleton) of crustaceans, some once in a lifetime, like the period when a fish larvae must capture its first prey to proceed. Crustaceans have been shown to demand more oxygen just before and after moulting (Alcaraz & Sarda 1981, McLeese 1956). The common shrimp (*Crangon*) showed a death rate similar to moulting rate when exposed to nitrite (Kirkerud *et al.* 1975). Behaviour is also affected, since many crustaceans are in need for shelter during the moulting process. A live-bearing fish (*Sebastes schlegeli*) showed 68 % increased oxygen consumption for gestating

females compared to non-gestating fish (Boehlert *et al.* 1991).

The eggs and larvae of Baltic cod are subject to hypoxia in their natural environment (Bagge & Thurow 1994, Nissling 1994). Hypoxic tolerance is about 30 % sat, and may be better than for fast-growing young fish (Scholtz & Waller 1992). However, the larvae were not tested beyond day 4 after hatching, while Serigstad (1987) - for larvae of Atlantic cod - found the respiration to increase sharply and peak 6 - 8 days after hatching, about the time when the larvae are in need for their first prey. The most vulnerable phase of a cods life, then, may not have been covered. This is the general situation, and implies that the critical levels listed do not necessarily serve as basis for safe levels on an yearly basis, i.e. that periodic hypoxia may still interfere with the organisms present in cases of coincidence between hypoxia and vulnerable phases of life.

Respiration

Respiratory response levels as mentioned in the introduction, affect the scope of metabolism of the animals, and thereby energy-requiring processes like activity, feeding, growth and reproduction. However, a couple of the parameters listed should rather be classified as lethal levels. This is the case for the oxygen level at ventilatory shutdown (asphyxia), tabulated as V3. Only the cease of water filling and expiration of *Holothuria forscali* and other echinoderms (Newell & Courtney 1965, Steen 1965) is somewhat doubtful. The critical level for build-up of anaerobic end products may also be considered as lethal on long exposure. In the long run expensive anaerobic metabolism will deplete the energy stores of the animal, or the end products reach lethal concentrations in tissue or blood. *Holothuria forscali* responded to experimental hypoxia with a shutdown of water filling and expiration at about 60 % sat, accompanied by the build-up of an oxygen debt (Newell & Courtney 1965). Although the physiology of this species seems to be poorly studied, it must be considered most vulnerable to hypoxia.

At moderate hypoxic levels, the onset of respiratory responses depend to some extent on the situation of the animal, their activity level, or whether they are stressed or not (see Spoek 1974 for an example with the lobster). Experiments with mussels revealed that the animals may show different degrees of respiratory homeostasis depending upon the aquarium environment and feeding (Bayne 1971). Differences in respiratory threshold levels may also arise from different hypoxic strategies of the species. Fig. 2a suggests that some species reduce their respiration at an early stage of progressive hypoxia compared to asphyxic level (*e.g.* wolf fish, cod and lobster), while others keep their resting respiration constant nearly till asphyxiated (the shrimps *Palaemon elegans* and *Crangon crangon*). Fig. 2b shows a better fit between critical level for respiratory homeostasis and sustaining survival. In the case of cod, the 24 hour L50 at 40 % sat obtained by Scholz & Waller (1992) seems to conflict the results of Sundnes (1957) and Schurmann & Steffensen (1992) who found asphyxic levels of 12 - 17 % sat at temperatures 10 - 15 ^{o}C. But with the differences in exposure time (24 hours compared to 2 - 3 hours) such differences should be at least partly explained.

Generally there is a potential of organisms to adapt to hypoxic environments when hypoxia is developing over some time. The two ecotypes of *Gammarus duebeni*, found within and outside a sewage plant, demonstrate a considerable potential of this species to adapt its respiration to function in severe hypoxia (Agnew & Jones 1986). Both fishes (Petersen & Petersen 1990) and crustaceans (Baden *et al.* 1990b) adapt to moderate hypoxia by increasing the oxygen carrying capacity of their blood. This will reduce the stress on the respiratory organs, but still it means redirecting energy from growth and reproduction to instead cope with an introduced environmental problem.

Though the information is limited, it suggests that the critical level for resting respiration, if properly obtained, should be further investigated as a possible protection level for sustained survival.

At the ecosystem level, reduced respiration of dominant populations will affect the progress of hypoxia, both temporally and spatially. When dominant biomasses reduce their metabolism, hypoxia will develop at a slower rate, and organic matter will to a greater extent accumulate at the water/sediment interface. Combined with reduced bioturbation, this will increase the stratification of the sediment (Diaz & Rosenberg 1995). The ultimate effect of reduced metabolism is a conservation of the oxygen pool of the overlying water, and thereby increasing probability of survival. But if the community of organisms is injured, or periods of sufficient oxygen are too short, organic accumulation is not exploited until the next hypoxic period. Organic material will then accumulate year by year, and the oxygen problems at the bottom likewise. In addition, a greater part of the nutrients, both fixed nitrogen and phosphorus, will probably be released from the bottom and thus accelerate the eutrophication problems (c.f. Diaz & Rosenberg 1995). For each area or basin there must exist a limit of eutrophication, beyond which such instability will occur. Determination of such limits may in part be based on more general descriptions of required oxygen conditions for the animal community, seasonal or periodic variation taken into account.

Behaviour

The ecological significance of emerge- and escape response levels are already mentioned and some examples included below. The Norway lobster (*Nephrops norwegicus*) is well studied under hypoxia, both in the laboratory and field. In the lab, it will leave its burrow at about the critical oxygen tension for maximum ventilation (Hagerman & Uglow 1985), and stand tiptoeing on the bottom (Baden *et al*. 1990b). In the field, the animals will leave their burrow at an earlier stage of hypoxia, as Bagge & Munch-Petersen (1979) obtained greatly increased trawl catches when the oxygen level was reduced only to 50 % sat. Exceptional trawl catches during hypoxic periods are seen for other infauna as well (Baden *et al.* 1990 a). The stomach content of fishes analysed by Pihl (1994) revealed that the hermit crab (*Pagurus bernhardus*) would leave their snail houses below 30 % sat with high risk of being eaten. Bond strength to the shelter differ among species, and the anomuran *Calocaris macandreae* would not leave its burrow even at oxygen tensions near zero (Anderson *et al*. 1991).

It must be concluded that critical oxygen levels for emerge responses are ecologically significant both due to natural predator - prey relationships and human trawl fishing.

The ability to escape hypoxic water do to a certain extent, allow motile or swimming animals to exploit enriched areas inter-mittently. Under hypoxic conditions they can leave the area and come back when conditions are favourable. But to some species this may cost too much energy, and, when repeated year by year, the populations will be decimated (see Beyer & Indrehus 1995 on the softbottom epi-/hyperfauna of the Oslofjord). Besides, the spatial development of hypoxia may cause the fauna to be trapped between a benthic and a midwater oxygen minimum, cover too big an area to flee, or move too fast into new areas. Such situations have led to widespread or local kills of fish and invertebrates (*e.g.* May 1973, Kirkerud & Magnusson 1977).

Feeding and growth

There are few results on growth in hypoxia of species from the North Sea and adjacent waters, but the flatfishes plaice and dab, showed reduced growth below 50 % sat (Petersen & Pihl 1995). The significance of the results was supported by field registration of mean length in the seasonally hypoxic Southeast Kattegat. Likewise, herring embryos were found to reduce their growth at about 50 % sat (Braum 1973). Experimental results on growth-limiting oxygen tension by Andrews *et al.* (1973), Stewart *et al.* 1967, Herrmann *et al.* (1962) and citations by Itasawa (1971) mainly on freshwater species all are in the range 30-60 % sat. Brett (1979) in his review article on fish growth arrived at a critical level for growth of 5 mg/l, or about 55-60 % sat.

In nature, feeding usually require more locomotory effort than when animals are fed in an aquarium. Sandberg (1994) studied the

effect of oxygen depletion on the predator-prey relationship between the isopod *Saduria entomon* as predator and the amphipods *Corophium volutator* and *Bathyporeia pilosa* as prey, all natural inhabitants of the Baltic Sea. Predation on *Corophium* was reduced between 30 and 17 % sat and on *Bathyporeia* between 50 and 35 % sat, indicating oxygen thresholds for each specific predator-prey relationship. This also illustrate that even if prey organisms may have their escape ability reduced in hypoxia, their predators must slow down as well. Similar explanations may account for the observation of Diaz *et al.* (1992) that periodic hypoxia in the York River estuary affected the structure of the benthic community less than community function.

General

Traditionally, critical levels or thresholds have been proposed for different fauna components and at different protection levels (*e.g.* Davis 1975). It would be possible from the accumulating data to improve on such levels.

Consideration of hypoxic responses alone might result in a critical level of >76 % sat (4,8 ml/l) for the welfare of all the species investigated. Below 65 % sat (4,1 ml/l) resting respiration of fish and fish larvae and some invertebrates start to reduce from about 50 % sat (3,2 ml/l), growth retardation is found for fish and fish embryos. From about 30-40 % sat (1,9 - 2,5 ml/l) escape reactions are found for epifauna and an increasing number of species ventilate at maximum. Long-term lethality is found for fishes. The first ventilatory responses are seen for infauna. From 20-25 % sat (1,3-1,6 ml/l) lethality is seen for epifaunal crustaceans, and infaunal crustaceans start to emerge. Fishes are asphyxiated (18 - 11 % sat). From 17 % sat (1,1 ml/l) lethality is found for infaunal crustaceans, and down to 5 % sat (0,3 ml/l) all the listed fishes and crustaceans are killed. This is comparable to the lethal levels for infauna estimated from the experimental study of Rosenberg *et al.* (1991) and field studies in seasonally hypoxic environments referred by Diaz & Rosenberg (1995) (0,8 - 1,1 ml/l).

The interval of about 65-50 % saturation (sat) is characterised by minor sublethal changes, e.g. reduced resting respiration in some species. In the interval of about 50-35 % sat more severe sublethal changes take place, like reduced growth in fishes. From about 35-20 % sat lethality may occur in the fish fauna in addition to severe sublethal responses in other hyper- and epifauna. Below about 20 % sat (1,2 ml/l) lethality also take place in epifauna, and severe sublethal responses and finally lethality take place in infauna, depending on duration. Such water may cause fish kills.

The above values refer to ambient water or sampling close to the sea-floor.

The detrimental effects of hypoxia in a real situation depend on other factors in addition to hypoxic severity. An obvious factor is duration of the hypoxic event that will also be augmented by eutrophication. Towards the fauna, hypoxic severity and duration act together as independent determinants of the biological effects. Mathematical combination of the two to form a single entity like ‘amount of hypoxic stress’ should not be anticipated, since there will be qualitative differences in effects along both axes (*e.g.* different species will be affected). But models based on two-dimensional or (see below) multi-dimensional mapping of species/effects seem to be a way to proceed.

Organic enrichment is another important factor, that usually go together with the other two (c.f. Mirza & Gray 1981). This factor should be included in the multi-dimensional mapping mentioned above. Gray (1992) discuss the possibility of quantifying this scale, and suggest that organic carbon, nitrogen and C/N ratio of surface sediments be further investigated for this purpose.

Factors that may be significant in some areas are salinity and temperature. In recipients of industrial waste, there may also be interfering chemicals (*e.g.* Weber 1993), and in some cases risk of recycling heavy metals from the sediment.

The causal relation between eutrophication and hypoxia is greatly influenced by topography. When applying the above type of information to set environmental goals, local natural restrictions, therefore, must be taken into account, such as geophysics, and natural nutrient loads and recycling. These may set limits as to the oxic status that may possibly be obtained (*e.g*. some basins are naturally anoxic).

In order to quantify the metabolism of organic matter at the sea-floor in relation to hypoxia and organic load, controlled experiments in basins would be highly profitable. Such experiments would also facilitate the study of benthic in-, epi- and hyperfauna, their population dynamics and behaviour, which should be included.

4. CONCLUSIONS

In an environment with fluctuating oxygen levels, care should be taken to secure a natural healthy fauna that can consume and metabolise the organic material supplied. This requires attention both to the *duration* and s*everity* of hypoxic periods, but also to *frequency* and *seasonal phase.* Average condition may be less relevant, since oxygen surplus in parts of the cycle do not generally outweigh lack in others. *Organic load* experienced by the bottom communities should also be included as one of the main factors. Temperature, salinity and industrial contaminants may be appropriate.

The interval of about 65-50 % saturation (sat) is characterised by minor sublethal changes, e.g. reduced resting respiration in some species. In the interval of about 50-35 % sat more severe sublethal changes take place, like reduced growth in fishes. From about 35-20 % sat lethality may occur in the fish fauna in addition to severe sublethal responses in other hyper- and epifauna. Below about 20 % sat (1,2 ml/l) lethality also take place in epifauna, and severe sublethal responses and finally lethality take place in infauna, depending on duration. Such water may cause fish kills.

In order to quantify the metabolism of organic matter at the sea-floor in relation to hypoxia and organic load, controlled experiments in basins would be highly profitable. Such experiments would also facilitate the study of benthic in-, epi- and hyperfauna, their population dynamics and behaviour, which should be included.

Seasonal phases of hypoxia should be related to seasonal phases of vulnerable stages in the life cycles of animals to identify possible temporal and spatial coincidence. Such cases are known for some important fish stocks, *e.g.* Baltic cod eggs and larvae, but more information is needed.

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