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Impacts of hypoxia on the structure and processes in the pelagic community (zooplankton, macro-invertebrates and fish)

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Abstract

Dissolved oxygen (DO) concentration in the water column is an environmental parameter that is crucial for the successful development of many pelagic organisms. Hypoxia tolerance and threshold values are species- and stage-specific and can vary enormously. While some fish species may suffer from oxygen values of less than $3\,\mathrm{ml\,L^{-1}}$ and show impact on growth, development and behaviour, other organisms such as euphausiids may survive DO levels as low as $0.1\,\mathrm{ml\,L^{-1}}$. A change in the average or the minimum or maximum DO in an area may have significant impacts on the survival of certain species and hence on the species composition in the ecosystem with consequent changes in trophic pathways and productivity.

Evidence of the deleterious effects of oxygen depletion on species of the pelagic realm is scarce, particularly in terms of the effect of low oxygen on development, recruitment and patterns of migration and distribution. While planktonic organisms have to cope with different DOs and find adaptive mechanisms, nektonic species may avoid areas of inconvenient DO and develop adapted migrational strategies. Planktonic organisms may only be able to escape vertically, above or beneath the Oxygen Minimum Zone (OMZ). In shallow areas only the surface layer can serve as a refuge, in deep waters many organisms have developed vertical migration strategies to use, pass and cope with the OMZ.

This paper elucidates the role of DO for different taxa in the pelagic realm and the consequences of low oxygen for foodweb structure and system productivity.

1 Introduction

Oxygen has come into the focus of science only recently as an environmental factor impacting physiology, behaviour and life cycles of marine organisms. While significant research has been done on oxygen consumption or transport, etc. on cellular or individual basis the impact of low oxygen conditions, i.e. hypoxia on the physiological

and behavioural capacity and life cycles is much less investigated (5200 hits in ASFA). About 35 percent of this work has been done on fish (1800 hits). The majority of the studies has been conducted in estuaries or semi-enclosed seas such as Baltic or Black Seas. The investigation of hypoxia in the pelagic ecosystems is a rather new topic.

5   The pelagic community includes representatives from nearly all zoological phyla. Most marine animals spend at least part of their lifetime in the pelagic environment, either as planktonic or nektonic organisms. Neglecting the primary producers (e.g. diatoms, dino-flagellates, green algae) at this stage we concentrate here on the consumers (e.g. copepods, jelly fish, euphausiids, decapods) and top preda-
10 tors (e.g. squid, fish, mammals), and within these groups we focus on the dominant species.

The impact of low oxygen or hypoxia ($<1.42\,\mathrm{ml}\,O_2\,L^{-1}$; $60\,\mu M$; $2\,\mathrm{mg}\,O_2\,L^{-1}$) can be twofold: on a macro-scale in the environment hypoxia constrains the vertical and horizontal distribution of species and forces them to depart from their normal behaviour;
15 and on a micro-scale it causes physiological changes and shifts and thus alters life-cycle performance, growth capacity and reproductive success and the vulnerability to diseases.

Hypoxia tolerance and threshold values are species- and stage-specific and can vary enormously (Miller et al., 2002). Fishes seem to be more vulnerable to low oxygen
20 levels than crustaceans and molluscs (Vaquer-Sunyer and Duarte, 2008). Even within species, different development stages may suffer differently from hypoxia. While some fish larvae may suffer at oxygen values of less than $3\,\mathrm{ml}\,O_2\,L^{-1}$ and show impact on growth, development and behaviour, other organisms such as euphausiids may survive to $0.1\,\mathrm{ml}\,O_2\,L^{-1}$. While sensitive species avoid even medium range oxygen levels,
25 others such as gobies have no problem to spend hours sitting on the oxygen-free mud at the sea floor! A change in the average and the minimum and maximum DO in an area may thus have significant impact on the survival of certain species and the species composition of an ecosystem with consequent changes in trophic relationships and productivity.

After elucidating the role of oxygen and the impact of hypoxia at the physiological level, we review in this paper the effects of hypoxic conditions on some of the dominant organism groups in the pelagic environment and discuss possible consequences for the structure of pelagic ecosystems and predator-prey-relationships in the pelagic ecosystem. Lluch-Cota et al. (2007) in their review of the Gulf of California still mention that "...no discrete sampling of the pelagic community of the water column as related to oxygen level..." has been performed. Only recent congresses and symposia have taken up this topic.

Depending on the scientific discipline, oxygen is presented in various units, mainly in DO concentration or saturation. Geochemical studies mostly use μmol per liter as unit for measured values, while mg or mL per liter are widely spread in physical and environmental studies. Physiological studies relate to partial pressure measured in hPa (mbar) or kPa, some are still in mm Hg. However, the oxygen demand of individuals is temperature-dependant and saturation is a unit including these two parameters. In many cases, temperature is not explicitly given by the authors and thus comparison between results is sometimes difficult. We have tried to harmonise the units in the review to a certain extent. Table 1 may help to transform and compare between units.

2 Physiological background of hypoxia tolerance in marine organisms

Ecophysiological studies aim to understand the physiological basis of zoogeographical patterns within the system of currents and in a latitudinal cline, as much as these distribution patterns are determined by the temperature regime and its interactions with other abiotic factors, like water velocities, oxygen levels etc. The responsible physiological mechanisms involve those limiting and adjusting cold and heat tolerance and these research topics have, in general, gained interest in the context of global warming and associated shifts in the geographical distribution of marine ectothermic animals.

Traditional concepts in animal physiology have considered the effects of individual

factors like oxygen, temperature, carbon dioxide or salinity and have addressed the specific responses in organisms from various habitats. For analyses of the complex interactions and effects of various environmental factors at the ecosystem level these traditional concepts need to be integrated in order to achieve more realistic estimates
5 of sensitivity to environmental change. Progress in recent years has identified how such integration may occur and can be implemented (e.g. Pörtner and Farrell, 2008). The traditional principles and their integration operate similarly across animal phyla and will accordingly be briefly summarized from a general point of view. Those principles are emphasized which provide a link between physiology and ecology and support an
10 understanding of ecosystem level processes.

In the context of organismic requirements for ambient oxygen and of the associated levels of hypoxia sensitivity the concepts of oxyconformity, oxyregulation, and the critical PO_2 have been revisited based on an integration of systemic and cellular processes in declining ambient oxygen tensions (Pörtner and Grieshaber, 1993). It has
15 been recognized early that animals may show different patterns of oxygen consumption in response to changes in ambient PO_2. Some keep their oxygen consumption more or less constant in a wide range of PO_2 and are called oxyregulators. Others reduce their oxygen uptake with decreasing oxygen tensions and have, consequently, been termed oxyconformers. Intermediate responses exist too (Mangum and van Winkle,
20 1973). Nonetheless, categorization is useful to identify metabolic patterns of oxyconformity and the underlying mitochondrial mechanisms. Circumstantial evidence for the presence of an alternative mitochondrial oxidase (cytochrome o) exists in lower marine invertebrates, e.g. sipunculids, annelids or bivalves (Pörtner et al., 1985; Buchner et al., 2001; Tschischka et al., 2000). This oxidase might represent an ancient mecha-
25 nism of oxygen detoxification used in animals which live in hypoxic environments. Only these aerobic oxyconformers, which display oxyconformity at cellular and mitochondrial levels should be considered as "true" oxyconformers, whereas the progressive drop in oxygen consumption seen during extreme hypoxia in both oxyconformers and oxyregulators is caused by oxygen supply being insufficient to completely cover energy de-

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mand. Variable intracellular oxygen levels drive variable rates of oxygen consumption in oxyconformers, whereas this rate remains constant above the Pc in oxyregulators. However, aerobic oxyconformers can be behavioral oxyregulators, once they manage to keep oxygen levels in their water burrow or in their body fluids constant through
5 compensatory adjustments in ventilatory (and circulatory) efforts. Irrigation of worm burrows in the sediment or ventilation of gill chambers in bivalves may in fact involve apparent oxyregulation in these animals. By keeping oxygen in their body fluids at minimal levels (e.g. Massabuau, 2001) they could minimize the extent to which oxygen detoxification by cytochrome o is necessary. Variable ventilatory capacities might thus
10 explain the variable responses elaborated by Mangum and van Winkle (1973).

    The terms oxyconformity and oxyregulation have been defined for quiescent animals, which display baseline or "standard" metabolic rate. Standard metabolic rate (SMR) is defined as the lowest rate of oxygen consumption for oxyregulators, "which would be obtained when all organs were absolutely at rest". The data available for
15 several oxyregulators suggest that this rate is maintained down to the critical PO_2 below which anaerobiosis starts (see below). This clear physiological definition of SMR excludes the "perturbing" effect of spontaneous muscular activity on the pattern of oxygen consumption during hypoxia. SMR is analysed (1) by correcting for the influence of spontaneous activity during long term measurements, (2) by extrapolating to zero
20 activity during analyses of aerobic metabolism at various activity levels, or (3) by determining metabolic rate at or slightly above the Pc, to exclude the effect of oxyconformity mechanisms. However, focusing on standard metabolic rate may not be satisfying, as animals need to perform and are active at ecosystem level such that the analysis falls short of providing complete ecosystem level implications. Nonetheless, for a principle
25 comparison of the responses of oxyconformers and oxyregulators to progressive hypoxia the concept of standard metabolic rate is relevant. According to a simple model the different patterns of conformity and regulation and associated metabolic transition phases can be analysed and some ecosystem level implications elaborated (Fig. 1).

    The concept of a critical PO_2 was introduced to characterize hypoxia sensitivity as

the oxygen tension below which an oxyregulating animal is no longer able to maintain its rate of oxygen consumption independent of the ambient oxygen tension and starts to exhibit a decreasing rate of oxygen uptake. This definition is not applicable to quantify hypoxia sensitivity in all animals including oxyconformers. Recent studies, which include an analysis of anaerobic processes at different oxygen tensions, demonstrate that this critical PO_2 is not only characterized by the transition from an oxygen independent to an oxygen dependent pattern of oxygen consumption, but also by the onset of an anaerobic energy metabolism. Thus the failure of oxyregulation as well as the onset of anaerobiosis coincide, the reason being insufficient capacity for oxygen uptake and transport via the blood (Pörtner and Grieshaber, 1993). This extended concept of the critical PO_2 (i.e. the ambient oxygen tension below which water oxygen concentration becomes limiting and anaerobic metabolism is needed to cover resting energy demand) becomes applicable in both oxyregulating and oxyconforming species. Combined analyses of changes in the overall rate of oxygen consumption, in oxygen transport via the body fluids, and in the transition from aerobic to anaerobic energy production are required to unequivocally establish the critical PO_2.

Anaerobic ATP production processes are located in the cytosol and within mitochondria leading to the formation of either lactate (opine) or succinate. These metabolites may, in most cases, be suitable cytosolic and mitochondrial markers of an anaerobic metabolism. However, muscular activity may lead to pyruvate and lactate or opine accumulation when mitochondria are still performing aerobically. This emphasizes the relevance of analyzing mitochondrial processes in quantifying hypoxia sensitivity. For example, long term incubation of oxyconforming *Sipunculus nudus* below the Pc demonstrated that succinate accumulation occurred before the opines were formed as glycolytic end products. Consequently, anaerobic glycolysis became involved in resting individuals of this species only when oxygen supply fell to an extent which no longer allowed (all of) the mitochondria to produce energy by aerobic means. This observation presents strong evidence that the animals exhibited their minimal aerobic metabolic rate at the critical PO_2. As a corollary, the metabolic rate at the Pc can be seen to

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represent the standard metabolic rate (SMR) of both oxyregulating and oxyconforming organisms. Furthermore, oxyregulators are able to maintain low metabolic rate (SMR) at PO_2-values higher than Pc (Pc_M in Fig. 1), whereas the oxygen consumption of "true" oxyconformers increases above Pc. These animals show a second critical PO_2 (Pc_R

5 in Fig. 1), above which the elevated rate of oxygen uptake finally remains constant.

Further observations characterize the Pc. On systemic and cellular levels, the transition from aerobic to anaerobic energy metabolism is either linked to the pronounced decrease or even increase in oxygen consumption, the latter as a result of a stimulatory response elicited by e.g. lactate accumulation (Pörtner at al., 1994; Pinz and

10 Pörtner, 2003). This again eliminates uncertainty in quantifying hypoxia sensitivity in oxyregulators. The critical oxygen tension is also characterized by the critical reduction of oxygen transfer via the blood or other body fluids. In those animals, which are able to tolerate long-term exposure to hypoxia, overall energy expenditure continues to fall below the critical PO_2. Furthermore, the Pc increases with organisational complex-

15 ity, from cellular organisms to complex organisms like animals because mechanisms causing additional limitations of oxygen provision become involved: (1) In a cell diffusion limitation of oxygen in the membrane and the cytoplasm together with the rate of mitochondrial respiration and, perhaps, the clustering of mitochondria in areas of high energy needs define the point at which the oxygen concentration finally becomes

20 limiting and anaerobiosis commences. (2) At tissue level capillary PO_2 (in animals with closed circulatory systems) or bulk venous PO_2 (in animals with an open circulatory system) are key parameters in determining whether oxygen provision is sufficient for the individual cell. The maintenance of the pressure head for sufficient oxygen supply depends upon the rate of perfusion, the density of the capillaries and on blood oxy-

25 gen transport. (3) For the whole organism the required pressure head, i.e. the Pc will also depend upon the structures and functions of the gas exchange organ and the circulatory system, and upon the O_2 affinity of the pigment and its regulation. These mechanisms alleviates the principle problem that body surface to volume ratios are low and unfavorable for oxygen diffusion at large body sizes.

A summary of the different patterns discussed for regulators and conformers leads to a simple model (see Fig. 1) where, generally, oxygen consumption at the Pc is equivalent to standard metabolic rate, even when considering that a potential increase in oxygen uptake below the Pc may occur as a response linked to the onset of anaerobic metabolism. SMR or Pc vary between species and their life stages as well as between individuals of the same species according to body size. SMR and Pc may even be variable in an individual animal according to its physiological state under the prevailing endogenous and exogenous conditions. For example, long term acclimatization to hypoxia may occur, such that the critical PO_2 and SMR may be lower for individuals of the same species exposed to hypoxia as compared to ones exposed to higher oxygen tensions. Once an animal displays a metabolic rate higher than SMR, the Pc of aerobic metabolism will rise and reach a high Pc_{max} at maximum metabolic rate (see Fig. 1).

From an integrative point of view these concepts of hypoxia sensitivity have become relevant in the context of thermal limitation and its role in understanding climate change effects on marine ecosystems. Temperature and hypoxia would traditionally be considered as different environmental factors, with specific implications for whole organism functioning. Studies of temperature-dependent oxygen supply, mode of metabolism and associated mechanisms of thermal adaptation in marine invertebrates and fishes across latitudes have suggested a role of oxygen supply in thermal limitation. Development of the concept of oxygen and capacity limited thermal tolerance in marine water breathers, however, has revealed how these factors are intertwined and become effective at the ecosystem level (Pörtner and Knust, 2007; Pörtner and Lannig, 2009). Thermal stress causes systemic hypoxemia at both ends of the thermal window. Temperature-dependent oxygen supply capacity sets the width of thermal window of an animal (Fig. 2). Thermally induced hypoxemia and associated stress and signaling mechanisms likely shape acclimation responses at various, molecular to whole organism levels (e.g. Kassahn et al., 2009). Thermal adaptation affects SMR and the cost of maintenance as well as energy budget of an organism.

The integration of the concepts of thermal and hypoxia sensitivity leads to new in-

sight and perspectives relevant for hypoxia tolerance (Fig. 2). These aspects require investigation in future research. The thermal optimum also reflects improved hypoxia tolerance. Close to upper pejus temperature the capacity of ventilatory and circulatory systems to provide oxygen to tissues is maximal and, accordingly, Pc_M results min-
5   imal. The positive balance between oxygen supply capacity and oxygen demand is maintained during cooling to lower pejus temperature. Cooling lowers the capacity for oxygen supply but also metabolic rate and provides elevated solubilities and levels of ambient oxygen. Hypoxemia setting in due to thermal limitation below both lower and upper Tp's causes a rise in Pc, thus indicating progressive reduction of hypoxia toler-
10 ance at the borders of the thermal window. At both critical temperatures, the Pc is maximal and becomes equivalent to ambient oxygen tensions (e.g. Zakhartsev et al., 2003). As a corollary, the species specific thermal window and the temperature sensitivity of Pc reflect the temperature dependence of hypoxia sensitivity and also the integration of thermal and hypoxia sensitivities. These relationships require consideration in analy-
15 ses of hypoxia resistance. Conversely, hypoxia and other stressors like carbon dioxide will affect thermal tolerance limits and also the processes involved in thermal acclimatization and adaptation, which counteract thermally induced hypoxemia and thereby also improve hypoxia tolerance. The specialization of whole organism functioning on limited temperature ranges emerges as a key element explaining current observations
20 of climate change effects on ecosystems. As a perspective, the operation of species and their sensitivity to environmental factors including hypoxia may in fact be best understood if analysed on a matrix of temperature dependent performance (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Pörtner et al., 2008, 2009).

3 Reaction of different taxonomic groups to hypoxic conditions in the pelagic system

3.1 Gelatinous plankton

Several taxonomic groups are subsumed as gelatinous plankton. Scyphozoa are the most dominant of these in the pelagic zone and represent the largest jellyfish. Hydromedusa, ctenophores and salps are other important members of this group.

Respiration rates of gelatinous zooplankton seem to be rather low. Rutherford and Thuesen (2005) found respiration rates of 0.18, 0.31, and 0.13 mmoles $O_2\,g^{-1}\,h^{-1}$ for the scyphomedusa *Aurelia labiata*, the hydromedusa *Aequorea victoria*, and the ctenophore *Pleurobrachia bachei*, respectively. These species were able to regulate oxygen consumption even below 10% saturation, which indicates that these species do very well in tolerating low oxygen conditions. Other species are not as hypoxia-tolerant. The authors found critical oxygen tension values P_c from 5.5 hPa ($\approx$3% saturation) in *Muggiaea atlantica* to 39.5 hPa ($\approx$19% saturation) in *Euphysa flammea*. They also tested the anoxia survival times and found values from <2 h for *E. flammea* and *Eutonina indicans* to >10 h for *A. victoria*.

The ctenophore *Mnemiopsis leidyi*, a species that originates from the east coast of the United States but has nowadays invaded the Black, Caspian, Mediterranean and Baltic Seas (in this sequence), shows a very sharp DO threshold (Keister et al., 2000). The species occurred at high densities at all DO>1.3–2 mg L^{-1}, but was nearly absent at <1 mg $O_2\,L^{-1}$.

The most obvious impact of hypoxia is that of reduced abundance or even disappearance of organisms because threshold values have been passed. However, other less visible impacts of hypoxia on physiological performance are also possible such as the impact on growth. In ctenophores, Grove and Breitburg (2005) found a significant reduction in growth at DO levels of 1.5 and 2.5 mg $O_2\,L^{-1}$, both in small (0.2 to 2.0 ml biovolume) and larger (8.0 to 17.6 ml biovolume) specimens. This phenomenon seems to occur especially at high prey densities. The same authors also found a significantly

reduced egg production in *Mnemiopsis leidyi* when exposed to low DO. Growth rates in *Chrysaora quinquecirrha* were comparable in low DO and normic conditions.

Gelatinous plankton is known as predator on fish larvae and other zooplankton and, at the same time, it competes with fish and fish larvae for zooplankton prey (Purcell and Sturdevant, 2001; Breitburg, 1994, 1997). It is argued that because of their higher tolerance against low oxygen (than e.g. finfish; Grove and Breitburg, 2005), they are predestined to take a dominant role in ecosystems with declining oxygen conditions. Especially ctenophores seem to have a high predation pressure on copepods (Purcell and Decker, 2005). Shoji et al. (2005) found doubling of ingestion rates of fish larvae by moon jellyfish (*Aurelia aurita*) with decreasing DO from 4 to $1\,\mathrm{mg\,O_2\,L^{-1}}$. A reason for that is argued to be the reduced ability of many prey organisms to escape under hypoxic conditions (Kodama et al., 2006; Dutil et al., 2007).

3.2 Crustacea

Crustacea belong to the most species-rich and diverse invertebrate taxa in the sea. The economically important species of decapods including lobsters, rock lobsters, shrimps, prawns and crabs usually have planktonic larval stages. Moreover, copepods and euphausiids dominate mesozooplankton communities in terms of abundance and biomass throughout the world ocean. They are of prime importance as trophic link from marine primary production to higher trophic levels, including fish. The following section focuses on potential effects of hypoxia on crustaceans in the marine pelagic environment.

3.2.1 Changes in spatial distribution

Oxygen minimum zones (OMZ) in the marine ecosystem have an important impact on the vertical distribution and migratory patterns of pelagic organisms (Saltzman and Wishner, 1997). Some species are virtually excluded from the OMZ, others are able to stay or cross it (Longhurst, 1967; Herring et al., 1998; Gonzalez and Quiñones,

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2002). Most zooplankton taxa show minimum abundances in the core of the OMZ, with higher abundances at the lower OMZ interface (Sameoto, 1986; Wishner et al., 1995; Böttger-Schnack, 1996; Saltzman and Wishner, 1997). A local maximum in zooplankton abundance or biomass at the lower OMZ interface seems to be a unique
5 feature of OMZ regions. Different, species-specific tolerances to hypoxic conditions influence zooplankton community composition in areas affected by OMZs (Saltzman and Wishner, 1997). In the Arabian Sea and in the California Current, zooplankton abundance and biomass decrease sharply, when the oxygen concentration falls below $0.2\,\mathrm{ml\,O_2\,L^{-1}}$ (Longhurst, 1967; Böttger-Schnack, 1996; Saltzman and Wishner, 1997).
10 Especially, deep-water oceanic species avoid the OMZ, while only a few species of copepods and euphausiids regularly occur within the OMZ. Often individuals found in the core of the OMZ are dormant stages of species with ontogenetic or diel vertical migrations (Longhurst, 1967).

Similarly, the abundance of calanoid copepods and the biomass of mesozooplank-
15 ton in general are severely reduced within the OMZ of the northern Benguela Current (Verheye et al., 2005; Auel and Verheye, 2007). The dominant copepod *Calanoides carinatus* shows a bimodal vertical distribution with parts of the population either concentrated in the surface layer (0–60 m), or copepodids C5 diapausing below 400 m depth apparently avoiding the OMZ in between (Auel et al., 2005; Verheye et al., 2005;
20 Auel and Verheye, 2007). Accordingly, abundances of other calanoid copepods are higher at the surface and below 300 m than in the centre of the OMZ.

Most euphausiids and some copepods avoid the core of the OMZ with less than $0.1\,\mathrm{ml\,O_2\,L^{-1}}$ (Sameoto, 1986; Sameoto et al., 1987; Saltzman and Wishner, 1997). Increasing abundances of copepods and euphausiids below the OMZ indicate that the
25 OMZ acts as a barrier for some species, although specifically adapted species regularly migrate through the OMZ (Saltzman and Wishner, 1997; Auel and Verheye, 2007, for *Euphausia mucronata* in the Humboldt Current see Escribano, 2006).

Among the specialists that regularly inhabit the OMZ is *Rhincalanus nasutus* (Castro et al. 1993; Sameoto, 1986) and non-calanoid copepods of the genus *Oncaea* (Böttger-

Schnack, 1996). In the Benguela Current, the group of hypoxia-tolerant copepods that inhabit the OMZ includes *Pleuromamma robusta*, *Heterorhabdus* sp., *Aetideopsis carinata* and again *Rhincalanus nasutus* (Auel and Verheye, 2007). Their adaptation to life at hypoxic conditions apparently allows them to seek refuge from competition and risk of predation by the majority of less tolerant copepods, other zooplankton and pelagic fish.

In the coastal upwelling system of the Humboldt Current off Chile, key copepod and euphausiid species are affected in their vertical distribution and migrating behaviour by the extent of the OMZ between 60 and 200 m depth. Several abundant species appear to be constrained by the OMZ and restricted to the upper 50 m layer, whereas others temporarily or permanently inhabit the OMZ and substantially contribute to the vertical flux of organic carbon from the euphotic zone through active vertical migration (Escribano, 2006). Among the few species permanently living in the OMZ and performing diel vertical migrations only within the OMZ are the copepods *Eucalanus attenuatus* and *Eucalanus inermis* as well as the euphausiids *Euphausia distinguenda*, *Stylocheiron affinis* and *Nematoscelis megalops*. Four more euphausiid species, i.e. *Euphausia mucronata*, *Euphausia eximia*, *Euphausia recurva*, and *Euphausia tenera*, perform extended diel vertical migrations, feeding at night in the upper OMZ (60–100 m) and descending below the OMZ during daytime. In contrast, the copepods *Pleuromamma gracilis* and *Euchaeta* spp. spend the night time below the OMZ and migrate upwards into the OMZ during daytime, thus conducting a kind of inverse diel vertical migration (Escribano, 2006).

Because of their abundance, biomass and vertical migration behaviour, the large-sized copepod *Eucalanus inermis* and the krill species *Euphausia mucronata* are especially important for the transport of organic carbon from the euphotic zone into the OMZ. There is a substantial daily exchange of >75% of total zooplankton biomass between the euphotic layer and the OMZ. *Eucalanus inermis* can actively exchange more than 10 mg C m^{-3} between the base of the thermocline (30–60 m) and the deeper OMZ layer (60–200 m), whereas *Euphausia mucronata* contributes nearly 1 g C m^{-3} to

the daily exchange from the upper 200 m to deeper layers (Escribano, 2006). The migration of zooplankton in and out of the OMZ could be a very efficient mechanism to incorporate freshly produced organic matter into the OMZ. Vertical migrations, population dynamics, life-cycle strategies and metabolic adaptations of key zooplankton species may contribute to the maintenance and persistence of the oxygen-depleted water mass (Escribano, 2006).

Increasingly hypoxic conditions and the expansion of the OMZ could lead to cascading effects on benthic and pelagic ecosystems, including habitat compression and community reorganization (Bograd et al., 2008). Mesopelagic organisms such as crustaceans and myctophid fishes that live in the upper boundary region of the OMZ or perform diel vertical migrations to feed in the surface layer at night may be affected (Childress and Seibel, 1998) with impacts on their epipelagic prey species.

Potential ecological effects of hypoxia include habitat loss and increased mortality (O'Connor and Whitall, 2007). In the northern Gulf of Mexico, the spatial extent of hypoxic areas is significantly negatively correlated with the fisheries' landings of brown shrimp *Farfantepenaeus aztecus* in the period of 1985 to 2004 (Zimmerman and Nance, 2001; Craig et al., 2005; O'Connor and Whitall, 2007).

The threshold level of dissolved oxygen concentration for the survival of juvenile mantis shrimp *Oratosquilla oratoria* was $2.78\,\mathrm{ml\,O_2\,L^{-1}}$, implying that hypoxia restricted the spatial distribution of juveniles and determined the seasonal colonisation of the species in Tokyo Bay (Kodama et al., 2006).

3.2.2 Physiological effects

The ability of certain zooplankton species to cross or even live in oxygen minimum zones is apparently linked to the presence and activity of enzymes of the anaerobic metabolism. The analysis of enzymatic activity of bulk zooplankton and of some dominant species revealed strong activity of both aerobic (ETS) and anaerobic (LDH) metabolic components within the OMZ (Escribano, 2006). In a comparative study on the specific lactic dehydrogenase (LDH) activity in *Euphausia mucronata* and *Calanus*

chilensis from the Humboldt Current upwelling system, the specific LDH activity in *E. mucronata* was two orders of magnitude higher than that of *C. chilensis*, consistent with *E. mucronata*'s ability to conduct daily vertical migrations through the oxygen minimum layer, whereas *C. chilensis* is restricted to oxygenated waters above the OMZ
₅ (Gonzalez and Quiñones, 2002). In *E. mucronata*, body size was positively correlated with the specific LDH activity.

Benthic crustaceans, which are regularly subject to hypoxic and anoxic conditions, such as the isopod *Saduria entomon* in deep basins of the Baltic Sea, are very tolerant to reduced levels of dissolved oxygen. A reduction in oxygen saturation to 15% did
₁₀ not show any significant effect on osmotic regulation, while anoxic conditions (oxygen saturation <1%) decreased the osmotic concentration of haemolymph in *S. entomon* only in conjunction with strongly reduced salinities and over extended exposure times (4 days; Dobrzycka-Krahel and Szaniawska, 2007).

In Atlantic blue crab, *Callinectes sapidus*, which inhabits coastal and estuarine envi-
₁₅ ronments, where it often encounters hypoxia, combinations of hypoxic conditions and hypercapnia (increased carbon dioxide) severely reduced the hemocyte phenoloxidase activity, an enzyme critical to antibacterial immune defence in crustaceans, implying that hypercapnic hypoxia compromises the ability of crustaceans to defend themselves against microbial pathogens (Tanner et al., 2006). Juvenile blue crabs *Callinectes*
₂₀ spp. showed significant decreases in feeding, growth, and moulting rates when exposed to prolonged episodes of hypoxia (10 to 28 days; Das and Stickle, 1993, 1994).

Freshwater crayfish of the three European native species *Austropotamobius pallipes*, *A. italicus* and *A. torrentium* demonstrated a disruption in the ion exchange process under hypoxia, but all tolerated very low oxygen concentrations for extended periods of
₂₅ time (Demers et al., 2006). Through physiological effects, hypoxia strongly enhances the rate of cadmium accumulation in gills and hepatopancreas of decapod shrimps, in particular when heavy metal concentrations are low (Pierron et al., 2007). The main mechanism of interaction between hypoxia and heavy metal contamination is related to chemical speciation.

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Individuals of the marine cladoceran *Moina micrura* not acclimated to oxygen deficiency showed a severely reduced scope of activity (62.5-fold reduction over the range of 10 to $0.3\,mg\,O_2\,L^{-1}$), when subjected to hypoxic conditions (Svetlichny and Hubareva, 2002). They stopped filtration and increased the time spent for swimming at concentrations of 0.7–$0.8\,mg\,O_2\,L^{-1}$. However, individuals that had been acclimated to hypoxic conditions via the accumulation of haemoglobin were less affected. They showed no response at this oxygen concentration and survived apparently unharmed at levels as low as $0.2\,mg\,O_2\,L^{-1}$, maintaining their filtering activity (Svetlichny and Hubareva, 2002). In the freshwater cladoceran *Daphnia magna*, hypoxia can disrupt the juvenoid hormone-mediated endocrine signalling (Gorr et al., 2006).

3.2.3 Reproduction

Studies on the effects of hypoxia on crustacean reproduction have focused on the egg production, hatching success and viability of copepods. Short exposure to near anoxia (1.78 to $3.56\,\mu mol\,O_2\,L^{-1}$) or a combination of anoxia with increased sulfide concentrations ($\sim 1\,mmol\,L^{-1}$) induced quiescence in the eggs of the planktonic copepod *Acartia tonsa*, but did not affect egg viability and subsequent growth and survival after restoration of normoxic conditions (Invidia et al., 2004). However, exposure times ≥ 15 days caused significant declines in hatching and strong reductions in life expectancy. In another study, eggs of *A. tonsa* stopped hatching at oxygen concentrations lower than $3.12\,\mu mol\,O_2\,L^{-1}$, but were not killed since they resumed hatching when transferred to normoxic seawater (Lutz et al., 1994). Experimental results obtained by various authors (Lutz et al., 1992, 1994; Roman et al., 1993; Marcus and Lutz, 1994; Marcus et al., 1997; Invidia et al., 2004) differ slightly in regard to the concentration of oxygen that induces quiescence and the maximum survival times for eggs exposed to hypoxic concentrations. In general, maximum survival time of *A. tonsa* eggs under anoxic conditions ranged from 20 to >32 days, related to variations in the developmental stages of the eggs and differences in the genetic and/or environmental histories of the females producing the eggs (Marcus and Lutz, 1994; Marcus et al., 1997; Invidia et al., 2004).

In *Acartia bifilosa*, a dominant copepod species in the Baltic Sea, low oxygen concentrations $<0.17\,\mathrm{ml\,O_2\,L^{-1}}$ induced dormancy in the eggs. Hatching was prevented by anoxic conditions, but subitaneous eggs survived well under these conditions for 10 to 12 months depending on the temperature. After 10 months of anoxia at 4°C, approximately 40% of the eggs still hatched, when brought back to normoxic conditions (Katajisto, 2004).

Since copepod recruitment from benthic eggs is prevented during anoxic events, the duration, area, and timing of anoxic events, as well as the species-specific tolerance of the eggs to low oxygen concentrations, will affect copepod population dynamics and zooplankton community composition in general (Roman et al., 1993; Katajisto, 2004). In contrast, temporarily anoxic conditions might even protect benthic eggs and resting stages from predation (McQuoid et al., 2002; Katajisto, 2004).

Besides hatching success and viability, egg production rate can also be affected by hypoxic conditions. At reduced dissolved oxygen concentrations of $1.5\,\mathrm{ml\,O_2\,L^{-1}}$, egg production of *A. tonsa*, but not survival, was significantly reduced as compared to normoxic controls (Marcus et al., 2004). At $0.7\,\mathrm{ml\,O_2\,L^{-1}}$, both adult survival and egg production were significantly reduced. These results suggest that, besides direct lethal effects of hypoxia, sub-lethal responses such as reduced egg production can have important repercussions on population and community dynamics of marine copepods and food webs (Marcus et al., 2004).

3.2.4 Ecological effects

Hypoxia can lead to a decoupling of predator-prey interactions and, thus, change trophic fluxes through food webs (Taylor and Rand, 2003). In a study on anchovies and copepods, hypoxia caused a spatial separation between plankton and planktivorous fishes. Since pelagic fish are more susceptible to hypoxic conditions than copepods, the spatial extent of the suitable habitat for fish was reduced during hypoxic events, while zooplankton may find refuges from predation. Thus, hypoxic conditions can reduce the predation risk of zooplankton by pelagic fish (Taylor and Rand, 2003).

Conversely hypoxic conditions can induce increased rates of predator-prey interaction (Kodama et al., 2006). Because some gelatinous species such as the ctenophore *Mnemiopsis leidyi* are more tolerant of low dissolved oxygen concentrations than their prey and competitors, hypoxia may have profound effects on trophic interactions (Decker et al., 2004). Under experimental conditions, clearance rates of zooplankton by large ctenophores were higher at low dissolved oxygen concentrations than under normoxic conditions. Ctenophore digestion rates seemed to be unaffected by hypoxic conditions of $1 \, \text{mg} \, O_2 \, L^{-1}$. In contrast, the jumping frequency of *A. tonsa* copepods decreased significantly with decreasing oxygen concentration (Decker et al., 2004). Such changes in prey behaviour under hypoxic conditions could affect encounter and capture rates, potentially making less-tolerant prey more vulnerable to predation in hypoxic waters. Since gelatinous species are more tolerant of hypoxia than fishes, they may be able to inhabit regions of low oxygen that are avoided by zooplanktivorous fishes with high oxygen requirements. This could lead to a dominance of gelatinous predators in areas affected by severe hypoxia and might alter trophic pathways in these systems (Decker et al., 2004).

3.3 Molluscs/squid

Information on oxygen requirements or hypoxia tolerance of pelagic molluscs is scattered. A reason maybe that these animals occur more in open waters and are not as amenable to experiments as other species. On the other hand we observe the increasing abundance of some squid species in the world ocean. Catches of squid have tripled during the last 30 years (FAO 2009) suggesting also an increasing role in the pelagic foodwebs of neritic and oceanic ecosystems.

Squid seems to be more tolerant against low oxygen than many other pelagic organisms, even if their energy requirements are higher due to their burst swimming method than in other organisms such as fish (Pörtner and Zielinski, 1998). Their oxygen consumption rises during exercise to fivefold above resting uptake (Hoeger et al., 1987). They are frequently found in the Oxygen Minimum Zones (OMZ), where they

can remain for long periods during the day (Gilly et al., 2006) floating around without movement and waiting for prey.

A critical oxygen partial pressure for squid seems to be 19% saturation (citation 29–30 mm Hg) (Hunt and Seibel, 2000). Howell and Simpson (1994) found reduced catches below a threshold value of $2.1 \, \text{ml} \, O_2 \, L^{-1}$ and Roberts and Sauer (1994) suggested $3 \, \text{ml} \, O_2 \, L^{-1}$ to be the threshold for squid to avoid low oxygen areas. However, this sensitivity is size-related showing a higher oxygen consumption rate and steeper decline at low DO for juveniles than for sub-adults. A significant reaction of the organism is observed at 25% saturation (40 mm Hg), but a dramatic decline in respiration is found only below 12% saturation (20 mm Hg). This is close to the tolerance values Zielinski et al. (2000) found for *Lolliguncula brevis*. As a measure of the vulnerability to hypoxia, the onset of anaerobic metabolism was investigated, which was detected at 49 and 41% saturation (9.4 to 7.9 kPa). The absolute DO limit for the species was identified at 13.2% saturation (2.8 kPa). Seibel et al. (1997) found even lower critical values of down to 2–12% saturation (3–19 mm Hg) for different species.

Direct field observations show the sensitivity of some squid against low oxygen. Rabalais et al. (2001) found squid in Remotely Operated Vehicle records only where DO was above $2 \, \text{mg} \, O_2 \, L^{-1}$, and Roberts (2005) showed that Chokka squid (*Loligo vulgaris*) selects its spawning ground on the eastern Agulhas Bank where temperature and oxygen are optimum for the embryonic stages with ranges of temperature between 11 and 20°C and oxygen above $3 \, \text{ml} \, O_2 \, L^{-1}$. Young stages seem to be more vulnerable to hypoxic conditions as shown by Hunt and Seibel (2000) who found juvenile squid *Gonatus onyx* at shallower depths with DO around $1 \, \text{ml} \, O_2 \, L^{-1}$ while the adults go deeper into the OMZ with DO less than $0.5 \, \text{ml} \, O_2 \, L^{-1}$.

It has been argued by different authors that the decline in oxygen concentration in the Eastern Pacific has induced an extension of the distribution range of the jumbo squid (*Dosidicus gigas*). Landing of the species has increased tremendously (Morales-Bojorquez et al., 2001; Field, 2008) and supports a large fishery. Vetter et al. (2008) assume that the shoaling of the OMZ could provide refuge from highly mobile predators

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such as mako sharks and thus support an increase of squid biomass. Squid, especially jumbo squid, has an enormous growth potential (Mejía-Rebollo et al., 2008) supporting a fast expansion of its distribution area. The extending OMZ may provide an increasing refuge space for hypoxia-tolerant meso-pelagic fish species and support this rapid biomass increase in jumbo squid off Chile and California (Field et al., 2007; Field, 2008). Argüelles et al. (2008) also argue that such increased food availability leads to a larger size-at-maturity in *D. gigas* and thus enhances the reproductive potential.

3.4 Fish

It is well known in fish biology, that low oxygen concentrations in the water have physiological impacts on the organisms, and these effects have been used e.g. in aquaculture to optimise the artificial production processes of these animals. Hypoxia is a highly effective inducer of hatching in mature Atlantic salmon eggs when applied less than 1 month prior to normal hatching (Oppen-Berntsen et al., 1990). This kind of stimulus is frequently used in aquaculture to synchronise hatching of larvae. We also know, that fish need well aerated water to remain healthy and use food efficiently for optimal growth. However, intensive aquaculture conditions are extreme and fish do not have any possibility to escape. Behaviour and reaction to low oxygen in the natural environment will be different. Kramer (1987) stated four principal categories of behavioural response to reduced dissolved oxygen in the environment: (1) changes in activity, (2) increased use of air breathing, (3) increased use of aquatic surface respiration, and (4) vertical or horizontal habitat changes. Not all of these categories are suitable for marine fish, responses 2 and 3 are more frequently observed in fresh water fishes. However change in activity such as swimming speed and growth and avoidance of low oxygen condition by changing the habitat have been found in the marine environment quite frequently. The following paragraphs concentrate on coastal and offshore waters even if some results are retrieved from freshwater species for comparative reasons.

3.4.1 Physiological effects

The general physiological processes resulting from varying dissolved oxygen concentration (DO) in the environment have been discussed in an earlier section of this paper. Here we give some additional examples on physiological constraints fish species may suffer from low DO.

Following Berschik et al. (1987), oxygen consumption represents the sum of different processes taking place in an organism. A decline below a certain threshold value is compensated by hyperventilation, but also results in a reduction in growth rate, as shown in demersal fish such as turbot (*Scophthalmus maximus*) or sea bass (*Dicentrarchus labrax*). These fish cope with low-oxygen conditions by reducing one of their physiological activities, growth. The underlying mechanism is likely to be a reduction in food intake (Boeuf et al., 1999; Pichavant et al., 2001). A decrease in ingestion may reduce the energy demands and therefore the oxygen requirements. Oxygen uptake in larval *Anchoa mitchilli*, *Archosargus rhomoidalis* and *Achirus lineatus* was directly related to their weight (Houde and Schekter, 1983).

King (1977) found a relationship between survival of *Sardinops sagax* larvae and DO combined with temperature. However, this correlation, albeit evident only if combined with temperature, was weak. This may be attributed to the limited number of experimental designs using only oxygen concentrations of 1.5, 3.5 and $5.2\,\mathrm{ml\,O_2\,L^{-1}}$. As a consequence, the critical range in oxygen concentration, found to be below 1.5–$2\,\mathrm{ml\,O_2\,L^{-1}}$ in other experiments (e.g. Keister et al., 2000; Miller et al., 2002) was covered only marginally by his experiments.

From other experiments it is known that *S. sagax* shows a low Q_{10} value indicative of a high eurythermy (van der Lingen, 1995). Lowest non-feeding swimming respiration rate of the species was $0.138\,\mathrm{mg\,O_2\,g^{-1}}$ wet wt $\mathrm{h^{-1}}$ which is ca. 50% more compared to other fish species (Brett and Groves, 1979). Filter feeding was found to be energetically cheaper than particulate feeding, which leads to the assumption that at a decreasing food concentration fish may have to switch from filter to particulate feeding and hence

increase their oxygen consumption to catch the same amount of food.

Physiological experiments examining responses to low oxygen concentration have primarily been conducted on adult fish. A direct influence of anoxic water conditions on the physiology has been observed in electric eels (Crampton, 1998). Field obser-vations showed that the fish avoid crossing areas with low oxygen concentrations of 2.1–2.8 ml O_2 L^{-1}. In many fish species, hypoxia leads to an increased ventilation fre-quency indicating a negative effect on their physiology (Powell and Perry, 1997). Plante et al. (1998) investigated the tolerance to hypoxia of adult Atlantic cod and found an LC_{50} at 21% saturation and no survival at 10%. Carp, normally a fish that is adapted to low environmental oxygen concentrations, showed a decrease of its critical DO (nor-mally 120 μM; ca. 2.7 ml O_2 L^{-1}) when exposed to higher salinities in brackish waters (De Boeck et al., 2000). Cichlids reared under normal oxygen conditions had higher metabolic rates than those reared under hypoxic conditions (Chapman et al., 2002). Kunzmann (personal communication) performed oxygen uptake and tolerance experi-ments with young horse mackerel. The species was able to survive to 10% DO satura-tion over a period of several hours and recovered within 2 h to repeat the exercises.

3.4.2 Reproduction and early life stages

Respiration and physiological processes in fish embryos are largely dependent on the overall external environment during incubation time. In general oxygen effects are difficult to separate from those of temperature, salinity or water flow. Considerable work has been done on combined impacts of temperature and low oxygen on early life-stages of commercially important freshwater species such as rainbow trout. Depeche and Billard (1994) in their review on the embryology in fish state that "Eggs are usually laid in an environment where oxygen is available". However some recent works have shown that in some ecosystems fish may have increasing problems to find enough oxygenated waters for their eggs to develop properly (Messieh and Rosenthal, 1989; Ekau and Verheye, 2005; Kreiner et al., 2009).

Studies focussing on the effect of hypoxia on the development of fish embryos found

low oxygen to cause early hatching in cultured coregonid fish (Czerkies et al., 2001), as it triggers the release of hatching enzyme in late-stage-egg embryos. Experiments on Atlantic salmon by Oppen-Berntsen et al. (1990) revealed a hatching of all eggs within a two hour time span instead of up to one week, when exposed to a partial

5 oxygen pressure of 5 mm Hg ($\approx$3% saturation). This procedure has to be applied carefully not to damage the embryos. The opposite can be achieved when maintaining the eggs under high oxygen pressure. Hatching is then delayed indefinitely (Hagenmaier, 1972). Other workers (Braum, 1973; Shang and Wu, 2004) have shown that under prolonged sub-lethal hypoxia conditions herring embryos are weakened and were neg-

10 atively impacted in their development leading to significantly increased malformation. The hatching length of the embryos decreased from 8.4 mm at 100% saturation to 6.1 mm at <50% (Braum, 1973). Weaker larvae would reduce the survival chance for the year classes. Widmer et al. (2006) found significantly reduced swimming abilities in zebrafish reared under hypoxic conditions and MacGregor and Houde (1996) found

15 that most anchovy eggs and larvae in the main stem of mid-Chesapeake Bay (>20 m water depth) were above the pycnocline when below-pycnocline DO was <2 mg O_2 L^{-1}. When Thomas et al. (2006) analysed the impact of low DO on Atlantic croaker (*Micropogonias undulatus*) they found a significant impairment of ovarian growth and a decrease in the production of fully grown oocytes.

20 The oxygen demand is changing significantly during ontogenesis. Pfeiler (2001) observed an increase in the sensitivity to hypoxia during the 10 day metamorphic period of leptocephalus larvae in the bonefish *Albula* sp. The metamorphosis is a physiologically highly intense period in the early development of a fish which requests a lot of oxygen. The larvae do not feed during that time but use their own reserves of lipids

25 and carbohydrates, yet oxygen demand is twice as high as normal and makes larvae vulnerable to hypoxic conditions.

Metamorphisis, the transition from a larva to a juvenile fish, is in general a critical period in the life cycle of fishes. This is the time where flat fishes change to bottom mode of life and where coral reef fishes select their future home reef and settle in their new

habitat. Several coral fish genera (*Gobiodon*, *Paragobiodon* and *Caracanthus*) show as adults a well developed hypoxia tolerance down to 3% air saturation to overcome low oxygen during night in their micro-habitats or they switch to air-breathing at low tides (Nilsson et al., 2007a). During their larval phase, especially during the pre-settlement phase, coral fish species such as the damselfishes *Chromis atripectoralis* and *Pomacentrus amboinensis* show extremely high rates of oxygen uptake and very low hypoxia tolerance (Nilsson et al., 2007b). Obviously these species change their physiological pathways during the transition time to adapt from a planktonic mode of life in an oxygen saturated environment to demersal mode of life under at least temporarily hypoxic conditions.

Not all species are able to change their metabolism in such a dramatic way. Ikejima et al. (1999) clearly found a correlation between the number of newly settled dragonet juveniles and the occurrence of summer hypoxia in Tokyo Bay. The unsuitable hypoxic habitat leads to the complete loss of the autumn spawning peak.

3.4.3 Vertical distribution and migration

Most obvious is the impact on the vertical and/or horizontal distribution pattern. Fish larvae and copepod nauplii (the staple food for larvae) abundances were lower throughout the water column when bottom-layer DO was $\leq 2\,\mathrm{mg\,O_2\,L^{-1}}$. Keister et al. (2000). Densities of naked goby larvae were less than one-third of those observed at $>2\,\mathrm{mg\,O_2\,L^{-1}}$ while density of copepod nauplii declined by >50%. Depth-distributions of several organisms also were affected by bottom-oxygen depletion to $\leq 2\,\mathrm{mg\,O_2\,L^{-1}}$: fish larvae, scyphomedusae, and copepods were much less common near the bottom with low DO. However, the ctenophore *Mnemiopsis leidyi* occurred in high densities at DO as low as $1.3\,\mathrm{mg\,O_2\,L^{-1}}$, and was nearly absent only at <1 mg/L. These results indicate the potential for substantial differences in organism interactions, especially predator-prey relationships, between times of high and low bottom-layer DO (Breitburg, 1994; Breitburg et al., 1994, 1997, 1999). While the vertical distribution of juvenile bay anchovies (*Anchoa* spp.) was generally restricted to the upper water layer

with $>2.5\,\mathrm{mg\,O_2\,L^{-1}}$ some specimens entered waters with DO down to $1\,\mathrm{mg\,O_2\,L^{-1}}$ (Tayler et al., 2007). These "outliers" were obviously looking for food in these near bottom water layers.

In Baltic cod the vertical distribution of eggs and larvae is highly correlated with the hydrographic situation in the water column. The suitable habitat for the early stages is constrained by the low salinity in the top layer and low oxygen in the bottom layers. Grønkjaer and Wieland (1997) in their investigations on Baltic cod larvae could not find larvae in layers deeper than 75 m. Oxygen below this depth drops rapidly to $<2\,\mathrm{ml\,O_2\,L^{-1}}$ (Nissing, 1994), and the authors argued that oxygen limits the depth distribution of these larvae. Buoyancy of the eggs is predetermined in the ovary of the mother fish by their lipid and water content, but after fertilisation with changing permeability of the chorion gravity of the egg may also change (Nissling and Vallin, 1994) and thus influence egg vertical distribution. The same authors found differences in the gravity of cod larvae depending on salinity and development stage. How these variations can be used by the species to reach better oxygen conditions is unclear.

Ekau and Verheye (2005) worked in open shelf waters on the vertical distribution of fish eggs and larvae and the relationship between their abundance and oxygen concentration. Results indicated that low oxygen in waters deeper than 40 to 60 m may significantly impact the vertical distribution of the species. At a threshold value of about 2.5 to $3\,\mathrm{ml\,O_2\,L^{-1}}$ larval abundance dropped sharply and their distribution was significantly more dependent on DO than on temperature or depth. Larvae are at the life-cycle stage known to be the most sensitve to low DO levels. Concentrations of 0.4 to $1.3\,\mathrm{ml\,O_2\,L^{-1}}$ to cause a 50% loss of larvae and juvenile fish, depending on the species and its lifestyle, with pelagic species being more sensitive than demersal ones (Miller et al., 2002). Survival time decreased about threefold over the metamorphic period in an *Albula* species with a leptocephalus larva (Pfeiler, 2001).

In the Northern Taiwan Strait the distribution of copepods as well as of fish larvae could be linked to hydrographical characteristics and a positive correlation between abundance and DO and temperature was found (Hsieh and Chiu, 2002). Unfortunately

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threshold values limiting the plankton distributions along DO gradients were not provided. Juvenile weakfish (*Cynoscion regalis*) followed the diel-cycling of low oxygen fronts in an estuary by avoiding areas of DO$<2\,\mathrm{mg\,O_2\,L^{-1}}$ (Tyler et al., 2007).

The critical saturation increases with temperature. In cod, the threshold moved from 16.5% at 5$°$C to 30% at 15$°$C (Schurmann and Steffensen, 1997), D'Amours (1993) found $3.4\,\mathrm{mg\,O_2\,L^{-1}}$ as a threshold value for adult cod at temperatures above 4$°$C. Thus not only the absolute oxygen concentration, but also temperature and salinity, and thus depth, will determine the distributional limits of the fish. 70% oxygen saturation seems to be a threshold above which substantially higher abundances of cod are encountered (Chabot and Claireaux, 2008). A special role is played by the thermocline where both temperature and oxygen saturation may drop considerably with depth. Fish larvae aggregate in such thermocline layers (Gray and Kingsford, 2003).

In the Northern Benguela upwelling system the temperature below the thermocline decreases rapidly to less than 15–17$°$C coinciding with a drop in oxygen to only 0.5–$1.5\,\mathrm{ml\,O_2\,L^{-1}}$ equivalent to oxygen saturation levels of 9–27% (Ekau and Verheye, 2005) This situation was encountered at a water depth mostly around 40–50 m resulting into a separation of a surface layer that was fairly populated with fish larvae and a poorly populated deeper layer at water depth $\geq$40 m. Especially sardine and anchovy larvae strongly preferred the upper 40 m (Kreiner et al., 2009).

3.4.4 Growth

Growth in fish is a physiological process that is closely related and strongly influenced by temperature, food availability and developmental stage. All physiological processes consume oxygen and thus the organisms are depending on oxygen supply from the surrounding environment, too. Hence decreased oxygen concentration in the water will lead to constraints in growth, movement and basic metabolism.

A correlation between growth performance and oxygen has been shown by different authors (e.g. Carlson et al., 1980; Brett and Blackwell, 1981; Chabot and Dutil, 1999; Braun et al., 2006). The growth rates in American Winter flounder (*Pseudo-*

pleuronectes americanus) kept in hypoxic waters reached less than 50% of those for specimens kept under normoxic conditions (Bejda et al., 1992). Boeuf et al. (1999) found a 20% reduction in growth of turbot under moderate hypoxic conditions, and Chabot and Claireaux (2008) have confirmed this threshold in laboratory studies and demonstrated that growth and food ingestion were significantly reduced below 70% saturation.

There is a significant impact of low oxygen on the reproduction and growth of the Gulf killifish (*Fundulus grandis*) (Landry et al., 2007). The authors explained this impact with the reduction of overall energy expenditure and an alteration of specific hormonal pathways that mediate the gamete production. They found the sex steroid hormone E2 being 50% reduced in females exposed to low oxygen, a consequence of this being ≈30% smaller gonads. The daily egg production dropped to about 26% of that in normoxic conditions!

Pichavant et al. (2001) compared the growh of European sea bass under hypoxic conditions but fed to satiation with another group of specimens reared in normoxic conditions but with restricted rations. They found no significant differences in growth and explained that the decrease in food uptake would be an indirect mechanism to save energy in a hypoxic environment and reduced growth thus would be an indirect effect, too. Feeding experiments by Jordan et al. (2007) showed that cod fed with 2.5 and 5% food rate under normoxic conditions used 40 and 55% of their oxygen uptake for specific dynamic action, while they used 69% under hypoxic conditions leaving much less oxygen for other metabolic activities. Similar results were found by Bejda et al. (1987) for red hake *Urophycis chuss*, where especially younger stages increased their swimming activity to escape low oxygen waters and all stages reduced food search activities with decreasing oxygen content.

3.4.5 Swimming behaviour and low oxygen avoidance

Besides physiological reaction to low DO, larval and adult fish have developed a number of adaptation mechanisms to cope with low oxygen conditions when they cannot

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escape. Freshly hatched trout larvae, for example, decrease their number of movements by 60% when exposed to hypoxia to reduce their oxygen consumption and total metabolism (Ciuhandu et al., 2007). Similar decreases in activity have been reported in other fishes. When exposed to anoxia, adult crucian carp (*Carassius carassius*) reduced activity by 50% relative to that in normoxia, and the distance travelled per minute was reduced by 75% (Nilsson et al., 1993). Juvenile white sturgeon (*Acipenser transmontanus*) decreased their activity by 70% when exposed to moderate hypoxia (Crocker and Cech, 1997). In adult carp, the decrease in activity was similar, with a gradual decrease, and a plateau was reached after 90–120 min of exposure to anoxia (Nilsson et al., 1993). Restricted mobility during hypoxia is probably a strategy to reduce oxygen demands and focus on vital functions rather than on locomotive activity. Some studies have reported an increase in activity with moderate hypoxia e.g. for sand goby *Pomatoschistus minutus* (Petersen and Petersen, 1990) or adult brook trout *Salvelinus fontinalis* (Tang and Boisclair, 1995), but these responses are rather interpreted as escape responses (Petersen and Petersen, 1990).

Various investigations from different areas in the world have shown that low DO levels have a severe impact on the composition and abundance of adult and larval fish fauna. Westernhagen and Dethlefsen (1983) and Dethlefsen and Westernhagen (1983) reported on dramatically low fish catches following a low-oxygen ($1.2–1.5\,\mathrm{ml\,O_2\,L^{-1}}$) water intrusion in the North Sea. A distinct stratification extended over several thousand square kilometres, inhibiting the aeration of deeper waters from the oxygenated surface waters. Fish catches were reduced to only $2–10\,\mathrm{kg\,h^{-1}}$ compared to $720–900\,\mathrm{kg\,h^{-1}}$ at a location with normoxic water ($2.7–3\,\mathrm{ml\,O_2\,L^{-1}}$). Direct video observations showed that all "mobile" fish species such as herring, sprat, cod, etc. had fled the area, while few of the strongly bottom-related species, e.g. flat fish, remained there in the area with many of them dying.

Howell and Simpson (1994) found a significant correlation between the mean catch and the mean species number with bottom dissolved oxygen concentrations in Long Island Sound showing a steep increase in catches at $2–2.9\,\mathrm{ml\,O_2\,L^{-1}}$ indicating move-

ments of the fish along suitable oxygen gradients. Similar behaviour was found by Burleson et al. (2001) who investigated the avoidance of hypoxia by large mouth bass. They found a close relationship between the site selection of the fish and oxygen saturation. At ca. 24°C the fish actively selected areas with >27% oxygen saturation
(2.4 mg O_2 L^{-1}) and avoided areas with lower levels. Preferred DO saturation was around 46%, corresponding to an oxygen concentration of 4 mg O_2 L^{-1}. This appears to be a common rule, when compared with data of Spoor (1990) and Wannamaker and Rice (2000).

Cod responds very clearly to short term decline of oxygen saturation from 100% to
20% in his swimming behaviour (Johansen et al., 2006). The fish initially increased its swimming speed significantly (29%) but then decreased swimming speed by 54%. Specimens showed severe stress symptoms during these experiments reflected in elevated cortisol and blood lactate values. Even if their experiments do not give a full picture of avoidance behaviour of cod as the experiment organisms had no choice to
select their preferred habitat, the results indicate that low oxygen levels are a stress situation for cod from which it tries to escape by increased swimming activity. Not able to do so in an experimental aquarium, it secondarily reduced swimming speed because of limited oxygen availability. Similar results were found by Herbert et al. (2005).

Weltzien et al. (1999) showed that if fish have a choice to select suitable oxygen con-
centrations they go for the high concentrations. In an oxygen-stratified setup silverside yolk-sac larvae (*Menidia beryllina)* were significantly attracted towards the upper well saturated layer when oxygen concentration in the lower layer was <3 mg O_2 L^{-1}. They remained in the lower layer only when the water was saturated. Similar results were shown Breitburg (1994) on larvae of bay anchovy (*Anchoa mitchelli*) and naked goby
(*Gobiosoma bosc*) in a stratified water column where both species exhibited a significant response to low DO. Good larval survival was found at 2.1 ml O_2 L^{-1} in naked goby and 1.5 ml O_2 L^{-1} in bay anchovy, whereas below these concentrations, larval mortality increased rapidly.

3.4.6 Schooling

Schooling is an important behavioural feature especially in pelagic fish. There are several advantages for the organisms to form and join schools, e.g. saving swimming energy (Herskin and Steffensen, 1998) or predator-deterrence behaviour.

Schooling behaviour can be affected by decreasing oxygen concentrations in the water (Moss and MacFarland, 1970). Anchovy (*Engraulis mordax*) reacts significantly with an increase in swimming velocity when oxygen concentration decreases rapidly. However, with a slow decrease in oxygen level, anchovies did not show any change in swimming speed. The mode of life also plays a role in the reaction to oxygen decrease. Sole (*Solea solea*) or sluggish eelpouts decrease their activity when exposed to hypoxia (Fisher et al., 1992; Dallavia et al., 1998) while fast swimming pelagic fish such as skipjack tuna increase their speed (Dizon, 1977) to escape the area.

Schools of Atlantic herring showed an increase in swimming speed at low oxygen saturation (15–34%) (Domenici et al., 2000). The authors hypothesized that the fish increase their swimming speed in order to rapidly escape from the unfavourable environment. Pihl et al. (1991) observed a similar response in adult cod. On the other hand schooling itself may cause decreased oxygen levels in the central and back part of the school just by the respiration of the organisms in the school and it may be a limiting factor for the size of a school (Steffensen, 1995, cited after Domenici et al., 2000). From several studies it can be concluded that lower oxygen also induces a wider spacing of the fish in the school leading to a looser network that may result in a complete disruption of the school. Domenici et al. (2000) observed such school disruption at 10–25% saturation in herring.

The overall impact of hypoxia on schools of pelagic fish such as herring is complex. The dimensions of schools increase, O-turning for changing position in the school is suppressed while shuffling rate remains constant leading to more specimens from the rear to change position by overtaking others, perhaps with negative energy impact (Domenici et al., 2002). The increase in school dimension leads to a larger inter-

individual distance causing lower communication and higher vulnerability to predators. In the extreme case, i.e. complete disruption of the school, reproduction success may be influenced by reduced probability of fertilisation.

4   Ecological effects

In the previous paragraphs, the impact of hypoxia on individuals or groups of species has been documented. The individual response of organisms to hypoxic conditions depends on the specific physiological limits and adaptations to the local environment. A change in the environmental conditions forces the organisms to re-adapt or to leave the habitat. The driving forces in this process can be direct on a physiological basis or indirect through a change of the biotic environment, i.e. the change of food organisms or predator spectrum. In any case, a change in the species composition of the system is a common response to changing oxygen conditions, the strength of which depends on the period and amplitude of the hypoxic event. Diaz (2001) listed 43 areas/ecosystems with aperiodic, periodic, seasonal or persistant hypoxia resulting sometimes in severe changes of the benthic fauna. We can assume that similar changes may occur in the pelagic environment if hypoxic conditions affect less mobile or less migratory specimens.

4.1   Changes in community structure

Several authors argue that oxygen content is shaping the communities of fish and other aquatic animals (e.g. Maes et al., 1998; Rosenberger and Chapman, 1999). Most of the work was done in estuaries or benthic/demersal communities where impact of hypoxic condition is very direct and species are forced to adapt quickly or perform migratory avoidance (Pihl et al., 1991; Keister et al., 2000). Nearly the complete communities may be substituted by hypoxia tolerant species from neighbouring habitats (Stevens et al., 2006). Such changes may result in dramatic or continuous changes

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in the catch of commercially valuable species such as brown shrimps in the northern Gulf of Mexico (O'Connor and Whitall, 2007) or demersal species in the Long Island Sound (Howell and Simpson, 1994) or the North Sea (Westernhagen and Dethlefsen, 1983). Evidence for the impact of hypoxia on pelagic communities in open coastal and offshore waters is scarce as hypoxia occurs in a different way, e.g. as a mid-water Oxygen Minimum Zone (OMZ) or an upward extending low oxygen bottom water layer on the shelf. Empirical evidence that low oxygen influences the distribution patterns of fish and zooplankton organisms was found by Ekau and Verheye (2005) and Auel et al. (2005) on the Namibian shelf in the Benguela upwelling region. A shift in the structure and composition of fish larvae over the last decade could be clearly related to changes in the extension of the OMZ along the Northern Namibian coast (Ekau and Bröhl, 2008).

4.2 Predator-prey relationships

A change in the community structure will definitely have consequences for the remaining species. Food organisms disappear, new prey species may not be as suitable or as nutritious as the former ones. Predator species may have changed forcing prey species to adapt to new hunting behaviour.

On the other hand predatory pressure may be reduced as top predators such as skipjack tuna need a minimum oxygen concentration of 3–3.5 ml O_2 L^{-1} (Barkley et al., 1978) to supply the fish with enough oxygen at consumption rates of 0.522 mg O_2 g^{-1} h^{-1} (Gooding et al., 1981). These constraints limit the overlap of the species with potential prey species (e.g. sardines and anchovies from eastern boundary upwelling areas). An argument that is also brought up in the discussion on the increase of jumbo squid off California and Chile (Field, 2008; Vetter et al., 2008). On the other hand reduced oxygen can directly influence the food uptake of fish, as shown in the paragraph above. Shoji et al. (2005) have reported on a reduced food uptake of juvenile Spanish mackerel *Scomberomorus niphonius* on red sea bream larvae with decreasing DO while the consumption of fish larvae by moon jellyfish (*Aurelia aurita*)

increased and hence contributed to a shift in the composition of the experimental community. An increase of predation by jellyfish on fish larvae in oxygen-depleted situations was explained by several authors with a reduction in the larvae's ability to escape (Breitburg et al., 1994, 1997; Shoji et al., 2005; Kodama et al., 2006). Decker et al. (2004) already argued that the higher tolerance of ctenophores and other gelatinous plankton against hypoxic conditions may outcompete young fish from their staple food copepods, lead to a dominance of gelatinous species and furthermore to a change in the trophic structure and pathways of the ecosystem. Lynam et al. (2006) have postulated such a shift to a jellyfish-dominated system in the Northern Benguela Current.

Striped bass are influenced in their predatory behaviour at a DO of $2.8\,\text{ml}\,O_2\,L^{-1}$, and that a level of at least $2.1\,\text{ml}\,O_2\,L^{-1}$ is required for the species to survive (Setzler-Hamilton and Hall, 1991; Breitburg et al., 1994). Much lower thresholds of $0.5\,\text{ml}\,O_2\,L^{-1}$ were found in naked gobies, although their feeding success or feeding attacks were reduced significantly (Breitburg et al., 1994). The authors concluded that low DO can strongly alter the absolute and relative importance of predators, especially on fish larvae in an estuary, but there is evidence that this argument can be generalised to other habitats and ecosystems.

Significant changes were also found in the diets of benthos feeders during and immediately after hypoxic events (Pihl et al., 1992, 1994). These predators seemed to have a strong benefit of the changing environment getting access to larger prey items which may have been driven out of the anoxic sediments. The mechanism behind this finding is that animals are forced to leave their normal habitat by hypoxic conditions and hence become more vulnerable to predators (Pihl et al., 1992, for benthic organisms and their predators).

Hedges (2007) investigated the predator-prey interactions in a freshwater fish community under the impact of hypoxia. He could clearly show that moderate hypoxic areas could already serve as refuge for prey organisms from predators as the latter did stop visiting these areas at certain threshold concentrations. All these findings indicate that the increasing hypoxic or even anoxic areas in the world ocean (Diaz and Rosenberg,

2008) and the extending OMZ in the eastern parts of the subtropical/tropical oceans (Stramma et al., 2008) have a strong impact on the horizontal and vertical distribution of the species and indirectly impact the relationships between predator and prey species. The trophic relationships are changed and thus the whole structure of the foodweb in the ecosystem. A driving force in this process is the time span and periodicity in which the oxygen conditions are changed and modulated. Mono-pulsed systems where hypoxic events occur once a year will react differently from multi-pulsed systems such as upwelling areas. Many systems have adapted to these conditions in one way or another. A completely different situation is expected in long-term climate driven changes like the extension and intensification of the OMZ in the eastern sub-/tropical oceans (Stramma et al., 2008).

5 Case studies

Most of the ocean areas vulnerable to hypoxia listed by Diaz (2002) are estuaries, coastal areas, enclosed or semi-enclosed seas. Some of these such as the Baltic Sea or Chesapeake Bay are extensively investigated and we know more or less what happens in these systems when oxygen is depleted. With increasing efforts to investigate the open ocean and to understand the variability in upwelling systems we realise that these open systems can also be or are vulnerable to the short and long term changes of DO in the water column and the sea floor. We take one example each from a semi-enclosed sea and an open upwelling area to demonstrate the consequences of hypoxia to fish and other pelagic organisms.

5.1 Baltic Sea

The Baltic Sea, certainly one of the most intensively studied seas in the world, is a strongly stratified water body with a sharp halocline at 70–90 m depth in the Baltic proper. Summarising reviews on the abiotic and biotic features of the Baltic Sea are

among others: Rheinheimer (1995), Lozan et al. (1996), Jansson (2003) and Lääne et al. (2005).

The strong stratification and an irregular inflow of fresh oxygenated North Sea water has lead to hypoxic or even anoxic conditions in the deeper water layers. Matthäus (1995) has described this development for several basins in the Baltic Sea, showing low DO of $1-3 \, \text{ml} \, O_2 \, L^{-1}$ in the first half of the 20th century in the Gotland Deep and a steady decrease into O_2 deficit/H_2S concentrations in the subsequent decades. Such a development is connected with the increased use of fertilisers in agriculture of the drainage basin countries, which has induced eutrophication in large parts of the Baltic Sea and as a consequence oxygen deficiency in the less mixed deep waters (Fig. 3).

The inflow of oxygenated waters from the North Sea has been less frequent since the mid 1970s (Matthäus, 1995) contributing to the decline of oxygen concentration in the deeper waters. The effect is a reduced or even absent benthic fauna in the deeper layers and high oxygen consumption by microbial organisms that degrade the detritus. As a consequence new settlement of larvae of benthic organisms is prevented by the low oxygen conditions and a repopulation is more difficult. The bottom area of these "dead zones" extended between $70\,000$ and $100\,000 \, \text{km}^2$ in the 1970s, fluctuating on a yearly basis with maximum values at the end of stagnation periods (Rumohr, 1995). In 2008 $DO < 2 \, \text{ml} \, O_2 \, L^{-1}$ were found from 70 m downwards filling the Gotland and Bornholm basins and with anoxic conditions (H_2S) at depths below 150 m (IOW 2009) (Fig. 4).

The stratification of the water column and the hypoxic/anoxic conditions in deeper water layers also have an impact on the pelagic species. The main commercially important fishes in the Baltic Sea are the pelagic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) and the demersal cod (*Gadus morhua*) with up to $>900\,000 \, \text{t}$ in 1984 and 1997 (FAO 2009). Herring is a substrate spawner laying their eggs in shallow, well ventilated coastal places. Sprat and cod are pelagic spawners of the open sea above the deep basins. Sprat eggs spawned in the upper 20 m have a high buoyancy and float in the near surface layers above the thermocline. The eggs are sensitive to

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low temperatures and need at least 5°C for a normal development (Schnack, 1995). A negative impact on sprat reproduction thus results more from long and cold winters than from low oxygen in deeper waters. We find the opposite situation in cod, a species more adapted to cold water temperatures and with less buoyant eggs than e.g. sprat. The spawning areas of cod are more dependent on salinity than on temperature and coincide with the deep basins of the Baltic proper. A critical issue for the reproduction success of this species is the interrelationship between buoyancy, salinity and dissolved oxygen concentration. Spawning products of cod need a minimum salinity of 11 PSU for a successful development. This is only found in greater depths around the thermocline. Egg concentrations occur at salinities between 9.5 and 16.5 PSU (Nissling, 1994; Wieland, 1995) which are found at depths >50–70 m. Higher salinities stimulate better egg development resulting in a need for the eggs to float as deep as possible and preferring the western basin such as that off Bornholm rather than the more easterly basins (Nissling, 1994). This author also suggested that 2.5 to 3 mg O_2 L^{-1} is the threshold concentration below which mortality of eggs increases significantly. However, the oxygen conditions in depths >50–70 m depth can be in that range and thus become very critical. Hence the spawning success is strongly dependent on the inflows of North Sea water renewing and oxygenating the deep zones of the basins.

Because of the different requirements of sprat and cod to the environment the changing conditions in the Baltic Sea induce a natural periodic fluctuation of the stocks driven predominantly by the periodicity and strength of the inflow of oxygenated North Sea water along the sea floor and the resulting vertical fluctuation of the thermo- and haloclines. Schnack and his co-workers have established a conceptual model to describe this fluctuating system and the variation in the biomass of the different components (Fig. 5).

The model shows how the species react to the changing environment in the pelagic Baltic Sea. In a cod-dominated system, the sprat stock is kept at a low level by cool temperatures (bad development conditions for eggs) and predation by cod and carnivorous zooplankton. The system may swap into the sprat status when high fishing

pressure on cod and long stagnation phases with low inflow of fresh North Sea water have diminished the cod stock. The stagnation lifts the oxycline upwards and cod eggs floating in the halocline get under hypoxic pressure reducing egg survival rates. Grazing of sprat eggs by cod is reduced and mild winters enhance recruitment success of
5　sprat. A sprat dominated system is built with increased predation on cod eggs. As long as the stagnation lasts, cod will have few chances to recover. Another change in the system may only occur if cold winters hinder sprat egg development and induce fresh water inflow to oxygenate the deeper layers where cod eggs develop. A clear correlation between the deep-water oxygen concentration and cod spawning success is
10　indicated by Jansson (2003) in his review on the Baltic Sea Large Marine Ecosystem.

　　Fishery landing values are normally following these changes with a phase-delay of few years impacting the economic importance of the species. The economic values of sprat and cod landings in the Baltic Sea are clearly correlated showing stable revenue between 200 and 300 mill. US$ for cod from 1955, when fisheries had recovered
15　after the war, to 1979 (Fig. 6). For this period a constant inflow of North Sea water (Matthäus, 1995) supported the recruitment and fisheries of cod in the area. A short period of elevated cod catches in the early eighties (perhaps as compensation for the reduced sprat catches) was followed by a dramatic decline in catch (100 000 t) and value (ca. 100 mill. US$) of cod since then accompanied by a period of minimum water
20　inflow (Matthäus, 1995). The sprat stock instead has recovered since the early 1990ies (Fig. 6) but cannot compensate the loss in cod fishery.

5.2　Northern Benguela upwelling system

The dynamics of the Benguela Current (BC) system has been described extensively (e.g. Shannon, 1985; Nelson and Hutchings, 1987; Lutjeharms and Valentine, 1987;
25　Fennel, 1999; Mohrholz et al., 2001; Monteiro et al., 2008) and is not repeated in detail here. There are several upwelling cells along the coast, the Lüderitz cell being the most prominent and perhaps the strongest upwelling cell in the ocean dividing the coastal upwelling system into two sub-systems, the northern and the southern Benguela up-

welling system (Rae, 2001). The northern boundary of the BC is the Angola-Benguela Frontal Zone (ABFZ) where the southerly flowing Angola current meets the northerly flowing BC. The oxygen conditions in the water column are quite different in these two sub-systems with a well developed Oxygen Minimum Zone (OMZ) in the northern part and well oxygenated waters in the southern. OMZ are found in other upwelling areas as well, but the special characteristic of the northern Benguela system is the southerly flowing Angola current that transports low oxygen water from the Angola gyre polewards. In upwelling systems the surplus of primary and secondary production that cannot be taken up by the higher trophic levels, dies off and sinks to deeper layers where they are decomposed by oxygen demanding microbial processes. In oceanic waters the OMZ ($<2\,\mathrm{ml\,L^{-1}}$) extends from about 50 to 500 m depth and represents a chemical barrier for vertically migrating species. The poleward transport of the hypoxic waters is driven by an undercurrent along the slope reaching southward to Lüderitz ($27°$ S) and flowing partly on the shelf, influencing and decreasing the oxygen concentrations of the bottom-waters (Monteiro et al., 2008). In addition to the low oxygen pre-conditions in neritic waters the sedimentation of organic material leads to strongly hypoxic or even anoxic conditions ("dead zones") at the sea floor and impacts the benthic fauna by selecting mostly low-oxygen resistant species in the benthos community. Flushing of the shelf areas depends on the dynamics of the regional currents and water masses and occurs when the poleward undercurrent is in a minimum and better oxygenated Cape Basin South Atlantic Central Water dominates the system (Monteiro et al., 2008).

Flushing and penetration of the shelf by hypoxic waters is an annually oscillating process with maximum oxygenated waters in September-November and a minimum in February-April (Hampton and Sweijd, 2008; Monteiro et al., 2008). Extreme situations in late austral summer may lead to the production of H_2S in the bottom layers and H_2S and methane eruptions are regular under certain conditions and contribute to persistent water column hypoxia. Massive gas charged sediments up to 480 km^2 wide were found by Emeis et al. (2004) in the near surface sediment layers along the coast of northern

Namibia. Such bubbles are strong enough to lift mud plaques up and release large amounts of gas into the water column. If this happens nearshore, benthic animals can be driven ashore as it has been observed in lobsters along the Namibian and South African coasts. Pelagic organisms may escape depending on the extension of the release area, but also may be trapped and washed ashore when they are encircled close to the shore.

The intensification of the hypoxic conditions in the water column is an issue that emerged only recently, according to investigations in the different upwelling systems (Bograd et al., 2008; Monteiro et al., 2008; Stramma et al., 2008). As laid out earlier in this chapter, the impact of such extension on the different organisms may not be visible in the dramatic way that we sometimes witness in benthic systems where we may observe "walkouts" of lobsters or in freshwater systems where even "jump-outs" of fish can be observed, as organisms try to escape from the hypoxic environment. Pelagic organisms may suffer from hypoxia in a very different way such as impact on early life development, feeding or predation that forces them to react in a very early stage at non-lethal levels. We can only look for indirect measures to investigate the impact of hypoxia on these species. Sardine and anchovy stocks have declined in the northern Benguela since several years and recruitment has been low with exceptions in a few years only. It has been postulated by Ekau and Verheye (2005) and Kreiner et al. (2009) that this decline is related to the aggravated oxygen condition in the spawning areas on the Namibian shelf. Early stages of small pelagics are known to be sensitive against low oxygen (Palomera, 1991; Breitburg et al., 1994, 2002), but e.g. horse mackerel (*Trachurus* spp.) or hake (*Merluccius* spp.) seem to be more resistant against hypoxia and recover much better than other organisms (Kunzmann, 2008). It is argued that the elevation of the upper oxycline of the OMZ impacts on the reproduction success of certain species and food availability (Fig. 7).

Shoaling of the oxycline has been observed in several areas. Figure 7 describes the situation in the Benguela upwelling area over the last 40 years. Bograd (2008) found a similar development in the California Current. The upward movement of the

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60 μmol O_2 L^{-1} isosurface ($\approx$2 mg O_2 L^{-1}) was 10 to 50 m in the offshore stations and up to 100 m at the inshore stations of the CalCOFI grid. The pattern in the Namibian area is more diverse and maybe not that strong with 10–30 m on the shelf especially between 18 and 21°30' S, the main spawning areas of sardine and anchovy. Empirical
5 studies on the distribution of fish larvae in the northern Namibian waters showed clear evidence that higher abundances of many species are restricted to water masses with >2.5 ml O_2 L^{-1} (Ekau and Verheye, 2005; Kreiner et al., 2009). Copepods divide into a number of different ecological groups using or avoiding the OMZ for feeding, hiding or migrating through. Several species remain in the oxygenated surface layer, others
10 enter the OMZ for resting/hiding from predators, and some perform vertical migrations through the OMZ to conclude their life cycle (Auel et al., 2005; Auel and Verheye, 2007). Changes in the absolute oxygen concentration or in the vertical extent of the OMZ will directly influence the copepod species in their activities and change the food spectra of their predators.

15 Several authors have explained the increase in jellyfish by the changes in the environmental conditions in the area, mainly temperature and oxygen, and human impacts such as fisheries or pollution (Purcell et al., 2007). They fear an overtake of jellyfish on fish under increasingly hypoxic conditions (Lynam et al., 2006). Graham (2001) reported on severe impacts of increased jellyfish populations on fisheries in the northern
20 Gulf of Mexico. As seen above an increase of jellyfish populations in the Benguela or other areas may be explained by two processes. Jellyfish are normally more resistant to low oxygen concentrations and remain or congregate in such areas. As predators on zoo- and ichthyoplankton an increase of their abundance will increase also the predation pressure and competition on other plankton which depresses the recovery
25 chances of hypoxia threatened other plankton populations. The ability to remain in or pass actively through the OMZ could be a crucial advantage in the future to survive and benefit from the large scale changes. Mincks et al. (2000) reported of four shrimp species (*Sergia* spp.) that live nearly exclusively in the OMZ between 150–1000 m in the upwelling influenced areas off Oman in the Arabian Sea. The species fed on other

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shrimps, euphausiids and copepods from the same water depths mostly not leaving the OMZ. It is likely that these species have special physiological adaptations that allow them to live in this environment. An extension of the OMZ would provide them with an extended habitat and increase their abundance in the area. A change in the over-
5 all community structure would be the result. Many of the shrimps with an estimated average abundance between 0.04–106/1000 m^3 serve as important food resource for pelagic and mesopelagic organisms (Karuppasamy et al., 2006). An increase of their biomass and distribution area would be beneficial to their predators as well.

We may observe such a development in the extending distribution area and biomass
10 of the giant or Humboldt squid in the eastern Pacific Ocean. Catches in the Gulf of California have increased from 6000 t in 1994 to 140 000 t in 1996 (Morales-Bojorquez et al., 2001). Two factors may be relevant, one being the developing fisheries, the other the extension of the distribution area. In the early 1980s the distribution area for the species ranged from 30° N to 50° S. In 2002 it was found up to 40° N, in 2003 up to 50° N
15 and in 2005/2006 it occurred off the coast of Alaska at 60° N (Gilly, 2005). An important factor in this expansion could be temperature as indicated by the ENSO phenomenon (Rodhouse, 2008) but Field (2008) also pointed out that this may not be the only factor responsible for the success of the squid in the high latitudes. The extending OMZ is argued to be an additional factor responsible for the development (Gilly et al., 2006).
20 However, Keyl et al. (2008) argue that the La Niña/El Niño combination from 1996 to 1998 considered as a "system reset" was a main trigger for the explosive development of the giant squid population in the east Pacific. The increase in biomass of giant squid along the Californian shelf privileges predator species such as sharks (Vetter et al., 2008), but creates competition to other predatory species such as hake that falls itself
25 into the role of prey! Holmes et al. (2008) argue that the appearance of giant squid as top predator in areas formerly dominated by hake leads to a dispersal of hake to avoid predation by squid. The side effect may be that fisheries effort on hake has to be increased to catch the same amount of fish.

6   Summary and conclusion

There are clear indications that tropical/subtropical Oxygen Minimum Zones are extending vertically and by intensity (Bograd, 2008; Stramma, 2008). Several studies have shown that degrading oxygen conditions are no longer restricted to semi-enclosed seas such as the Baltic or the Black Sea or estuaries such as Chesapeake Bay but also occur in the open ocean. The underlying processes seem to happen on different time scales and periodicities compared to the coastal or enclosed systems. Degradation may extend over decades as shown by Stramma (2008) and driving forces are not pollution and eutrophication but long-term climatic changes.

The reaction of the living communities in the respective areas is highly complex and far from understood. Complex effects happen on different levels of biological organisation: from direct physiological reactions to changing temperature, oxygen and salinity via alterations on the individual level such as behaviour, growth or feeding to changes in the population. The cumulative effect will be seen on community level where species composition and biomass distribution will change and percolate into the fisheries, tourism or other socio-economic aspects of maritime uses.

We have proof that organisms are sensitive against changes in the oxygen concentrations in their environment. We have evidence that this sensitivity of the species leads to changes in the community composition, structure, trophic flows and species behaviour. However, we have not really incorporated oxygen in our models and do not really understand what quantitative impact a changing oxygen concentration might have. In this last section we summarize possible scenarios in the pelagic zone resulting from a decreasing oxygen concentration in the water.

– The frame for adaptation and behavioural response of the species is set by their very basic physiological characteristics. Here are the key factors that guarantee the survival of the species under changing conditions or lead to disappearance. We know some of the mechanisms that play a key role in these processes and some principle differences between taxonomic groups or modes of life, but we are

far from having these parameters on hand for all (key) species in the ecosystems to incorporate it in our models.

- From our knowledge on the physiological processes and empirical observations we know that there will be winners and loosers in the changing ecosystems. Increasing hypoxia seems to privilege gelatinous plankton and/or squid as observed in the Benguela and California current regions. Disadvantaged are the components of the "classical" marine foodweb: certain copepods and fish. Within these groups the response is very complex. In general, small pelagic fish species such as the clupeids could be more vulnerable than higher evolved and more adaptable species such as gobies or flat fish. There is no systematic investigation whether higher evolved fishes are more tolerant and have better adaptability to hypoxic conditions than less evolved. We know from young sea bass, that this species is able to adapt its respiratory surface of the gills depending on different DO conditions over a three month period (Saroglia et al., 2002), but we cannot say if this is a general feature in fish or for which group it refers?

- Predator species are particularly depending on higher oxygen concentrations (Worm et al., 2005) as hunting as their mode of life requires high amounts of oxygen. Tuna species are forced to permanent swimming to cover their high oxygen demand. In a changing environment they will have to leave the area as one of the first species. Prince and Goodyear (2006) found evidence that shoaling of the OMZ is reducing the habitat of Atlantic blue and white marlin and sailfish significantly.

- The intra-specific competition for oxygen is won by the smaller specimens that out-compete larger because the body-mass-oxygen-consumption ratio is better for the smaller specimens (Burleson et al., 2001). Larger specimens will leave the area first. This has impact on the age composition of the stocks and may change recruitment abilities as well as predation pressure on food organisms. Hence, trophic interactions will change and carbon fluxes will follow different pathways.

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Other species or even taxonomic groups will use the free resources, increase in biomasses and open up new pathways to use or deposit the incorporated carbon. Not all of this biomass, e.g. jellyfish, will be usable for mankind.

– The economic consequences of hypoxia concerning pelagic resources are difficult to estimate. There will be winners and losers in the systems and whether they will be attractive for our fisheries or not is not predictable. Every square km of additional hypoxic area in the Gulf of Mexico reduces brown shrimp catch by 214 kg (O'Connor and Whittall, 2007). Standard fish catches in the Danish North Sea after the intrusion of hypoxic waters dropped from 700–900 kg h^{-1} to nearly nil (Detlefsen and Westernhagen, 1983). The decline of the small pelagics in the Northern Benguela Upwelling system may partly be related to the shoaling of the OMZ resulting in the almost complete disappearance of the sardine fishery in Namibia. Remaining predator species such as horse mackerel seem to have switched to mesopelagic fish and other organisms for food. As a consequence of the shoaling of the OMZ in the eastern tropical Pacific (Prince and Goodyear, 2006), there is evidence that the vertical range of tuna decreased making tuna stocks more vulnerable to purse seine as well as pole and line fisheries (Green, 1967; Barkeley et al., 1978) with an overall increase of the catch. The increase in jumbo squid biomass and distribution with a fourfold catch magnification between 2000 and 2005 may be an example for a positive economic side-effect (Field, 2008). These examples may show that the economic consequences of expanding hypoxia in the ocean and along the coast are based on very complex relationships and small non-linear changes in the parameters may result in drastic regime shifts of marine ecosystems.

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region stored in the data base of the National Museum Information and Research Center (Nat-MIRC) in Swakopmund, Namibia. Our thanks go to Anja Kreiner and Anja van der Plas who made the data available for us.

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Table 1. Conversion factors between different units of dissolved oxygen (DO) concentrations.

Dissolved oxygen (DO) concentration						
μMol O_2		mg-at O_2		mg O_2		mL O_2 (STP)
1000	=	2	=	32.00	=	22.39
500	=	1	=	16.00	=	11.20
31.25	=	0.0625	=	1	=	0.7
44.66	=	0.0893	=	1.429	=	1
Partial pressure						
mm Hg		kPa		hPa/mBar		% Saturation
160	=	21	=	210	=	100
7.6	=	1	=	10	=	4.76
1	=	0.13	=	1.31	=	0.625

$\dot{Q}$

- anaerobic heat
- aerobic heat

Pc_{max}
Pc_R
MMR

Pc_{min}

Pc_M

excess heat ?

$\dot{Q} \cong \dot{M}O_2 \gtreqqless \dot{M}_{ATP}$

SMR

0

0 PO_2
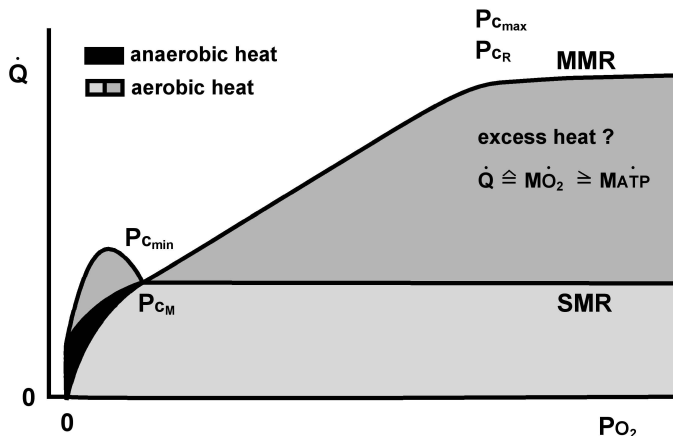
Comparing oxyconformers and oxyregulators

Pc_R: critical PO_2 of constant aerobic metabolic rate

Pc_M: critical PO_2 below which anaerobiosis starts

aerobic Oxyregulator:
able to maintain SMR above Pc_M, $Pc_M = Pc_R$

aerobic Oxyconformer:
regularly exceeds SMR above Pc_M, $Pc_M < Pc_R$

Fig. 1.

Fig. 1. Graphical presentation of a model used for the comparison of the physiological responses of oxyconforming and oxyregulating animals in declining oxygen tensions (modified after Pörtner and Grieshaber, 1993). For the sake of clarity, oxygen consumption rates and critical oxygen values are compared in absolute terms, neglecting the fact that standard metabolic rates are variable between species and individuals. Pc_M is the critical PO_2 below which anaerobiosis starts, Pc_R is the critical PO_2 of constant aerobic metabolic rate. SMR is the standard metabolic rate, the minimum metabolic rate in complete aerobiosis (at Pc_M), excluding locomotory activity. An increase in oxygen consumption may occur in oxyregulators below Pc_M (see text). An aerobic oxyregulator is able to maintain SMR at PO_2 values above Pc_M, Pc_M equals Pc_R. However, it is able to reach maximum metabolic rate during phases of maximum aerobic exercise. Maximum aerobic metabolic rate is reached by full exploitation of energy turnover capacity (high energy consumption and associated production). Maintaining this maximum leads to higher levels of Pc (Pc_{max}) and thus, enhanced hypoxia sensitivity than at SMR. In contrast, an aerobic oxyconformer regularly exceeds SMR once exposed to high ambient oxygen levels and passively exploits its aerobic scope above Pc_M, $Pc_R > Pc_M$.
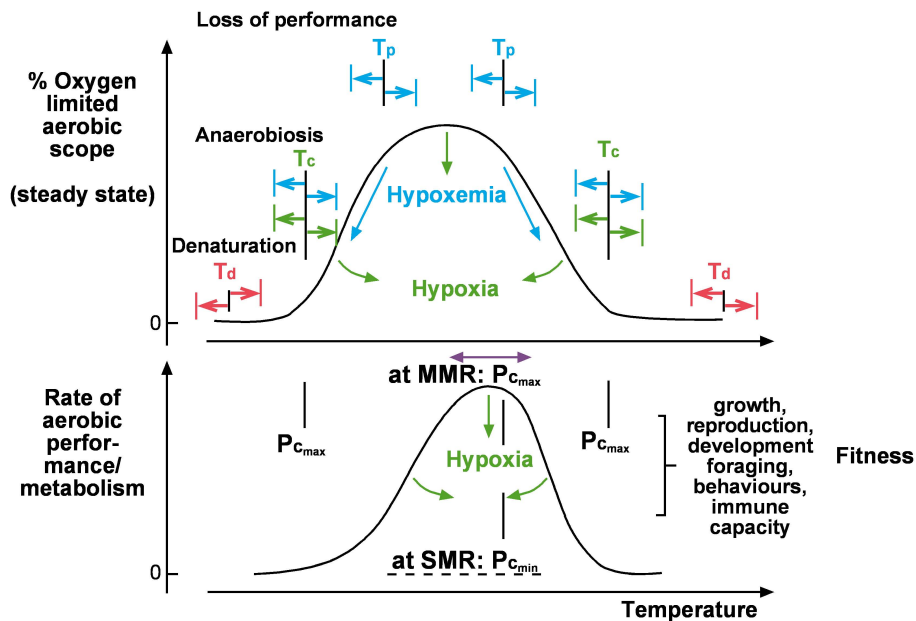
Fig. 2.

Fig. 2. Conceptual model of how ocean warming and hypoxia as interacting stressors shape the thermal window of performance of a species, population or life stage, based on the concept of oxygen and capacity limited thermal tolerance (after Pörtner and Knust, 2007; Pörtner et al., 2009). Optimized oxygen supply to tissues between low and high pejus temperatures (top) combined with the kinetic stimulation of performance rates by warming supports temperature dependent performance and a functional optimum (i.e. an optimum of aerobic scope) close to upper pejus temperature (bottom). This reflects fitness due to functional capacity in ecosystem level processes such as competition, foraging, immune response, growth and behaviours. Ambient hypoxia causes a narrowing of thermal windows and possibly, lower performance optima due to lower functional capacities at reduced systemic oxygen tensions (green arrows). The graph depicts acute performance levels and limitations in response to short term temperature fluctuations. On longer time scales, changing temperatures elicit acclimatization as a limited shift of performance optima and limits on the temperature scale (horizontal arrows). Low and high limits of thermal acclimatization (vertical lines) delineate the thermal niche of a species. Note that the passive tolerance range (beyond pejus and critical temperatures) is a relevant component of the niche in some cases, when it is exploited under extreme conditions, e.g. in invertebrates exposed to combined hypoxia and temperature extremes in the intertidal zone. Hypoxia tolerance is maximum in the thermal optimum, due to optimal oxygen supply capacity causing Pc to be minimal. Hypoxia sensitivity is enhanced at thermal extremes when oxygen supply capacity falls in relation to oxygen demand, and the Pc rises towards its maximum, indicated by the onset of anaerobic metabolism at ambient, even normoxic oxygen tensions.
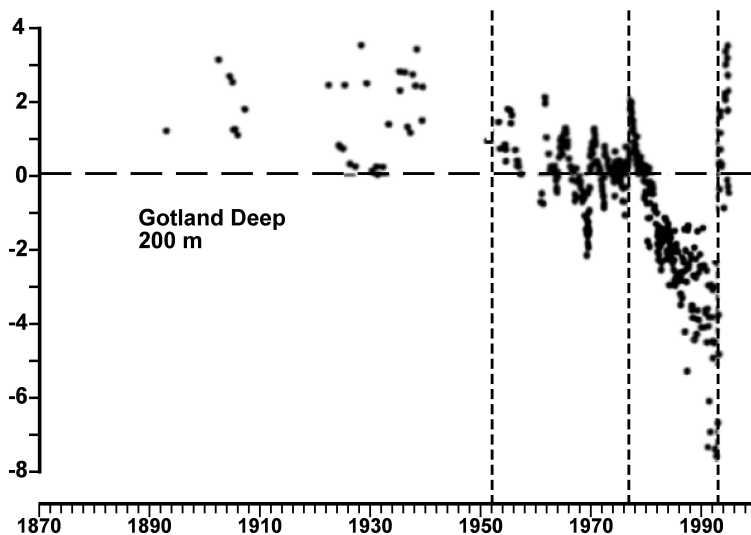
Fig. 3. Long-term variation in oxygen and hydrogen sulphide concentrations in the central Baltic Gotland Deep water during the last century (hydrogen sulphide expressed as negative oxygen equivalents) (extracted from Matthäus, 1995, slightly modified).
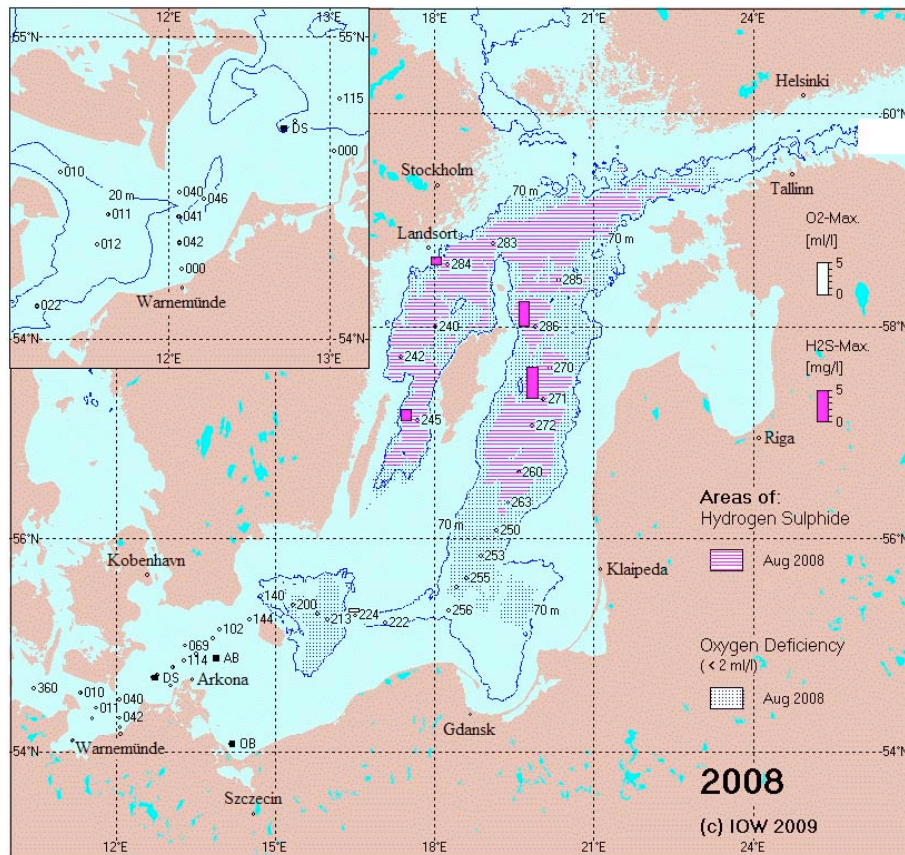
Fig. 4. Oxygen Deficiency ($<2\,\mathrm{ml\,O_2\,L^{-1}}$) and anoxic ($H_2S$) conditions in the Baltic Sea in August 2008. The deep areas ($>70\,\mathrm{m}$) in the Baltic proper are filled with low oxygenated water. Pink areas indicate hydrogen sulphide distribution with maximum of ca. $5\,\mathrm{ml\,H_2S\,L^{-1}}$ at indicated positions (http://www.io-warnemuende.de/suboxische-und-anoxische-bereiche-im-tiefenwasser-der-ostsee.html, IOW 2009).
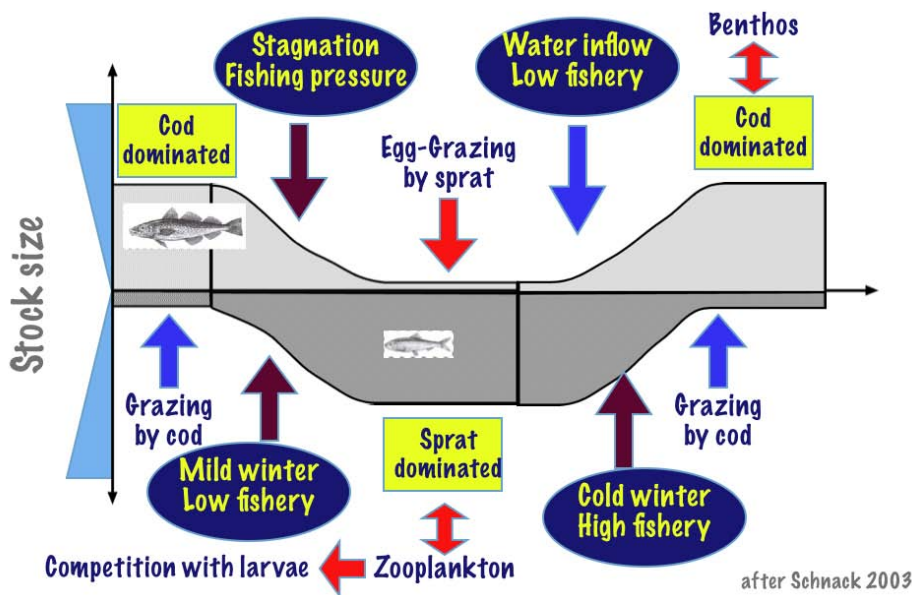
Fig. 5. Interrelationships between sprat and cod stocks, environmental factors and grazing in the Baltic Sea. The system swaps from cod dominated to sprat dominated and back driven by environmental factors (North Sea water inflow – stagnation, cold winter – mild winter), biological drivers (egg grazing cod-sprat, zooplankton competition) and human activities (cod-sprat fisheries) (modified after Schnack, 2003).

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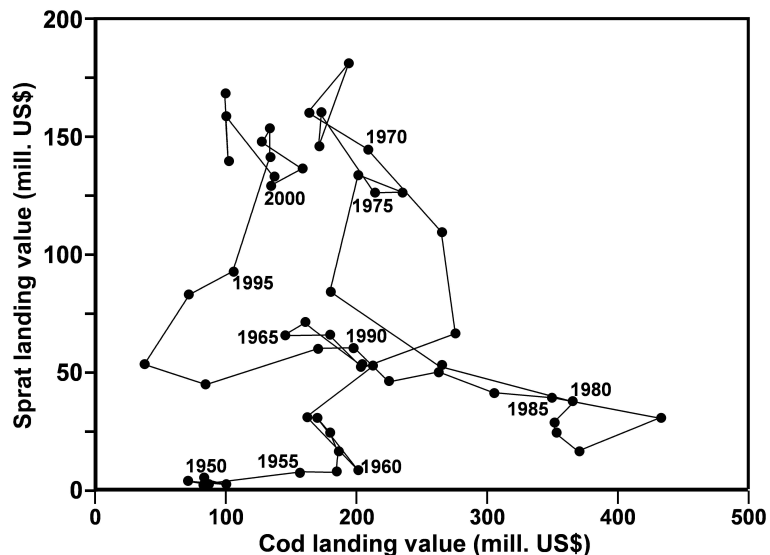
Fig. 6. Correlation between landing values of cod and sprat in the Baltic Sea in the years 1950 to 2004. Catches from 1955 to 1979 are rather stable in quantity and value. A short period of intensified fisheries ends in 1985 with a sharp decline in catch and landing value coinciding with the lack of fresh North Sea water inflow. Catches and value are stable again on a lower level (data from www.seaaroundus.org).
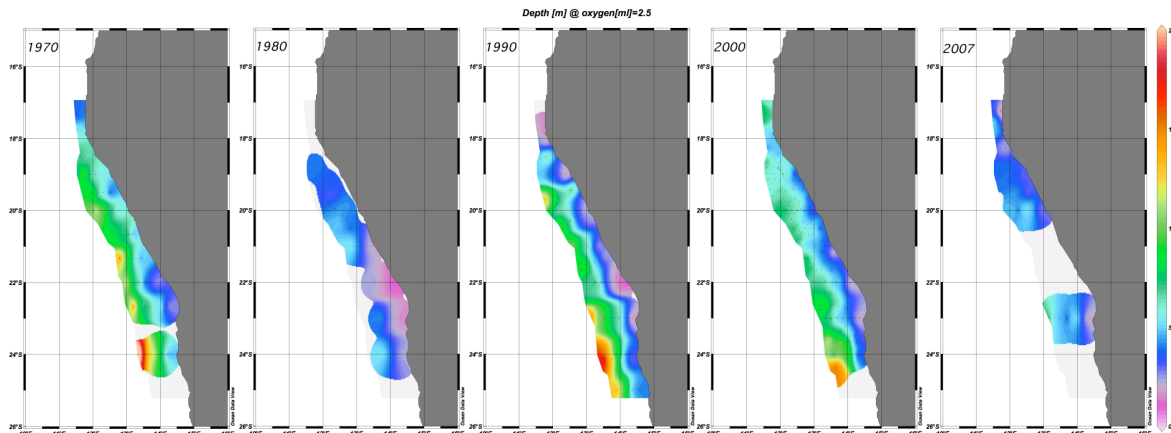
Fig. 7. Development of O_2=2.5 ml iso-surface from 1970 to 2007. The general trend can be described as a shoaling of the 2.5 ml iso-surface over the last 40 years (data from NODC, courtesy of Kreiner, NatMIRC and Ekau, 2007, 2008).