Ecosystem thresholds with hypoxia

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Abstract Hypoxia is one of the common effects of
eutrophication in coastal marine ecosystems and is
becoming an increasingly prevalent problem world-
wide. The causes of hypoxia are associated with excess
nutrient inputs from both point and non-point sources,
although the response of coastal marine ecosystems is
strongly modulated by physical processes such as
stratification and mixing. Changes in climate, particu-
larly temperature, may also affect the susceptibility of
coastal marine ecosystems to hypoxia. Hypoxia is a
particularly severe disturbance because it causes death
of biota and catastrophic changes in the ecosystem.
Bottom water oxygen deficiency not only influences the
habitat of living resources but also the biogeochemical
processes that control nutrient concentrations in the
water column. Increased phosphorus fluxes from sed-
iments into overlying waters occur with hypoxia. In
addition, reductions in the ability of ecosystems to
remove nitrogen through denitrification and anaerobic
ammonium oxidation may be related to hypoxia and
could lead to acceleration in the rate of eutrophication.
Three large coastal marine ecosystems (Chesapeake
Bay, Northern Gulf of Mexico, and Danish Straits) all
demonstrate thresholds whereby repeated hypoxic
events have led to an increase in susceptibility of
further hypoxia and accelerated eutrophication. Once
hypoxia occurs, reoccurrence is likely and may be
difficult to reverse. Therefore, elucidating ecosystem
thresholds of hypoxia and linking them to nutrient
inputs are necessary for the management of coastal
marine ecosystems. Finally, projected increases in
warming show an increase in the susceptibility of
coastal marine ecosystems to hypoxia such that hypoxia
will expand.

Keywords Hypoxia · Biogeochemistry ·
Nitrogen · Phosphorus · Regime shift ·
Resilience

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Introduction

Hypoxia is one of the common effects of eutrophi-
cation in coastal marine ecosystems, and dead zones

created by hypoxia have spread exponentially glob-
ally since the 1960s (Díaz & Rosenberg, 2008).
Increased prevalence of hypoxia is directly a result of
excess nutrient inputs from both point and diffuse
sources, thus increasing the production of organic
matter. The increased flux of organic matter to
bottom waters changes the balance between oxygen
supply through physical forcing and oxygen con-
sumption from decomposition of organic material. It
should be stressed that hypoxia in coastal marine
ecosystems is strongly modulated by physical pro-
cesses such as stratification and mixing (Smith et al.,
1992; Hagy et al., 2004); without stratification or with
intense mixing renewing oxygen supplies, hypoxia
will not occur. Hypoxia is a particularly severe
disturbance because it causes death of organisms and
catastrophic changes in the ecosystem (Gray et al.,
2002).

In this review, we will explore the consequences of
hypoxia to changes in the remineralization of organic
matter and to the modification of the biogeochemical
cycles of phosphorus and nitrogen, and show how
they act as feedback mechanisms to further eutrophi-
cation. In addition, we will demonstrate that repeated
hypoxic events will increase the susceptibility of
coastal marine ecosystems to further hypoxia through
alteration of ecosystem functioning of the sediments
and show that this has already occurred in a number
of coastal marine ecosystems. Finally, we will
examine the effects of predicted increases in global
temperature on hypoxia.

Biogeochemical consequences

Hypoxia and bottom water oxygen deficiency not
only negatively influence organisms (Vaquer-Sunyer
& Duarte, 2008) and the habitat of living resources,
but also the biogeochemical processes that control
nutrient concentrations in the water column. Internal
feedbacks on biogeochemical processes occur with
oxygen depletion, with one of the most prominent
being the effect on the phosphorus (P) biogeochem-
ical cycle. Increased P fluxes from sediments into
overlying waters with hypoxia is a classic response
observed in freshwater systems (Mortimer, 1941) and
has been well documented in coastal marine ecosys-
tems (Nixon et al., 1980; Conley et al., 2002). When
oxygen conditions in sediments become low,

dissolved inorganic phosphorus (DIP) is released
from iron-bound phosphorus in sediments (Jensen
et al., 1995). In the Baltic Sea, which is the largest
coastal area in the world to suffer from eutrophica-
tion-induced hypoxia, large internal P loading occurs
with hypoxia (Fig. 1). The amount of DIP released
from sediments in the Baltic is an order of magnitude
larger than external inputs from rivers (Conley et al.,
2002). The increased sediment–water fluxes of phos-
phorus with hypoxia return DIP to surface waters
alleviating P limitation (Conley, 1999), stimulating
phytoplankton production and acting as a positive
feedback to increase hypoxia.

Hypoxia also influences rates of denitrification and
anaerobic ammonium oxidation (anammox). Denitri-
fication is one of the major routes of loss of fixed
nitrogen (N) in the oceans (Seitzinger & Giblin,
1996); however, its measurement is difficult (Groff-
man et al., 2006). Denitrification is the reductive
respiration of nitrate or nitrite to N_2 or nitrous oxide
(N_2O). In addition, fixed nitrogen removal also
occurs through the anammox process (Dalsgaard
et al., 2003). The rates of denitrification are depen-
dent on a variety of factors, but the availability of
starting products, for example nitrate (Kemp et al.,
1990) and carbon (Smith & Hollibaugh, 1989; Sloth
et al., 1995), is a major controlling factor.

In a review of continental shelf sediments, Seitz-
inger & Giblin (1996) found a linear relationship
between denitrification rate and sediment oxygen
uptake. In general, the efficiency rate of denitrifica-
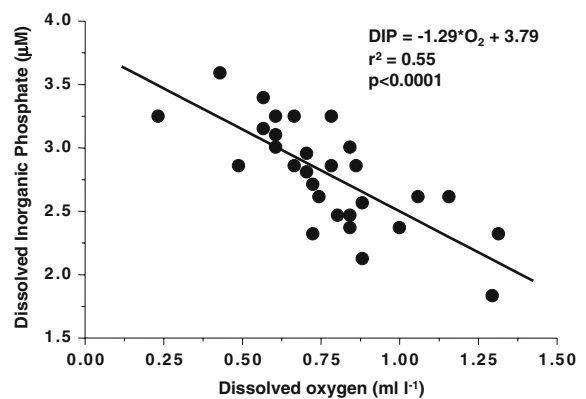tion increases with sediment respiration. However, as

Fig. 1 Relationship between bottom water oxygen concentra-
tions and DIP concentrations in hypoxic bottom waters from
the Baltic Sea (redrawn from Conley et al., 2002)

the sediments become more reducing and more N is remobilized as ammonium and less as nitrate, the rates of denitrification slow such that denitrification can be shut down at high respiration rates. Several studies have demonstrated that in estuarine systems, denitrification displays a threshold-like behavior (Webster & Harris, 2004; Eyre & Ferguson, 2009), increasing to a maximum of carbon decomposition, and then decreasing as sediments become more reducing (Fig. 2). Thus, when coastal and estuarine systems become hypoxic, there is a large risk that the loss of nitrogen will decrease (Smith & Hollibaugh, 1999), thus increasing the availability of DIN and acting as a positive feedback that increases the potential for eutrophication.

The conventional belief that the efficiency of denitrification is reduced when oxygen conditions are low has been challenged with the recent observation that massive amounts of denitrification occur in the water column of hypoxic zones in the open ocean (Deutsch et al., 2007). Recently, Vahtera et al. (2007) found a negative correlation between hypoxic water volume and the total dissolved inorganic nitrogen pool in the Baltic Sea. This suggests greater overall nitrogen removal as the area of hypoxia increases, although current measurements of water column denitrification do not support this hypothesis (Hannig et al., 2007). However, we have no information on the potential for denitrification in the sediments prior to large-scale water column hypoxia in the Baltic Sea. The enhancement or reduction in the rate of denitrification and anammox may depend upon whether systems are seasonally hypoxic or permanently hypoxic and the development of these processes in
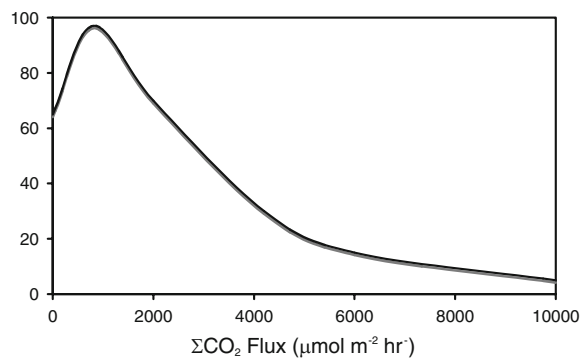
the water column or the sediments. The other important controlling factor governing the loss of nitrogen is certainly the availability of nitrate (Kemp et al., 1990), which is low in many hypoxic zones.

Thresholds of ecosystem hypoxia

The relationship between nutrient inputs and hypoxia may not be a simple one, as there is evidence that once an ecosystem experiences hypoxia, it becomes more vulnerable to future hypoxic events (Conley et al., 2007; Díaz & Rosenberg, 2008). This suggests that the relationship between ecosystem hypoxia and nutrient inputs may show a threshold-like behavior, with a regime shift (Scheffer et al., 2001) involving an abrupt transition from oxic to hypoxic status upon exceeding specific thresholds of nutrient inputs. Regime shifts derive from non-linear responses in ecosystems (Muradian, 2001) where qualitative changes, involving changes in ecosystem buffers and ecosystems processes, lead to an abrupt change in status. These non-linear responses to pressures also imply that ecosystems displaying a threshold-like behavior typically show resistance to return to the original status, resulting in a hysteresis in the recovery to reduced pressures (Muradian, 2001). We argue here that the development of coastal hypoxia can be best conceptualized and examined as a case for ecosystem thresholds conducive to a regime shift that may affect the reversibility of the problem.

As shown above, hypoxia can act as a positive feedback to enhance the effects of eutrophication. In the Baltic Sea, for example, excess DIP remaining after the spring bloom stimulates the growth of large nuisance blooms of nitrogen-fixing cyanobacteria during the summer, with fixation of new nitrogen and the sinking carbon further enhancing hypoxic conditions (Vahtera et al., 2007). Large sediment–water fluxes of DIP occur with hypoxia, returning DIP to a partially P-limited water column, stimulating phytoplankton growth and acting as a positive feedback to increase hypoxia. It has been hypothesized that the Baltic Sea has experienced several ecosystem states with respect to fish production, with eutrophication and enhanced DIP release from anoxic bottoms together with enhanced nitrogen fixation providing a stabilizing mechanism (Österblom et al., 2007).

Fig. 2 System average denitrification efficiency as a function of ΣCO_2 efflux for 22 shallow coastal Australia systems (redrawn from Eyre & Ferguson, 2009)

Recent studies in other coastal marine ecosystems suggest that repeated hypoxic events can help to sustain future hypoxic conditions (Hagy et al., 2004; Kemp et al., 2005). Large-scale changes in benthic communities occur with hypoxia reducing the abundance of large, slow-growing, deeper-dwelling animals, and changing to smaller, fast-growing species that can colonize surface sediments rapidly following hypoxia (Díaz & Rosenberg, 1995). These smaller species do not have the capability to irrigate and bring oxygen downward into the sediments, so that the change in the community structure implies a change in functioning, with the loss of a major buffer against hypoxia. The loss of benthic communities and the inability of the communities to recover with repeated hypoxic events (Karlson et al., 2002) may render ecosystems more vulnerable to future development and persistence of hypoxia. A further loss of sediment-buffering capacity against hypoxia results from the consumption of electron acceptors during the onset of hypoxia (NO_3, O_2, Fe^{2+}, and Mn^{2+}). Once these are depleted during hypoxic events, there is a qualitative change in the sediment metabolism from aerobic to anaerobic pathways involving profound changes in the rates and processing of organic matter (Soetaert & Middelburg, 2009). Once sediments and water become anoxic, anaerobic metabolism leads to the accumulation of reduced metabolites such as sulfides in the system, which titrate oxygen diffusing into the system, thus acting as buffers preventing re-oxygenation of the environment. For example, sulfide accumulation has been shown to be a major buffering process acting to maintain sediments anoxic under seagrass beds that receive excess organic inputs, as sulfide is rapidly oxidized thereby consuming oxygen inputs (Holmer et al., 2003).

Hence, ecosystem hypoxia leads to the loss of important ecosystem buffers that favor the maintenance of oxic conditions (sediment bio-irrigation and electron acceptors) and the appearance of new buffers that act in the opposite direction to maintain ecosystems hypoxic (Fig. 3). Ecosystem buffers are responsible for the resilience of ecosystems. Once they are changed with hypoxia, the resilience of the ecosystems against hypoxia is eroded and new buffers, acting to build resilience to the hypoxic state, appear that increase ecosystem vulnerability to this disturbance and tend to perpetuate hypoxia.
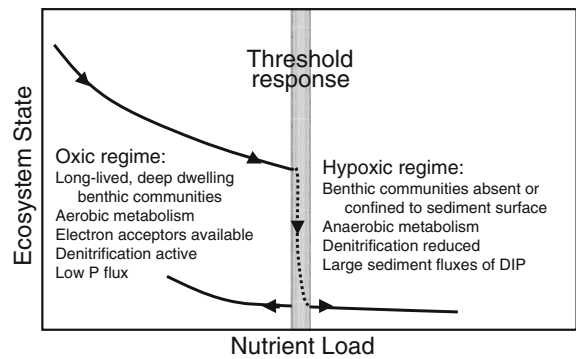

Fig. 3 Hypothetical diagram showing change in ecosystem state as represented by bottom water oxygen concentrations versus nutrient concentrations. An ecosystem is believed to reach a threshold when bottom-living organisms are killed and the system switches to one dominated by anaerobic processes

We have tested for changes in ecosystem state in three large coastal marine ecosystems that have experienced hypoxia over the last decades (Fig. 4A–C): the Danish Straits (Conley et al., 2007), Chesapeake Bay (Hagy et al., 2004), and the Gulf of Mexico (Rabalais et al., 2002). We used a change-point detection method (Gombay and Horvath, 1996) to test for the significance of thresholds in time-series data assuming observations to be normally distributed and a change in the mean or in the linear relation to the driver to occur at an unknown point in time. For the Danish Straits, two significant change points were detected (Fig. 4A): in 1986 (Conley et al., 2007) and again after the record hypoxia in 2002 (HELCOM, 2003). Note that the second shift in 2002 was not found in Conley et al. (2007) because there were not as many observations reported following the 2002 event. In the Danish Straits, hypoxia has worsened following the appearance of large-scale hypoxic events (Fig. 4A; Conley et al., 2007). For Chesapeake Bay, we determined that the significant change occurred in 1986 (Fig. 4B). A persistent increase in the susceptibility of Chesapeake Bay has previously been noted by Hagy et al. (2004) and Kemp et al. (2005), although the time-point of change was not previously pinpointed. Finally, the Gulf of Mexico has exhibited a significant increase in hypoxia (Fig. 4C) following the 1993 record flooding in the Mississippi River (Rabalais et al., 2002). Higher sedimentary oxygen demand in the Gulf of Mexico has been hypothesized
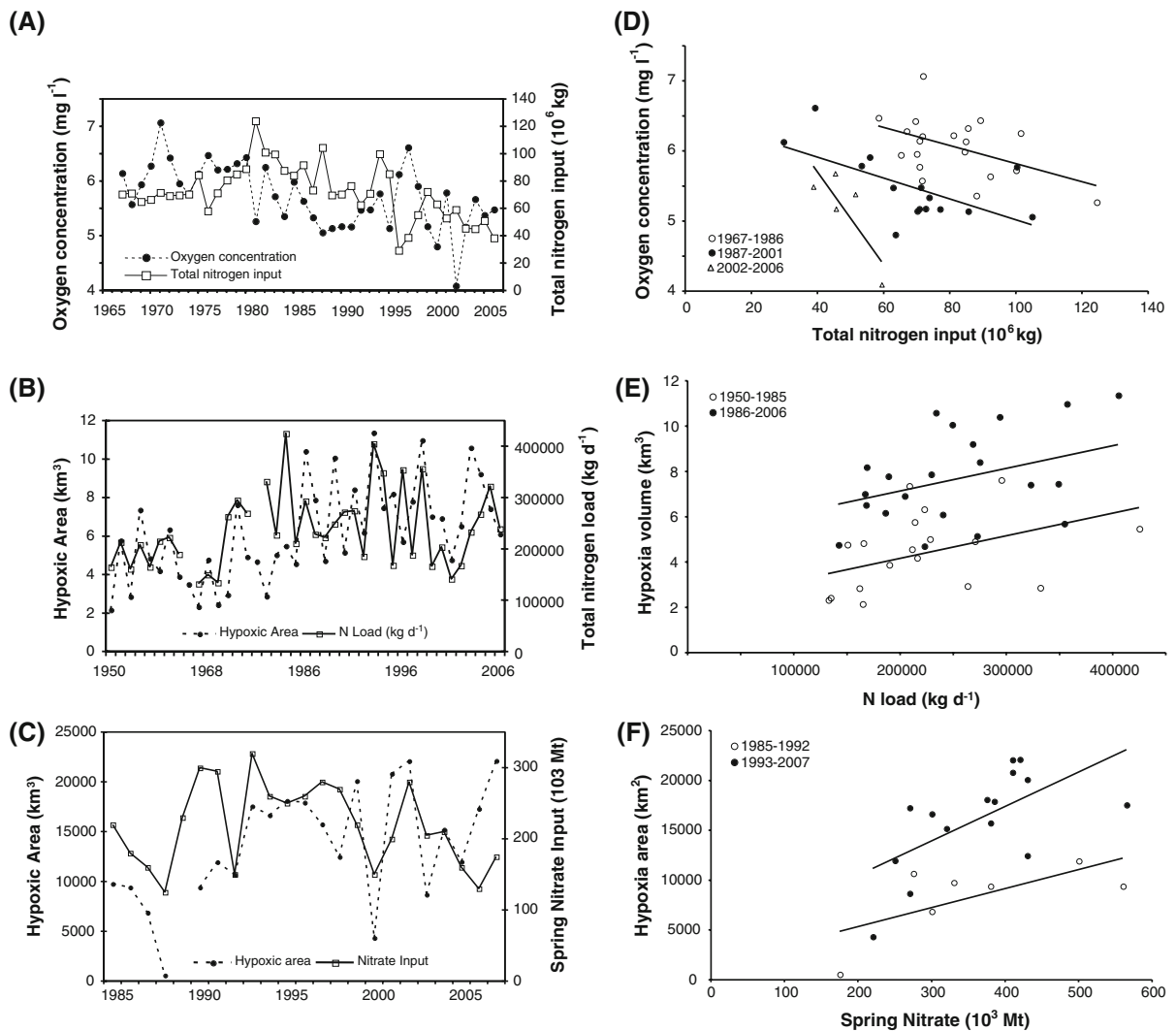
Fig. 4 Systems displaying significant thresholds ($P < 0.05$) in hypoxia through time (**A–C**). The significance of the thresholds was tested with a change-point detection method (Gombay & Horvath, 1996). **A** and **D**: Danish Straits (Conley et al., 2007); **B** and **E**: Chesapeake Bay (Hagy et al., 2004; Scavia et al., 2006; D. Scavia, University of Michigan, unpubl. data); and **C** and **F**: size of the hypoxic zone in the northern Gulf of Mexico (N.N. Rabalais, Louisiana Universities Marine Consortium

(LUMCON), unpubl. data, http://www.gulfhypoxia.net/) and spring (April, May, June) nitrate + nitrite inputs from the Mississippi and Atchafalya rivers (Alexander et al., 2008). **D–F** examines the relationship between nitrogen loading and hypoxia. Slopes for the separate periods were not significantly different, and therefore, the thresholds were manifested as a change in the mean of hypoxic conditions only. (The unit Mt signifies metric tonnes)

to result in an increase in the size of the hypoxic zone and can be considered a shift to an alternative steady state (Turner et al., 2008). Hypoxia in the Gulf of Mexico has worsened after 1993; for example, smaller river flows have induced a larger response in hypoxia since then (Fig. 4C), with the occurrence of large hypoxic areas over 15,000 km^2 observed in many of the following years. Subsequently, we examined the slope of nitrogen loading versus oxygen

concentration for the different periods (Fig. 4D–F). In all cases, significant relationships were observed between hypoxia and nitrogen loading, although the slope of the relationship was not significantly different, and therefore, the thresholds were manifested as a change in the mean hypoxic conditions only.

These changes suggest that a regime shift occurs in coastal marine ecosystems affected by large-scale hypoxia (Conley et al., 2007). Regime shifts are often

rapid transitions that occur in an ecosystem state to new alternative states, with changes in biological variables that propagate through several trophic levels (Scheffer et al., 2001; Collie et al., 2004). Regime shifts can have large consequences for fisheries (Collie et al., 2004; Oguz & Gilbert, 2007). The recovery of ecosystems from hypoxia may occur only after long time periods (Díaz, 2001) or with further reductions in nutrient inputs. Although it is possible for coastal marine ecosystems to respond rapidly to large reductions in nutrient loading (Rask et al., 1999; Mee, 2006), experience has generally shown recovery to be greatly delayed, taking years to decades for ecosystems to recover after nutrient inputs are reduced, and probably less than complete recovery is possible (Díaz, 2001; Duarte et al., 2009). One potential concern with regime shifts is that the condition is not easily reversible. The ability of coastal marine ecosystems to recover from hypoxia may be partly related to the ability of organisms to recolonize and the availability of nearby refuges. These observations suggest that the thresholds for hypoxia are dynamic, and that once trespassed, the changes in internal buffers discussed above render the ecosystems more prone to experience future hypoxia, effectively lowering the thresholds of nutrient inputs at which hypoxia takes place and increasing the recurrence of the problem.

Impact of global warming

Coastal hypoxia has been primarily linked to increased nutrient inputs. Yet, this is not the sole control on hypoxia. Temperature is one of the major factors controlling the extent of hypoxia (Conley et al., 2007), acting through a multitude of interacting processes. Temperature increases may enhance stratification, thereby reducing the supply of oxygen to bottom waters by vertical mixing. However, stratification also potentially reduces the upward mixing of nutrients across the pycnocline, which constitutes a considerable source for production, and consequently decreases the export of particulate organic matter to bottom waters, particularly in the summer period. Temperature also affects the respiration of organisms in the water column. A consequence of this could be higher remineralization of organic matter in the upper mixed layer and lower sedimentation of particulate organic matter, whereby a larger fraction of the organic matter sedimenting out of the upper mixed layer may be respired instead of permanently buried. Increasing temperature may also affect phytoplankton grazing, but it is not clear whether matching of primary production and grazing will improve or worsen. Finally, the solubility of oxygen decreases with temperature, reducing the margin in oxygen concentration separating well-ventilated waters from hypoxia, such that there will be less oxygen for replenishing bottom waters, no matter whether this occurs by vertical mixing or advective transport of subducted surface water.

The latter process is probably the most important effect in relation to temperature for coastal waters with estuarine character. Conley et al. (2007) analyzed long-term oxygen concentrations in the Danish straits with respect to temperature and found, using multiple regression, that they declined by 0.238 (± 0.084) mg O_2 $l^{-1}{}^{\circ}C^{-1}$, as predicted by the effect of temperature on the solubility of oxygen (approximately -0.26 mg O_2 $l^{-1}{}^{\circ}C^{-1}$). The effect of temperature on oxygen production and consumption may also be important. Harris et al. (2006) calculated, using metabolic theory, that a 4°C increase in the summer water temperatures of a northeastern Atlantic estuary will result in a 20% increase in net primary production and a 43% increase in respiration, resulting in an increasing likelihood of system hypoxia. However, in contrast to the effect of temperature increases on oxygen solubility, which is well known and precise, the effects on ecosystem metabolism still need to be verified. In the text below, consequences of global warming on hypoxia will be assessed assuming oxygen solubility to be the major effect of temperature increase and that the other temperature-dependent processes more or less even each other out.

Over the last decades, substantial evidence from both observations and model results has documented an ongoing global warming (Christensen et al., 2007), which is now generally accepted as a fact in the scientific community. However, there is still much debate about how much the globe will warm. Here, we used the temperature projections obtained by the ECHAM4/OPYC3 model (Roeckner et al., 1999) that couples atmosphere, sea-ice, and oceans assuming the atmospheric pCO_2 level to reach 750 µatm by 2100. Using this model, Hansen & Bendtsen (2006) obtained regional forecasts for the Danish straits of

surface water temperature increases around 3.5°C, with seasonal variation from 4°C in winter to 3°C in summer. Physical models of the area using aging tracers have shown that bottom waters in the hypoxia areas (July–October) originate as Skagerrak surface waters penetrating into the straits during winter and spring (Hansen & Bendtsen, 2006). With a temperature increase of 4°C, oxygen solubility is lowered by 0.96 mg O_2 l^{-1}, which corresponds well to the extrapolated value (0.95 mg O_2 l^{-1}) using the regression analysis in Conley et al. (2007).

The spatial coverage of hypoxia in the Danish straits has been analyzed with a weekly resolution from 1998 to 2005 using a spatial and temporal interpolation technique of oxygen profiles described in HELCOM (2003). The effect of a 4°C temperature increase was analyzed by subtracting 0.952 mg O_2 l^{-1} from the estimated oxygen concentrations at the bottom. Areas exposed to hypoxic conditions (<2 mg O_2 l^{-1}) any time during a specific year were identified. During the 8-year period, 1998 had the best oxygen conditions with 968 km^2 exposed to hypoxia, whereas 2002 was the worst year with 8256 km^2 (Fig. 5). With a projected decrease in oxygen solubility with warming and all other factors unchanged, the area of hypoxia would have been 2269 km^2 and 16,720 km^2 for the 2 years, respectively. In the latter case, this corresponds to 38% of the entire bottom area and, in fact, most of the Danish straits except the Kattegat would be hypoxic below the pycnocline located at 15–20 m depth. In a normal year, 5–10% of the bottom area exposed to hypoxia under present conditions will increase to 10–15% for the projected temperature increase. Overall, the area of hypoxia will approximately double with a temperature increase of 4°C.

Future perspectives

Hypoxia is becoming an increasingly widespread phenomenon throughout the world (Díaz, 2001), and evidence for eutrophication as an important causal factor is increasing (Scavia et al., 2003; Hagy et al., 2004; Conley et al., 2007). Despite nutrient reductions in some areas affected by hypoxia (e.g., Carstensen et al., 2006), there has still been no reported recovery from hypoxia in coastal ecosystems. This does not mean that nutrient reductions are
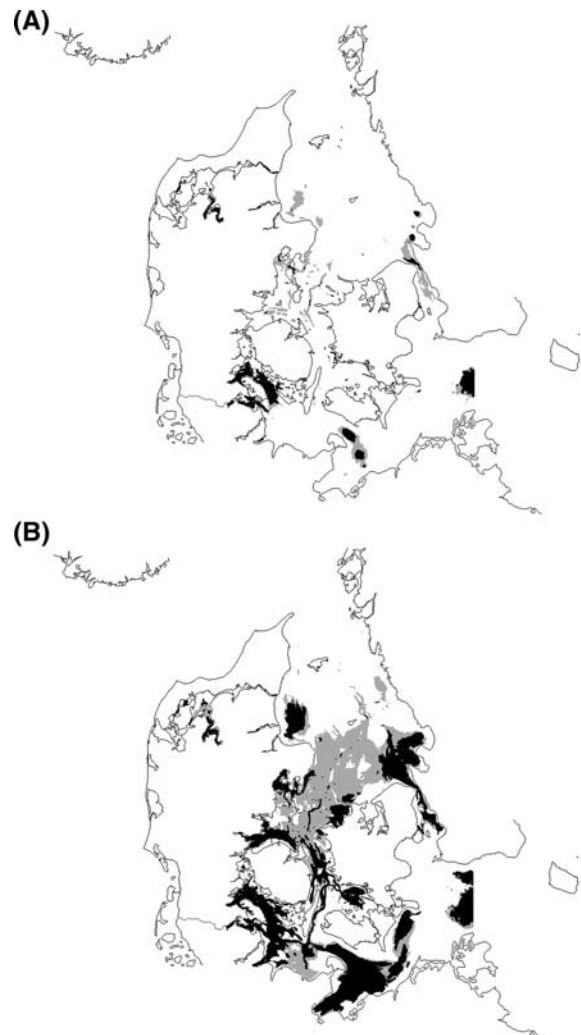

Fig. 5 Areas exposed to hypoxic conditions at present (*black shading*) and projected for a 4°C temperature increase (*grey shading*) in the best year, 1998 (**A**), and in the worst year, 2002 (**B**)

not important for improving oxygen concentrations; hypoxia would have been even worse if nutrient inputs had not been reduced. Nutrient reductions may to some extent have been counteracted by temperature increases and regime shifts in the sequestering of organic material, making hypoxia a self-sustaining process. Failure to reduce nutrient inputs may lead to cascading effects of increasing hypoxia with the return to a desired status becoming more and more unlikely, and nutrient reduction is the only realistic management measure for improving oxygen conditions. Consequently, hypoxia can only be remedied by reducing nutrient inputs to levels that will allow

for recolonization of macrozoobenthos and a balance between nutrient input and removal rates. The sooner significant reductions are implemented, the more likely is the recovery. Finally, monitoring of oxygen conditions and nutrient management responses are important for coastal ecosystems showing early signs of beginning hypoxia. Nutrient reductions required to restore coastal ecosystem health may be larger if thresholds of hypoxia are exceeded.

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