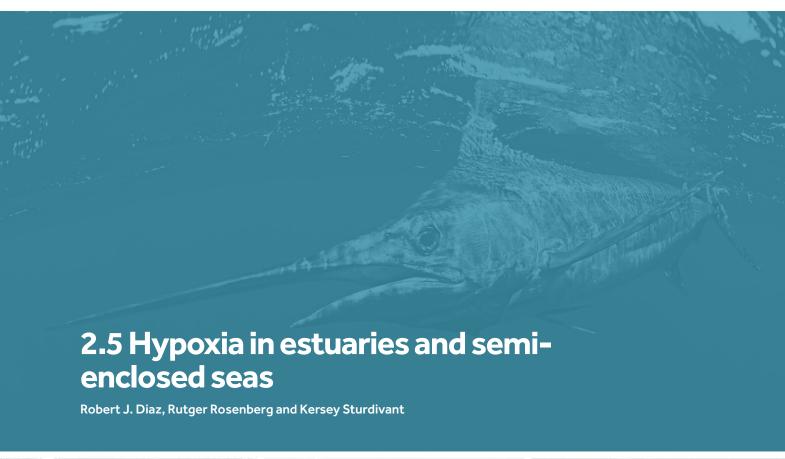


Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions Edited by D. Laffoley and J.M. Baxter









ILICN GLOBAL MARINE AND POLAR PROGRAMME









2.5 Hypoxia in estuaries and semi-enclosed seas

Robert J. Diaz¹, Rutger Rosenberg² and Kersey Sturdivant³

¹Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt., VA, USA. Email: robertdiaz@icloud.com ²Kristineberg Marine Research Station, University of Gothenburg, Gothenburg, Sweden. Email: rutger.rosenberg@bioenv.gu.se ³Duke University Marine Lab, Nicholas School of the Environment, Beaufort, NC, USA. Email: kersey.sturdivant@duke.edu

Summary

- In the last 65 years, over-enrichment of waters with nutrients or organic matter (eutrophication), has emerged
 as a problem that threatens and degrades coastal ecosystems, alters fisheries, and impacts human health in
 many areas around the world. Hypoxia is one of the most acute symptoms of this eutrophication and harmful
 algal blooms another.
- The global extent of eutrophication-driven hypoxia and its threats to ecosystem services are well documented, but much remains unknown relative to human health, social, and economic consequences.
- The importance of maintaining adequate levels of oxygen in coastal systems is best summarized by the motto of the American Lung Association: "if you can't breathe nothing else matters".
- Over 900 areas around the world have been identified as experiencing the effects of eutrophication. Of these, over 700 have problems with hypoxia, but through nutrient and organic loading management about 70 (10%) of them can now be classified as recovering.
- There is no other environmental variable of such ecological importance to coastal ecosystems that has changed so drastically in such a short period of time as a result of human activities as dissolved oxygen.

Coastal hypoxia effect	Potential consequences
Loss of biomass.	 Direct mortality of fisheries species. Direct mortality of prey species. Reduced growth and production. Reduced recruitment.
Loss of biodiversity.	 Elimination of sensitive species. Reduced diversity. Increased susceptibility to disease and other stressors. Lower food web complexity.
Loss of habitat.	 Crowding of organisms into suboptimal habitats. Increased predation risks from both natural and fishing pressure. Forced departure from preferred habitat. Altered or blocked migration routes.
Altered energy and biogeochemical cycling.	 Increased energy flow through microbes. Production of toxic hydrogen sulphide. Release of phosphorus and other nutrients from sediments that fuels algal blooms. Loss of denitrification.

2.5.1 Introduction

The human population is rapidly expanding, recently passing 7 billion and will likely exceed 10 to 12 billion by the year 2100 (Gerland et al., 2014). This expansion has led to extensive modification of landscapes at the expense of ecosystem function and services, including pervasive effects on coastal primary production from excess nutrients to overfishing (Ripple et al., 2017). Long-term records of nutrient discharges provide compelling evidence of a rapid increase in the fertility of many coastal ecosystems starting in the 1960s. On a global basis, by 2050, coastal marine systems are expected to experience at least a doubling in both nitrogen and phosphorus loading compared to current levels, with serious consequences to ecosystem structure and function (Foley, 2017; Foley et al., 2005).

The question asked by Foley et al. (2005) is: 'Are land use activities degrading the global environment in ways that undermine ecosystem services, which in turn undermine human welfare?' When it comes to dissolved oxygen the answer is yes. In marine ecosystems, oxygen depletion has become a major structuring force for communities and energy flows at global scales.

Eutrophication can be defined as an increasing rate of primary production and organic carbon accumulation in excess of what an ecosystem is normally adapted to processing (Nixon, 1995). It is one part of a complex of stressors that interact to shape and direct ecosystem processes. The most obvious ecosystem response to eutrophication is the excessive greening of the water column and overgrowth of algae and vegetation in coastal areas, a direct response to nutrient enrichment. The unseen response to eutrophication is the decrease in dissolved oxygen in bottom waters created by decomposition of the excess organic matter delivered to the sea bed, which can lead to hypoxia or dead zones (i.e. areas where dissolved oxygen levels drop to 2.8 mg O₂ L⁻¹ or lower). In the past this eutrophicationinduced low oxygen or hypoxia was mostly associated with rivers, estuaries, and bays. But dead zones now develop in continental seas, such as the Baltic Sea, Kattegat, Black Sea, Gulf of Mexico, and East China Sea.

Much of the sensitivity of organisms to low oxygen is related to the fact that oxygen is not very soluble in water and that small changes in oxygen concentration lead to large percentage differences. For fresh water at 20 °C, 9.1 mg of oxygen (O_2) will dissolve in a litre of water. This would be 100% saturation. A 1 mg O_2 L⁻¹ drop is about a 11% decline in saturation. In addition, oxygen solubility is strongly dependent on temperature and the amount of salt dissolved in the water. Saturation declines about

1 mg $\rm O_2$ L⁻¹ from 20 to 26 °C and about 2 mg $\rm O_2$ L⁻¹ from fresh water to sea water at similar temperatures (Benson & Krausse, 1984). So, depending on temperature and salinity, water contains 20-40 times less oxygen by volume and diffuses about ten thousand times more slowly through water than air (Graham, 1990).

Thus, what appear to be small changes in oxygen can have major consequences for animals living

in an oxygen-limited milieu. Physiologically, higher temperatures also increase metabolic requirements for oxygen and increase rates of microbial respiration and, therefore, oxygen consumption. For salmonid fishes, oxygen can become limiting at higher temperatures when oxygen solubility declines (Fry, 1971). Concentrations of dissolved oxygen below 2 to 3 mg $\rm O_2$ L $^{-1}$ are a general threshold value for hypoxia for marine and estuarine organisms, and 5 to 6 mg $\rm O_2$ L $^{-1}$ in fresh water. However,

Table 2.5.1 Planetary boundary processes (Rockström et al., 2009) and how exceeding them will affect dissolved oxygen.

Earth-System Process	Parameters (units)	Proposed Boundary	Current Status	Pre-Industrial Value	Consequences for oxygen
Climate change	(i) Atmospheric carbon dioxide concentration (parts per million by volume)	350	387	280	More carbon dioxide in water reduces oxygen concentration
	(ii) Change in radiative forcing (watts per metre squared)	1	1.5	0	Warmer water holds less oxygen
Rate of biodiversity loss	Extinction rate (number of species per million species per year)	10	>100	0.1-1	Lower oxygen will stress more species
Nitrogen and Phosphorus Cycles	(i) Amount of N ₂ removed from the atmosphere for human use (millions of tonnes per year)	35	121	0	More N and P entering coastal systems will increase primary production, which will in turn decompose and lower oxygen increasing hypoxia
	(ii) Quantity of P flowing into the ocean (millions of tonnes per year)	11	8.5-9.5	~1	
Stratospheric ozone depletion	Concentration of ozone (Dobson unit)	276	283	290	Unknown
Ocean acidification	Global mean saturation state of aragonite in surface sea water (Ω)	2.75	2.9	3.44	More acidic waters contain less oxygen
Global freshwater use	Consumption of freshwater by humans (km³ per year)	4,000	2,600	415	Reduced river flow would improve low oxygen conditions
Change in land use	Percentage of global land cover converted to cropland (%)	15	11.7	Low	More cropland leads to more nutrient runoff, see Nitrogen and Phosphorus Cycles
Atmospheric aerosol loading	Overall particulate concentration in the atmosphere on a regional basis		To be determined		Unknown
Chemical pollution	Amount emitted or concentration of persistent organic pollutants, plastics, endocrine disrupters, heavy metals and nuclear waste in the global environment, or the effects on ecosystem and functioning of Earth systems		To be determined		Unknown

species and life stages differ greatly in their basic oxygen requirements and tolerances (Vaquer-Sonyer & Duarte, 2008).

The relatively low solubility of oxygen in water combined with two principal factors lead to the development of hypoxia and at times anoxia. These factors are water column stratification that isolates the bottom water from exchange with oxygen rich surface water and decomposition of organic matter in the isolated bottom water that reduces oxygen levels. Both factors must be at work for hypoxia to develop and persist in bottom waters.

2.5.2 Geographic definition

Hypoxia caused by human activities occurs on every continent, including Antarctica (Conlan et al., 2004). Over the last 60 to 70 years alarming global trends of declining oxygen concentrations have emerged both in coastal areas and in the open oceans (Gilbert et al., 2009; Ito et al., 2017; Schmidtko et al., 2017). Similar trends have been documented for lakes, starting over 100 years ago, some 70 years prior to the spread of hypoxia in coastal regions (Jenny et al., 2016). Many of these declining oxygen trends have been linked to human activities directly or indirectly. Rockström et al. (2009) proposed that there are boundaries which if exceeded will negatively impact global ecosystems including humanity. While oxygen was not one of the nine boundaries discussed, it is influenced by many of the processes discussed (Table 2.5.1). The expanding size of the human population has led to three of the boundaries being crossed, which are climate change, rate of biodiversity loss, and the nitrogen cycle. Of these, alterations to the nitrogen cycle have the most direct consequences for dissolved oxygen, followed by climate change. The more nutrients added to the sea the more organic matter will be produced, which will create a greater oxygen demand when it is decomposed, potentially leading to more hypoxia.

Since the 1960s, the global number of hypoxic systems has about doubled every ten years up to 2000 (Figure 2.5.1). Prior to 1960, there were about 45 systems with reports of eutrophication-related hypoxia. During the 1960s, another 60 systems were added. The 1970s saw estuarine and coastal ecosystems around the world becoming over-enriched with organic matter from expanding eutrophication and the number of oxygendepleted ecosystems jumped from about 100 to 180. In

the 1980s many more systems reported hypoxia for the first time bringing the total to about 330. More hypoxic areas were reported in the 1990s than any other decade and the total rose to about 500 systems. By the end of the 20th century the total was about 500 and hypoxia had become a major, worldwide environmental problem. About 15% of these hypoxic systems (70) are now showing signs of improvement (Conley et al., 2011; Diaz et al., 2010). At the end of the first decade of the 21st century another 140 sites reported hypoxia, bringing the total to about 640. This total of 640 does not include about 65 sites that Conley et al. (2011) identified from the Baltic region. When these are added the total number of dead zones jumps to about 700. An additional 230 coastal sites were identified as areas of concern that currently exhibit signs of eutrophication and are at risk of developing hypoxia (Diaz et al., 2010).

2.5.3 Trends and impacts

The past 65 years have witnessed a ten-fold increase in the number of eutrophication-driven hypoxic areas. There are signs of a slowing in the growth of the number of hypoxic systems, mostly because North America and Europe are well studied and almost completely reported. Altieri et al. (2017) examined latitudinal trends in the number of known dead zones and research effort and concluded that there are hundreds of tropical dead zones yet to be identified, particularly in Asia, the Indo-Pacific, and oceanic islands. It is highly likely that globally there are over 1,000 dead zones based on the very strong correlation between human population centres and the presence of hypoxia, and the underreported ecosystems in those locations. The distribution of coastal oxygen depletion is either centred on major population concentrations, or closely associated with developed watersheds that deliver large quantities of nutrients. The distribution of dead zones closely matches the deposition of nitrogen from human activities in North America, Europe, and South America (Figure 2.5.2). While some of the highest deposition rates are in India and China, there is little information on water quality to assess oxygen conditions.

Since the early 2000s many assessments of global environmental and resource health identify hypoxia as one of the factors threatening coastal and ocean life, for example the Millennium Ecosystem Assessment (2005). In addition, climate model predictions and observations reveal regional declines in oceanic dissolved oxygen linked to global warming (Deutsch et al., 2011; Ito et

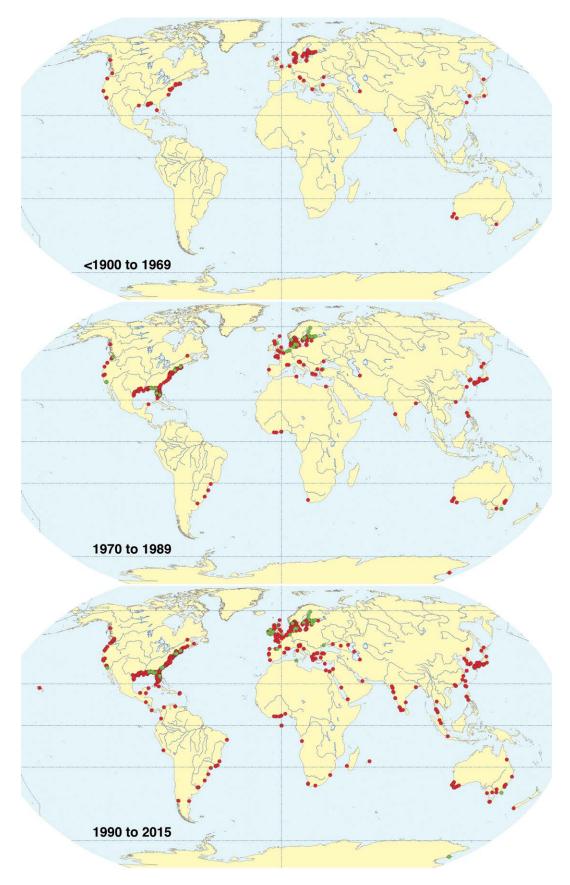


Figure 2.5.1 Global pattern in the cumulative development of coastal hypoxia through time. Each red dot represents a documented case related to human activities. Green dots are sites that have improved. Based on Diaz & Rosenberg (2008), Diaz et al. (2010), and Conley et al. (2011).

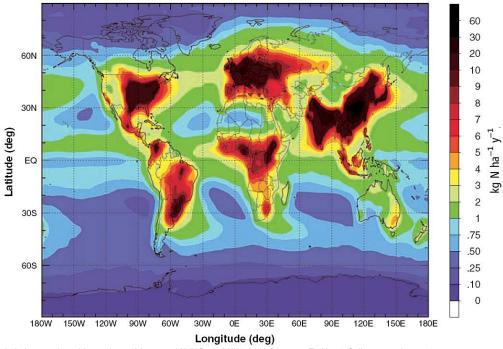


Figure 2.5.2 Global nitrogen deposition estimated from total N (NO, and NH,) emissions, 105 Tg N yr⁻¹ (Galloway et al., 2008).

al, 2017). To understand hypoxia and its effects on ecosystems requires several perspectives that start at a local level, move to regional, and finally to a global perspective. The most important scale is local for stressors like coastal development, nutrients, pollution, and eutrophication. At local scales (<1 to 1,000 km²) impacts are most pronounced and where there is most information. At regional scales (>1,000 to 1,000,000 km²) it is a mix of influences from land and sea. This involves local land-based impacts and processes bleeding into regional seas, and large-scale open ocean processes at the boundaries of regions, such as upwelling and water column stratification depth. Much of the problem with hypoxia at local and regional levels can be directly tied to concentrations of human populations and agriculture, both of which have significantly altered the global nitrogen cycle (Gruber & Galloway, 2008; Seitzinger et al., 2010), (Figure 2.5.3). Global scales factors that influence oxygen and hypoxia are changes in circulation patterns, climate, temperature, and pH.

Climate change, whether from global warming or from microclimate variation, will have consequences for eutrophication-related oxygen depletion that will progressively lead to an onset of hypoxia earlier in the season and possibly extending it through time. The influence of multiple climate drivers needs to be considered to understand what future change to expect (Table 2.5.2). Climate change may make systems more susceptible to development of hypoxia through its direct

effects on water column stratification, precipitation patterns, and temperature. These effects will likely occur primarily through warming, which will lead to increased water temperatures and subsequent decreases in oxygen solubility. Warmer surface waters will extend and enhance water column stratification, a key factor in the development of hypoxia (Laurent et al., 2018). Warmer water will increase organism metabolism, which is the key process for lowering oxygen concentrations. In addition to warming, future climate predictions include large changes in precipitation patterns. If changes in precipitation lead to increased runoff to estuarine and coastal ecosystems, stratification and nutrient loads are likely to increase and worsen oxygen depletion (Justic'et al., 2007; Najjar et al., 2010). Conversely, if stratification decreases due to lower runoff or is disrupted by increased storm activity or intensity, the chances for oxygen depletion should decrease (Table 2.5.2).

Much of how climate change will affect hypoxia in the coastal zone will depend on coupled land-sea interactions with climate drivers (Table 2.5.2). But the future pervasiveness of hypoxia will also be linked to land management practices and expansion of agriculture to feed an ever-increasing human population. Land management will affect the nutrient budgets and concentrations of nutrients applied to land through agriculture (Sinha et al., 2017). If in the next 50 years humans continue to modify and degrade coastal systems as in the previous 100 years (Halpern et al.,

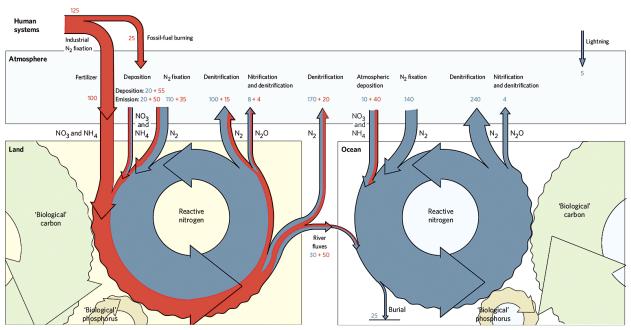


Figure 2.5.3 The global nitrogen cycle on land and in the ocean from Gruber & Galloway (2008). Major processes that transform molecular nitrogen into reactive nitrogen are shown. There is also a tight coupling between the nitrogen cycles on land and in the ocean with those of carbon and phosphorous. Blue fluxes denote 'Natural' (unperturbed) fluxes; orange fluxes denote anthropogenic perturbation. Numbers are in Tg N yr⁻¹ and are for the 1990s.

2008), human population pressure will likely continue to be the main driving factor in the persistence and spread of coastal dead zones. Overall, climate drivers will tend to magnify the effects of expanding human population.

Climate related changes in wind patterns are of great concern for coastal systems as wind direction and strength influence the strength of upwelling/downwelling, which in turn affect stratification strength and delivery of deepwater nutrients into shallow coastal areas. Even relatively small changes in wind and current circulations could lead to large changes in the area of coastal sea bed exposed to hypoxia. Changes in the pattern of upwelling on the Pacific coast off Oregon and Washington due to shifts in winds that affected the California Current systems appeared to be responsible for the recent development of severe hypoxia over a large area of the inner continental shelf (Chan et al., 2008; Grantham et al., 2004).

Thus, the future status of hypoxia and its consequences for the environment, society and economies will depend on a combination of climate change (primarily from warming, and altered patterns for wind, currents and precipitation) and land-use change (primarily from an increasing human population, agriculture and nutrient loadings). Expanding energy demands associated with population growth now drive climate change that threatens all ecosystems at all scales from local to global.

2.5.4 Ecosystem consequences

Relative to oxygen, we do not know where the boundaries are for ecosystem catastrophe (Table 2.5.1). The amount, severity, and duration of hypoxia and anoxia must all be factored in. While there are, at times, spectacular events such as mass mortalities of sessile organisms, less is known about population level effects of hypoxia and anoxia. Exposure to hypoxia can reduce reproduction over sufficiently large spatial scales as to affect the dynamics of populations and fisheries production (Bianucci et al., 2016; Breitburg, 2002; Rose et al., 2009), and can even trigger genetic changes in future generations, even if these generations themselves are not exposed to hypoxia (Wang et al., 2016). We also know that when hypoxia develops fish, crabs, shrimp, and other mobile marine life will swim away to areas of higher oxygen concentration, often congregating in dense assemblages right along the boundary of low oxygen zones (Craig & Crowder, 2005). This phenomenon is the origin of the term dead zone, a place where fishermen cannot find anything to catch due to the migration of mobile animals out of the affected area. As a dead zone forms, suitable habitat is compressed and the resulting "escape" by mobile fauna comes at a cost. Individuals suffer lost growth potential (due to a shift to less-suitable habitat and increased competition for resources through crowding), increased vulnerability to predation (as fauna are restricted to

Table 2.5.2 Influence of climate drivers on the extent and severity of hypoxia (Modified from Boesch et al., 2007).

Climate Driver	Direct Effect	Secondary Effect	Influence on Hypoxia
Increased temperature	More evaporation	Decreased stream flow	+
		Land-use & cover changes	-/+
	Less snow cover	More nitrogen retention	-
	Warmer water	Stronger stratification	+
		Higher metabolic rates	+
More precipitation	More stream flow	Stronger stratification	+
		More nutrient loading	+
	More extreme rainfall	Greater erosion of soil P	+
Less precipitation	Less stream flow	Weaker stratification	-
		Less nutrient loading	-
Higher sea level	Greater depth	Stronger stratification	+
		Greater bottom water volume	-
		Less hydraulic mixing	+
	Less tidal marsh	Diminished nutrient trapping	+
Summer winds and storms	Weaker, less water column mixing	More persistent stratification	+
	Stronger, more water column mixing	Less persistent stratification	-
	Shifting wind patterns	Weaker/stronger upwelling potential	-/+

shallower, better-lighted waters), higher susceptibility to fishing (by predictably aggregating individuals at the edge of hypoxic zones), etc. (Table 2.5.3). As a result,

hypoxia indirectly influences harvest, both through effects on processes underlying production such as growth and mortality (including effects on juveniles



Figure 2.5.4 Mersey Estuary \bigcirc Shutterstock.com.

Table 2.5.3 Generalized response of populations to hypoxia and potential economic effect.

Factor	Result	Potential economic Effect
Mortality	Loss of stock, may take years to recover	Lower landings Increased time fishing
Reduced recruitment	Smaller populations, effect may be long lasting	Lower landings Increased time fishing
Reduced growth	Smaller individuals	Lower individual value
Poor body condition	Weaker individuals	Lower value
Increased migration	Energy resources diverted to movement	Smaller individuals Increased time fishing
Aggregation	Exposure to increased risks of predation and exploitation	Less time fishing Easier to catch
Altered behaviour	More/Less susceptible to fishing gear	Increased or decreased catchability

Direct effects on fisheries stocks related to reduced growth, movement to avoid low oxygen, aggregation and predation pressure.

Direct effects on fishers related to increased time on fishing grounds, cost of searching for stocks, and market forces that control dock side prices.

before they are subject to fishing pressure), and on processes influencing catchability (e.g. emigration, avoidance behaviour).

Mechanistically hypoxia is linked to other stressors, e.g. global warming, ocean acidification, and pollution, and it is often the combined effects of these perturbations that shapes marine ecosystems (Breitburg et al., 2015; Farrell, 2016; Gobler et al., 2016). Because hypoxia limits energy acquisition, it is likely to exacerbate the effects of co-occurring stressors that increase energy demands. Additionally, the development and persistence of ocean dead zones can also create toxic hydrogen sulphide (H₂S) that negatively affects marine life separately from the physiological limitations of a decrease in oxygen.



Figure 2.5.5 Bluefish *Pomatomus saltatrix* © Paolo Oliveira - Alamy stock photo.

All of these factors complicate efforts to identify direct population level responses to hypoxia.

The earliest accounts of hypoxia-stressed systems are from European fjords, such as the Drammensfjord and rivers with population and industrial centres, such as the Mersey Estuary (Figure 2.5.4), where a combination of factors including hypoxia led to the elimination of salmon by the 1850s (Alve, 1995; Jones, 2006). In the USA the earliest account of ecological stress associated with hypoxia come from Mobile Bay, Alabama, where in the 1850s, hypoxic bottom water pushed by tides and wind into shallow water caused mobile organisms to migrate and concentrate at the water's edge. These events became known as "Jubilees" as it was easy for people to pick up the hypoxia stressed fish and crabs that had congregated along the shoreline (May, 1973). In all cases, hypoxia caused the movement of mobile fauna, which has energetic consequences, and reduced or eliminated the trophic base for bottom-feeding species, which has adverse consequences for a system's higher level energy flows (Baird et al., 2004).

If it is important for fish and shrimp to reach critical nursery or feeding areas at certain times in their life cycle, then hypoxia may affect population dynamics by delaying arrival or shortening time spent on spawning or feeding grounds. In such cases, the cost of delayed migration in terms of population mortality and production is not known. For example, in 1976 continental shelf hypoxia in the New York-New Jersey Bight blocked the northward migration of bluefish (*Pomatomus saltatrix*) (Figure 2.5.5). Fish that encountered the hypoxic

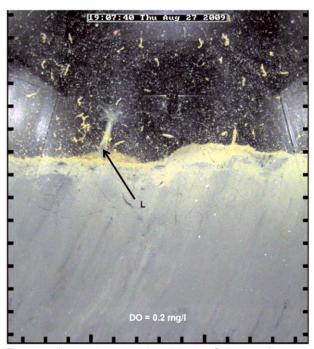


Figure 2.5.6 Hypoxia's impact on infauna behaviour. Sediment profile image of the holothurian, *Leptosynapta tenuis* (L), extending out of the sediment during near-anoxic conditiuons as it tries to reach water with more dissolved oxygen. Scale around image is in cm units. Light artefacts from reflections are visible on the edge of the image. Modified from Sturdivant et al. (2012).

zone did not pass through or around it but stayed to the south waiting for the hypoxia to dissipate and then continued their migration which was delayed by weeks. On the continental shelf of the northern Gulf of Mexico, hypoxia interfered with the migration of brown shrimp (Farfantepenaeus aztecus) from inshore wetland nurseries to offshore feeding and spawning grounds. Juvenile brown shrimp leaving nursery areas migrated farther offshore when hypoxia was not present but were compressed inshore when hypoxia was present. In avoiding hypoxia, brown shrimp aggregated both inshore and offshore of low oxygen areas losing about a quarter of their shelf habitat for as much as six months (Rabalais et al., 2010). The population consequences of this are unknown.

There is a similarity of faunal response across systems to varying types of hypoxia that range from beneficial to mortality (Diaz & Rosenberg, 1995; Vaquer-Sunyer & Duarte, 2008). Consequences of low oxygen are often sublethal and negatively affect growth, immune response, and reproduction (Rabalais et al., 2014). While mobile fauna has to contend with a loss of habitat as they are forced to migrate, and must adjust to changes in prey resources, they are able to at least escape the affected area. Fauna that have limited mobility must

develop physiological and behavioural adaptations (e.g. extract, transport and store sufficient oxygen; maintain aerobic metabolism; reduce energy demand; tolerate H₂S) if they are to survive a declining oxygen environment (Wu, 2002). As hypoxia develops sessile animals initiate a graded series of behaviours to survive (Figure 2.5.6) but will eventually die as oxygen declines or persists through time (Diaz & Rosenberg, 2008). The result is a hypoxia-based habitat compression as hypoxia tends to overlap with essential habitat such as nursery areas, feeding grounds, or deeper, cooler refuge waters during the summer (Craig & Bosman, 2013; Eby & Crowder, 2002).

The development and persistence of dead zones does not have universally negative consequences for ecosystems. Habitat compression from hypoxia may also enhance trophic efficiency contributing to increased fish productivity (Bertrand et al., 2011). We also know that some fauna has adapted to take advantage of oxygen-depleted habitats, utilizing these areas for predator avoidance or feeding on hypoxiastressed prey. These mobile fauna hover at the edge and migrate into and out of hypoxic zones, using the time out of the dead zone to reoxygenate (Ekau et al., 2010). However, despite documentation of some positive ecosystem responses to deoxygenation, hypoxic habitats are largely lost to the ecosystem for varying lengths of time and have significantly diminished productivity (Sturdivant et al., 2014).

Small and large systems exposed to long periods of hypoxia and anoxia have lower annual secondary production with productivity a function of how quickly benthos can recruit and grow during periods when oxygen is normal (Diaz & Rosenberg, 2008). The extreme case would be the perennial hypoxic/anoxic areas of the Baltic Sea that cover about 70,000 km² where benthic invertebrate production is near zero (Figure 2.5.7). Under normal oxygen conditions this area of the Baltic Sea should be producing about 1.3 million metric tons (mt) wet weight of potential benthic prey for bottom feeding predators (Elmgren, 1984, 1989). In Chesapeake Bay, which has about 3,500 km² of seasonal hypoxia that lasts about three months, about 75,000 mt wet weight of potential prey for fish and crustacean predators is lost (Sturdivant et al., 2014). In the northern Gulf of Mexico severe seasonal hypoxia covers about 20,000 km² and leads to approximately a 210,000 mt wet weight loss of prey from the fisheries forage base. The question remains as to what happens to the "lost" production?



Figure 2.5.7 Dead zone on sea bed in Baltic Sea © Peter Bondo Christensen.

Is it consumed by the microbial community, was it ever produced (benthic production is regulated by growth and recruitment which is stymied during hypoxia), or is it displaced to other areas in the system? If the production isn't displaced but is truly lost, the unknown is whether a system recovers from the secondary production lost to hypoxia during periods of normal oxygen. The Chesapeake Bay has about nine non-hypoxic months to make-up for lost production and the northern Gulf of Mexico six months.

The elimination of benthic prey and hypoxia-based habitat compression can have profound effects on ecosystem functions as organisms die and are decomposed by microbes. Up food chain energy transfer is inhibited in areas where hypoxia is severe as benthic resources are killed directly and mobile predators avoid the area (Figure 2.5.8). As mortality of benthos occurs, microbial activities quickly dominate energy flows (Baird et al., 2004). This energy diversion tends to occur in ecologically important places and at the most inopportune time for predator energy demands (i.e. during the warmer months) and causes an overall reduction in an ecosystem's functional ability to transfer energy to higher trophic levels and renders the ecosystem potentially less resilient to other stressors (Diaz & Rosenberg, 2008). Systems reporting mass mortality provide primary examples of degradation in trophic structure (Oliver et al., 2015).

There is an inherent resiliency to perturbations in marine ecosystems which can make resolving ecosystem level consequences to disturbance difficult (Downing et al., 2012). Hypoxia has clear mortality effects on sessile, and at times mobile, organisms but its population level effects in coastal environments remain uncertain. Much of the evidence supporting negative effects from hypoxia comes from laboratory experiments, localized effects in nature, fish kills, and our intuition that a lack of oxygen can lead to dire consequences (Rose et al., 2009). Scaling to predict effects on food webs and fisheries production is confounded by compensatory mechanisms such as increased production of planktonic prey, increased encounter rates between predators and prey compressed into smaller oxygenated habitat space, and co-occurring stressors that have similar ecosystem responses (Breitburg et al., 2009b; De Mutsert et al., 2016; Rose et al., 2009). As a result, conclusive evidence of wide-spread population level response to hypoxia is lacking. Quantifying the effects of hypoxia on fish populations, whether large or small, is critical for effective management of coastal ecosystems and for cost-effective and efficient design of remediation actions. The potential for interaction of direct and indirect effects, and subtle changes in vital rates (such as reproduction and recruitment) leading to population responses complicates field studies and management but does not excuse us from quantifying the population losses due to hypoxia. As coastal ecosystems continue to decline their capacity to deliver ecosystem services will also decline providing a level of urgency to resolving this question to better enhance future conservation efforts.

2.5.5 Societal consequences

As climate and land-use continue to change, the future forecast is that coastal hypoxia will worsen, with increased occurrence, frequency, intensity, and duration (Diaz & Rosenberg, 2011). The ecological impacts of hypoxia have been assessed (Diaz & Rosenberg, 2008; Levin et al., 2009; Vaquer-Sunyer & Duarte, 2008), but how these ecological effects translate into societal costs is unknown. Human population distribution is increasingly skewed, with the overwhelming bulk of humanity concentrated along or near the coast on just 10% of the earth's land surface. Thus, it is logical that anthropogenic disturbances to coastal ecology will feedback to socioeconomics. An economic valuation of hypoxia involves multiple academic fields and the responses can be subtle and difficult to quantify, even when mass mortality

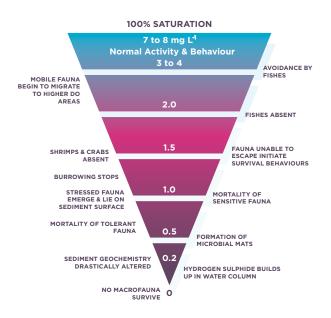


Figure 2.5.8 Range of behaviour and ecological impacts as dissolved oxygen levels drop from saturation to anoxia.

events occur, making quantification difficult (Smith & Crowder, 2011). However, from assessing ecological effects of hypoxia it is known that populations can experience a range of problems that at some point will negatively affect economic interests (Table 2.5.3). Much of the problem in assessing economic consequences is related to the multiple stressors acting on targeted commercial populations (habitat degradation, overexploitation, pollution) and also factors that stress fisher's economics (aquaculture, imports, economic costs of fishing, fisheries regulations). Hypoxia is not priced in the market, but fish are, and provide a useful measure to quantify economic impact.

Because of their devastating effects on stocks and fishermen, hypoxia-induced mass mortality events are a logical place to begin any assessment. Losses from hypoxia-related mortality of oysters in Mobile Bay, USA, in the early 1970s was estimated at the time to be US\$500,000, but greater economic losses were associated with the declining stocks and poor recruitment of oysters (Crassostrea virginica) associated with recurring severe hypoxia (May, 1973). Estimated losses to marine related industries from the New York Bight hypoxic event in the summer of 1976 were over US\$570 million (Figley et al., 1979). Much of this loss was in surf clams that accounted for >US\$430 million. Factored by the area of hypoxia (987 km²) the 1976 event cost about US\$580,000 km⁻² for resources and fisheries related activities and US\$165,000 km⁻² for just the resources lost.

Lack of identifiable economic effects in fisheries landing data does not imply that declines would not occur should conditions worsen. In the northern Gulf of Mexico brown shrimp landings appear to be inversely related to the area of hypoxia (O'Connor & Whitall, 2007). Whether this relationship will remain linear or transform into a catastrophe function (Jones & Walters, 1976) at some critical point is not known. Other large systems have suffered serious ecological and economic consequences from seasonal hypoxia; most notable are the Kattegat with localized loss of catch and recruitment failures of Norway lobsters (Nephrops norvegicus) (Figure 2.5.9) in the late 1980s, and the north-west continental shelf of the Black Sea which suffered regional loss of bottom fishery species also in the 1980s (Karlsen et al., 2002; Mee, 1992, 2006).

Economic valuation of losses from hypoxia seem small relative to the total value of fisheries, but the key point is that losses from hypoxia are measurable in economic terms (Huang & Smith, 2011). For example, the valuation of recreational fishing relative to hypoxia in the Patuxent River, a tributary in Chesapeake Bay, showed that as oxygen declined to mild hypoxic levels total losses for striped bass (Morone saxatilis) fishing was about US\$10,000 for the annual hypoxic event with a net present value of about US\$200,000. If the same water quality was allowed to occur in the entire Chesapeake Bay, the net present value of the losses due to hypoxia would be >US\$145 million annually (Lipton & Hicks, 2003). A similar analysis of recreational fishing in northeast and middle Atlantic regions found that overall as oxygen declined capture rate of fish declined (Bricker et al., 2006). The effects of hypoxia on recreational fishing for one species suggests that similar effects are likely being experienced by commercial fishers. This has been documented for shrimp and crab fisheries in North Carolina. Huang et al. (2010) found that hypoxia may reduce annual shrimp harvest by about 13%, valued at about US\$1.2 million annually, and Smith and Crowder (2011) documented that just a 30% reduction in nutrient loading would abate hypoxia potentially adding US\$2.6 million annually to the crab harvest.

Experience with other hypoxic zones around the globe shows that both ecological and fisheries effects become progressively more severe as hypoxia worsens (Caddy, 1993; Diaz & Rosenberg, 1995), suggesting that at some point economic loses will become more obvious and costly. However, currently the direct connection of hypoxia to fisheries landings at large regional scales



Figure 2.5.9 Nephrops norvegicus © Bernard Picton.

is not always clear (Baustian et al., 2009); this is complicated by the fact that many fisheries experience heavy fishing pressure simultaneous with hypoxic zone growth, making it difficult to identify the primary cause of the decline in harvest rates (Breitburg et al., 2009a). There are also a number of factors that include confounding effects of eutrophication, overfishing, and compensatory mechanisms that alter or mask effects of hypoxia on landings. Breitburg et al. (2009b) found a hint of a connection with a possible decline in landings of benthic species in systems where ≥40% of bottom area becomes hypoxic. Hypoxia has also been documented to increase the landings of less valuable pelagic fish relative to more valuable bottomdwelling fish and shellfish (Caddy, 1993; Rabotyagov et al., 2014). Most recently Smith et al. (2017) found the persistence of hypoxia in the Gulf of Mexico can skew a population's size distribution toward smaller individuals reshaping seafood markets; as a result of this population skew, hypoxia increased the relative price of large shrimp compared with small shrimp. These findings translate into tangible responses from the fishing industry in terms of fishing behaviour and effort and are further confounded by other economic considerations (e.g. fuel).

There is a counter-argument that a causality of hypoxia (namely eutrophication) could have positive economic opportunities. Bricker et al. (2014) determined that the nutrient rich Chesapeake Bay could be utilized to productively foster shellfish aquaculture. They suggest that if ~40% of the estuary bottom is cultivated for shellfish aquaculture it would promote growth of a now depleted oyster stock, remove eutrophication impacts directly from the estuary through harvest, and as a consequence remediate hypoxia. Bricker et al. (2014) suggest this approach could be applied to estuaries around the USA, particularly river-dominated low-flow systems with moderate to high levels of nutrient-related degradation, as a means for nutrient remediation, replenishment of diminished bivalve stocks, and enhancement of economic output. The plausibility of this approach would be largely dependent on the rate of return on investment. Would harvest and sales of oysters be sufficient to cover initial capital costs and costs associated with aquaculture management? These are big unknowns that would need to be resolved to address the viability of this approach. As it currently stands, eutrophication and hypoxia are only documented to negatively impact aquaculture practices resulting in large die-offs and economic hardship (San Diego-McGlone et al., 2008).

2.5.6 Implications of continuing ocean deoxygenation

Within the last 60 years over-enrichment of our waters primarily with nutrients from fertilizers has emerged as one of the leading causes of water quality impairment. These nutrients have led to a greening of our seas and are an indirect consequence of agricultural and municipal activities that support a rapidly expanding human population. On a global basis, humans have been adding more nitrogen to land or ocean than is supplied by natural biological nitrogen fixation (Figure 2.5.3). It is estimated that as a result of human activities the flux of nitrogen has more than doubled over natural values while the flux of phosphorus has tripled (Foley et al., 2005; Gruber & Galloway, 2008).

Virtually all the ocean's food provisioning ecosystem services for humans require oxygen to support organism growth and production. Oxygen is just absolutely necessary to sustain the life of all the fishes and invertebrates we have come to depend upon for food and recreation. By the early 1900s dissolved oxygen was a topic of interest in research and management, and by the 1920s it was recognized that a lack of oxygen was a major hazard to fishes. But it was not obvious that dissolved oxygen would become critical in shallow coastal systems until the 1970s and 1980s when large areas of low dissolved oxygen started to appear with associated mass mortalities of invertebrate and fishes. From the middle of the 20th century to today, there have been drastic changes in dissolved oxygen concentrations and dynamics in marine coastal waters. Diaz and Rosenberg (1995) noted that no other environmental variable of such ecological importance to estuarine and coastal marine ecosystems as dissolved oxygen has changed so drastically from human activities, in such a short period of time.

Accounts of environmental problems related to low dissolved oxygen pre-date our ability to measure oxygen concentration in water. For example, the Drammensfjord in Norway appears to have been persistently hypoxic and anoxic since at least the 1700s based on foramaniferan proxies (Alve, 1995). Even in this small fjord with extended residence time of deep water, historical naturally occurring anoxia has been made worse over the last two centuries by eutrophication. Improvements were observed only after reductions in organic loading. Another example would be the Mersey Estuary, England, which had poor water

quality and hypoxia since at least the 1850s but is now recovered through concerted management efforts (Jones, 2006).

2.5.7 Conclusions / Recommendations

Recognizing the negative consequences of coastal eutrophication and related hypoxia, nations have to make socio-economic commitments for reducing nutrient loads to the adjacent estuaries, bays and seas, upon which they depend. Worldwide there are currently over 700 coastal hypoxia systems, about 70 have responded positively to remediation. All but one improved as a result of management of point discharges. The north-west continental shelf of the Black Sea is the only exception, which responded positively to a reduction in nutrient runoff after the collapse of the Soviet Union. Once the second largest anthropogenic hypoxic area on earth, it is now reduced through concerted efforts to reduce point discharges and runoff from agricultural lands (Capet et al., 2013; Langmead et al., 2008; Mee, 2006).

The management and reduction of hypoxia can only be accomplished by reducing the general problem of eutrophication from a combination of sewage/industrial discharge and nutrient runoff. Nutrients generally increase biological production, while hypoxia acts in the opposite direction, reducing biomass and habitat quality. Overall, the combination of stressors associated with eutrophication has and continues to degrade our coastal systems.

The impacts of hypoxia and nutrient enrichment on food webs and fisheries will be strongly influenced by the extent to which they co-occur. Unless the leakage of nutrients from land-based sources to the sea can be reduced, the future for our estuarine and coastal resources looks bleak. Where applied, nutrient management has reversed the effects of hypoxia. But concerted effort in the future will be needed to allow more systems to recover, particularly for those systems affected primarily by land-runoff.

For hypoxia in Europe and North America much is known about its occurrence in coastal areas, including spatial and temporal patterns. Less is known from the other continents, where most of the human population lives, and oceanic islands. For all systems, less is known about long-term trends, factors controlling dissolved oxygen depletion and replenishment, impacts on ecological processes, and economic losses. To

formulate effective strategies for remediating coastal hypoxia it is essential to have an understanding of what the specific drivers are and what responses to expect with various remediation approaches. Some of these drivers are under state or national control, while others lack defined ownership/responsibility. However, management of hypoxia including the control of drivers of eutrophication is often a transboundary issue.

At some point degraded habitat as a result of eutrophication and hypoxia will lead to reduced fisheries landings or possibly collapse of regional stocks. The bad news is that the overall forecast is for all forms of hypoxia to worsen in the future, with increased occurrence, frequency, intensity and duration. The good news is that the consequences of local and regional eutrophication-induced hypoxia can and have been reversed with long-term and persistent efforts to manage and reduce nutrient loads, which in all cases has led to the restoration of ecosystem services.

2.5.8 References

- Altieri, A., Harrison, S., Seemann, J., Collin, R., Diaz, R.J., & Knowlton, N. (2017). Tropical "dead zones" and mass mortalities on coral reefs. Proceedings of the National Academy of Sciences of the United States of America, 114, 3660-3665. https://doi. org/10.1073/pnas.1621517114
- Alve, E. (1995). Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Dramrnensfjord, southern Norway. *Marine Micropaleontology*, 25, 169-186. https://doi. org/10.1016/0377-8398(95)00007-N
- Baird, D., Christian, R.R., Peterson, C.H., & Johnson, G.A. (2004). Consequences of hypoxia on estuarine ecosystem function: Energy diversion from consumers to microbes. *Ecological Applications*, 14, 805-822. https://doi.org/10.1890/02-5094
- Baustian, M.M., Craig, J.K., & Rabalais, N.N. (2009). Effects of summer 2003 hypoxia on macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, 381, 31-37. https://doi.org/10.1016/j.jembe.2009.07.007
- Benson, B.B., & Krause, D. (1984). The concentration and isotopic fractionation of gases dissolved in freshwater in equilibrium with the atmosphere: 1. Oxygen. *Limnology and Oceanography, 25*, 662-671. https://doi.org/10.4319/lo.1980.25.4.0662
- Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti, F., & Chavez, F.P. (2011). Oxygen: a fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. PLoS ONE, 6, e29558. https://doi. org/10.1371/journal.pone.0029558
- Bianucci, L., Fennel, K., Chabot, D., Shackell, N., & Lavoie, D. (2016). Ocean biogeochemical models as management tools: a case study for Atlantic wolffish and declining oxygen. *ICES Journal of Marine Science*, 73, 263-274. https://doi.org/10.1093/icesjms/fsv220

- Boesch, D.F., Coles, V.J., Kimmel, D.G., & Miller, W.D. (2007). Ramifications of climate change for Chesapeake Bay hypoxia. In: Pew Center (ed.), *Regional impacts of climate change, four case studies in the United States,* Pew Center on Global Climate Change, Arlington, Virginia, pp. 57-70.
- Breitburg, D. (2002). Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries and Coasts*, 25, 767-781. https://doi.org/10.1007/BF02804904
- Breitburg, D.L., Craig, J.K., Fulford, R.S., Rose, K.A., Boynton, W.R., Brady, D.C., ... Targett, T.E. (2009a). Nutrient enrichment and fisheries exploitation: Interactive effects on estuarine living resources and their management. *Hydrobiologia*, 629, 31-47. https://doi.org/10.1007/s10750-009-9762-4
- Breitburg, D.L., Hondorp, D.W., Davias, L.W., & Díaz, R.J. (2009b). Hypoxia, nitrogen and fisheries Integrating effects across local and global landscapes. *Annual Review Marine Science*, 1, 329– 350. https://doi.org/10.1146/annurev.marine.010908.163754
- Breitburg, D.L., Salisbury, J., Bernhard, J.M., Cai, W.-J., Dupont, S., Doney, S.C., ... Tarrant, A.M. (2015). And on top of all that... Coping with ocean acidification in the midst of many stressors. *Oceanography*, 28, 48–61. https://doi.org/10.5670/oceanog.2015.31
- Bricker, S., Lipton, D., Mason, A., Dionne, M., Keeley, D., Krahforst, C., ... Pennock, J. (2006). Improving methods and indicators for evaluation coastal water eutrophication: a pilot study in the Gulf of Maine. NOAA Technical Memorandum NOS NCCOS 20, National Ocean Survey, Silver Springs, Maryland. 81 pp. https://repository.library.noaa.gov/view/noaa/17774
- Bricker, S.B., Ricer, K.C., & Bricker III, P.O. (2014). From headwater to coasts: influence of human activity on water quality of the Potomac River Estuary. *Aquatic Geochemistry*, 20, 291-323. https://doi.org/10.1007/s10498-014-9226-y
- Caddy, J.F. (1993). Towards a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Review of Fisheries Science*, 1, 57–95. https://doi.org/10.1080/10641269309388535
- Capet, A., Beckers, J.M., & Grégoire, M. (2013). Drivers, mechanisms and long-term variability of seasonal hypoxia on the Black Sea northwestern shelf–is there any recovery after eutrophication? Biogeosciences, 10, 3943-3962. https://doi.org/10.5194/bg-10-3943-2013
- Chan, F., Barth, J., Lubchenco, J., Kirincich, J., Weeks, A., Peterson, H., ... Chan, B.A. (2008). Emergence of anoxia in the California Current Large Marine Ecosystem. *Science*, *319*, 920. https://doi.org/10.1126/science.1149016
- Conlan, K.E., Kim, S.L., Lenihan, H.S., & Oliver, J.S. (2004). Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. *Marine Pollution Bulletin*, 49, 43-60. https://doi.org/10.1016/j.marpolbul.2004.01.007
- Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., ... Zillen, L. (2011). Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science and Technology*, 45, 6777-6783. https://doi.org/10.1021/es201212r
- Craig, J.K., & Crowder, L.B. (2005). Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown

- shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series*, 294, 79–94. https://doi.org/10.3354/meps294079
- Craig, J.K., & Bosman, S.H. (2013). Small spatial scale variation in fish assemblage structure in the vicinity of the northwestern Gulf of Mexico hypoxic zone. *Estuaries and Coasts*, 36, 268-285. https://doi.org/10.1007/s12237-012-9577-9
- De Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan Jr., J.H., & Christensen, V. (2016). Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecological Modelling*, 331, 142-150. https://doi.org/10.1016/j.ecolmodel.2015.10.013
- Deutsch, C., Brix, H., Ito, T., Frenzel, H., & Thompson, L. (2011). Climate-forced variability of ocean hypoxia. *Science*, 333, 336-339. https://doi.org/10.1126/science.1202422
- Diaz, R.J., & Rosenberg, R. (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology, an Annual Review, 33, 245-303.
- Diaz, R.J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. Science, 321, 926-928. https://doi.org/10.1126/science.1156401
- Diaz, R.J., & Rosenberg, R. (2011). Introduction to environmental and economic consequences of hypoxia. *International Journal of Water Resources Development*, 27, 63-74. https://doi.org/10.1080/07900627.2010.531379
- Diaz, R., Selman, M., & Chique, M. (2010). Global Eutrophic and Hypoxic Coastal Systems. World Resources Institute. Eutrophication and Hypoxia: Nutrient Pollution in Coastal Waters. http://www.wri.org/project/eutrophication.
- Downing, A.S., van Nes, E.H., Mooij, W.M., & Scheffer, M. (2012). The resilience and resistance of an ecosystem to a collapse of diversity. *PLoS ONE*, 7, e46135. https://doi.org/10.1371/journal.pone.0046135
- Eby, L.A., & Crowder, L.B. (2002). Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 952-965. https://doi.org/10.1139/f02-067
- Elmgren, R. (1984). Trophic dynamics in the enclosed, brackish Baltic Sea. *Rapports et procès-verbaux des reunions ICES*, 183, 152-169.
- Elmgren, R. (1989). Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. *Ambio*, 18, 326-332.
- Ekau, W., Auel, H., Pörtner, H.-O., & Gilbert, D. (2009). Impacts of hypoxia on the structure and processes in the pelagic community (zooplankton, macro-invertebrates and fish). Biogeosciences Discussion, 6, 5073-5144. https://doi.org/10.5194/ bgd-6-5073-2009
- Farrell, A. (2016). Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning. *Journal of Fish Biology, 88*, 322-343. https://doi.org/10.1111/jfb.12789
- Figley, W., Pyle, B., & Halgren, B. (1979). Socioeconomic impacts. In R.L. Swanson, & C.J. Sindermann (Eds.), Oxygen depletion and associated benthic moralities in New York Bight, 1976, NOAA Professional Paper 11, U.S. Government Printing Office, Washington, D.C., pp. 315-322.

- Foley, J. (2017). Living by the lessons of the planet. *Science*, 356, 251-251. https://doi.org/10.1126/science.aal4863
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., ... Snyder, P.K. (2005). Global consequences of land use. *Science*, 309, 570-574. https://doi.org/10.1126/ science.1111772
- Fry, F.E.J. (1971). The effect of environmental factors on the physiology of fish. Academic Press, New York, NY. https://doi.org/10.1016/ S1546-5098(08)60146-6
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., ... Sutton, M.A. (2008). Transformation of the nitrogen cycle Recent trends, questions, and potential solutions. *Science*, 320, 889–892. https://doi.org/10.1126/science.1136674
- Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., ... Wilmoth, J. (2014). World population stabilization unlikely this century. Science, 346, 234-237. https://doi.org/10.1126/science.1257469
- Gilbert, D., Rabalais, N.N., Díaz, R.J., & Zhang, J. (2009). Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences Discussion*, 6, 9127–9160. https:// doi.org/10.5194/bgd-6-9127-2009
- Gobler, C.J., & Baumann, H. (2016). Hypoxia and acidification in ocean ecosystems: coupled dynamics and effects on marine life. *Biology Letters*, 12, 1-8. https://doi.org/10.1098/rsbl.2015.0976
- Graham, J.B. (1990). Ecological, evolutionary, and physical factors influencing aquatic animal respiration. *American Zoologist*, 30, 137–146. https://doi.org/10.1093/icb/30.1.137
- Grantham B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., ... Menge, B.A. (2004). Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature*, 429, 749-754. https://doi.org/10.1038/nature02605
- Gruber, N., & Galloway, J.N. (2008) An earth-system perspective of the global nitrogen cycle. *Nature*, 451, 293-296. https://doi. org/10.1038/nature06592
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., ... Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319, 948–952. https:// doi.org/10.1126/science.1149345
- Huang, L., & Smith, M.D. (2011). Management of an annual fishery in the presence of ecological stress: The case of shrimp and hypoxia. *Ecological Economics*, 70, 688–697. https://doi. org/10.1016/j.ecolecon.2010.11.003
- Huang, L., Smith, M.D., & Craig, M.D. (2010). Quantifying the Economic Effects of Hypoxia on a Fishery for Brown Shrimp Farfantepenaeus aztecus. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 2, 232-248. https://doi.org/10.1577/C09-048.1
- lto, T., Minobe, S., Long, M.C., & Deutsch, C. (2017). Upper ocean $\rm O_2$ trends: 1958–2015. *Geophysical Research Letters*, 44, 4214-4223. https://doi.org/10.1002/2017GL073613
- Jenny, J.-P., Francus, P., Normandeau, A., Lapointe, F., Perga, M.-E., Ojala, A., ... Zolitschka, B. (2016). Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused

- by rising local human pressure. *Global Change Biology, 22*, 1481–1489. https://doi.org/10.1111/gcb.13193
- Jones P.D. (2006). Water quality and fisheries in the Mersey estuary, England: A historical perspective. *Marine Pollution Bulletin*, 53, 144-154. https://doi.org/10.1016/j.marpolbul.2005.11.025
- Jones, D.D., & Walters, C.J. (1976). Catastrophe theory and fisheries regulations. *Journal of the Fisheries Research Board of Canada*, 33, 2829-2833. https://doi.org/10.1139/f76-338
- Justic', D., Bierman, V.J., Jr, Scavia, D., & Hetland, R.D. (2007).
 Forecasting gulf's hypoxia: the next 50 years? Estuaries and Coasts, 30, 791-801. https://doi.org/10.1007/BF02841334
- Karlson, K., Rosenberg, R., & Bonsdorff, E. (2002). Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters a review. Oceanography and Marine Biology, an Annual Review, 40, 427-489. https://doi.org/10.1201/9780203180594
- Langmead O., McQuatters-Gollop, A., Mee, L.D., Friedrich, J., Gilbert, A.J., Gomoiu, M-T., ...Todorova, V. (2009). Recovery or decline of the northwestern Black Sea: a societal choice revealed by socio-ecological modelling. *Ecological Modelling*, 220, 2927–2939. https://doi.org/10.1016/j.ecolmodel.2008.09.011
- Laurent, A., Fennel, K., Ko, D.S., & Lehrter, J. (2018). Climate change projected to exacerbate impacts of coastal eutrophication in the northern Gulf of Mexico. *Journal of Geophysical Research: Oceans, 123*, 3408–3426. https://doi.org/10.1002/2017JC013583
- Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., ... Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences*, 6, 2063–2098. https://doi.org/10.5194/bg-6-2063-2009
- Lipton, D., & Hicks, R. (2003). The cost of stress: low dissolved oxygen and economic benefits of recreational striped bass (*Morone saxatilis*) fishing in the Patuxent River. *Estuaries*, 26, 310-315. https://doi.org/10.1007/BF02695969
- Matear, R.J., & Hirst, A.C. (2003). Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. Global Biogeochemical Cycles, 17, 1125. https://doi. org/10.1029/2002GB001997
- May, E. (1973). Extensive oxygen depletion in Mobile Bay, Alabama. Limnology and Oceanography, 18, 353-366. https://doi. org/10.4319/lo.1973.18.3.0353
- Mee, L. (2006). Reviving dead zones. *Scientific American*, 295, 78-85. https://doi.org/10.1038/scientificamerican1106-78
- Mee, L.D. (1992). The Black Sea in crisis: a need for concerted international action. *Ambio*, *21*, 278-286.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC. 155 pp.
- Najjar, R.G., Pyke, C.R., Adams, M.B., Breitburg, D., Kemp, M., Hershner, C., ... Wood, R. (2010). Potential climate-change impacts on the Chesapeake Bay. *Estuarine, Coastal, and Shelf Science*, 86, 1-20. https://doi.org/10.1016/j.ecss.2009.09.026
- Nixon, S.W. (1995). Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia*, 41, 199-219. https://doi.org/10.1080/00785236.1995.10422044

- O'Connor, T., & Whitall, D. (2007). Linking hypoxia to shrimp catch in the northern Gulf of Mexico. *Marine Pollution Bulletin*, *54*, 460-463. https://doi.org/10.1016/j.marpolbul.2007.01.017
- Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B., & Bullock, J.M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, 6, 1-8. https:// doi.org/10.1038/ncomms10122
- Rabalais, N.N., Díaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., & Zhang, J. (2010). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, 7, 585–619. https://doi.org/10.5194/bg-7-585-2010
- Rabalais, N.N., Cai, W.-J., Carstensen, J., Conley, D.J., Fry, B., Hu, X., ...Turner, R.E. (2014). Eutrophication-driven deoxygenation in the coastal ocean. *Oceanography*, 27, 172–183. https://doi.org/10.5670/oceanog.2014.21
- Rabotyagov, S.S., Kling, C.L., Gassman, P.W., Rabalais, N.N., & Turner, R.E. (2014). The economics of dead zones: causes, impacts, policy challenges, and a model of the Gulf of Mexico hypoxic zone. Review of Environmental Economics and Policy, 8, 58-79. https://doi.org/10.1093/reep/ret024
- Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Christ, E., ... Laurance, W.F. (2017). World Scientists' Warning to Humanity: A Second Notice. *BioScience*, 67, 1026-1028. https://doi.org/10.1093/biosci/bix125
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., ... Foley, J.A. (2011). A safe operating space for humanity. *Nature*, 461, 472-476. https://doi.org/10.1038/461472a
- Rose, K.A., Adamack, A.T., Murphy, C.A., Sable, S.E., Kolesar, S.E., Craig, J.K., ... Diamond, S. (2009). Does hypoxia have population-level effects on coastal fish? Musings from the virtual world. *Journal of Experimental Marine Biology and Ecology*, 381, S188-S203. https://doi.org/10.1016/j.jembe.2009.07.022
- San Diego-McGlone, M.L., Azanza, R.V., Villanoy, C.L., & Jacinto, G.S. (2008). Eutrophic waters, algal bloom and fish kill in fish farming areas in Bolinao, Pangasinan, Philippines. *Marine Pollution Bulletin*, 57, 295-301. https://doi.org/10.1016/j.marpolbul.2008.03.028
- Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature*, 542, 335-339. https://doi.org/10.1038/nature21399
- Seitzinger, S.P., Mayorga, E., Bouwman, A.F., Kroeze, C., Beusen, A.H.W., Billen, G., ... Harrison, J.A. (2010). Global river nutrient export: A scenario analysis of past and future trends. *Global Biogeochemical Cycles*, 24, GB0A08. https://doi. org/10.1029/2009GB003587
- Sinha, E., Michalak, A.M., & Balaji, V. (2017). Eutrophication will increase during the 21st century as a result of precipitation changes. *Science*, *357*, 405-408. https://doi.org/10.1126/science.aan2409
- Smith, M.D., & Crowder, L.B. (2011). Valuing ecosystem services with fishery rents: a lumped-parameter approach to hypoxia in the Neuse River Estuary. Sustainability, 3, 2229-2267. https://doi. org/10.3390/su3112229
- Smith, M.D., Oglend, A., Kirkpatrick, A.J., Asche, F., Bennear, L.S., Craig, J.K., & Nance, J.M. (2017). Seafood prices reveal impacts of a major ecological disturbance. *Proceedings of the National*

- Academy of Sciences of the United States of America, 114, 1512-1517. https://doi.org/10.1073/pnas.1617948114
- Sturdivant, S.K., Diaz, R.J., & Cutter, G.R. (2012). Bioturbation in a Declining Oxygen Environment, *in situ* Observations from Wormcam. *PLoS ONE*, 7, e34539. https://doi.org/10.1371/journal.pone.0034539
- Sturdivant, S.K., Diaz, R.J., Llansó, R., & Dauer, D.M. (2014). Relationship between hypoxia and macrobenthic production in Chesapeake Bay. *Estuaries and Coasts*, *37*,1219-1232. https://doi.org/10.1007/s12237-013-9763-4
- Vaquer-Sunyer, R., & Duarte, C.M. (2008). Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences of the United States of America, 105, 15452–15457. https://doi.org/10.1073/pnas.0803833105
- Wang, S.Y., Lau, K., Lai, K.-P., Zhang, J.-W., Tse, A.C.-K., Li, J.-W., ... Wu, R.S.-S. (2016). Hypoxia causes transgenerational impairments in reproduction of fish. *Nature Communications*, 7, 12114. https://doi.org/10.1038/ncomms12114
- Wu, R.S. (2002). Hypoxia: from molecular responses to ecosystems responses. *Marine Pollution Bulletin*, 45, 35-45. https://doi. org/10.1016/S0025-326X(02)00061-9