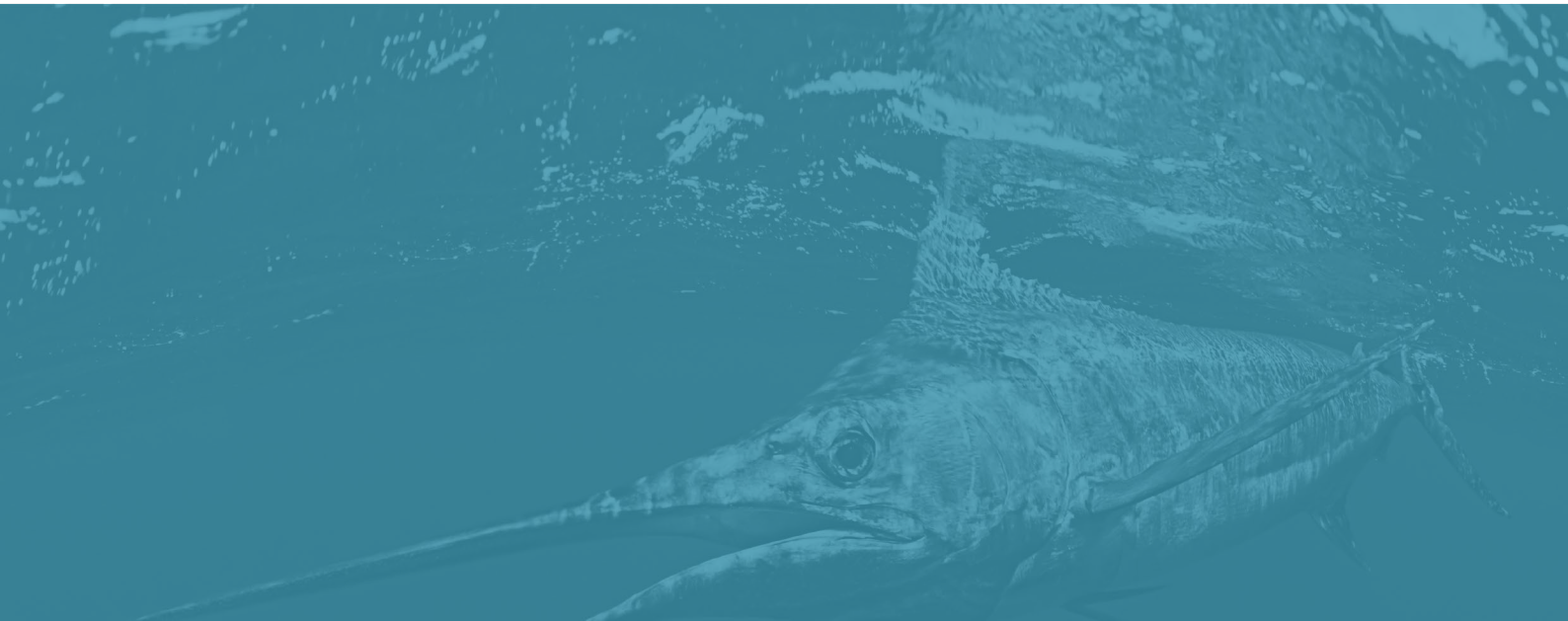




Ocean deoxygenation: Everyone's problem

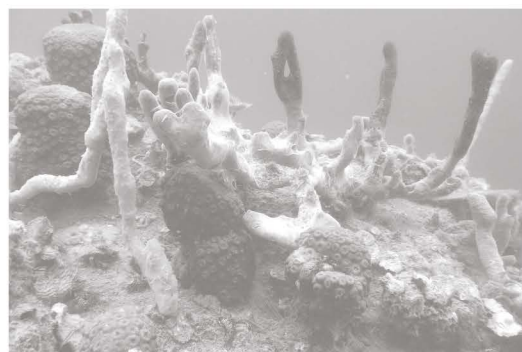
Causes, impacts, consequences and solutions

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10. Impacts of ocean deoxygenation on fisheries

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IUCN GLOBAL MARINE AND POLAR PROGRAMME



Impacts of ocean deoxygenation on fisheries

10

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Summary

- Fisheries (commercial, artisan, recreational harvest) are an ecosystem service that provide employment and nutrition in the global food system. Worldwide production of capture fisheries has levelled off, while demand continues to increase. Over-harvesting and effects on habitats and the food web switches fisheries from an ecosystem service to a stressor.
- Deoxygenation is anticipated to expand over the next decades, and can affect fisheries through negative effects on growth, survival, and reproduction affecting biomass, and movement of fish affecting their availability to harvest. The extent of the deoxygenation effects on fisheries is anticipated to increase because the areas of the ocean that will show increasing deoxygenation overlap with the coastal and oceanic regions that support high fisheries production.
- Quantifying the effects of deoxygenation on fisheries is complicated by the effects of co-varying environmental factors and other stressors that also affect the population dynamics of the species of interest, and because the dynamics of oxygen and fisheries (fishers and vessels) are highly site-dependent. Global climate change involves simultaneous changes in temperature, acidity, and oxygen, as well as effects caused by other stressors such as sea-level rise.

- Isolating a direct hypoxia effect on fisheries landings using a correlation-based analysis of landings and nitrogen loadings across coastal ecosystems was difficult, but trophic efficiency (landings per unit nitrogen loading) was lower in systems with extensive hypoxia.
- Eight case studies show the various ways deoxygenation affects fisheries. Examples include low oxygen effects on the target fish population itself through reduced recruitment and population abundance and examples of spatial distribution effects on the fish and crustaceans resulting in changes in the dynamics of fishing vessels. Analyses range from circumstantial evidence based on field data to extensive data and modelling.
- Modelling analyses demonstrate that in those situations when hypoxia alone may have small to moderate population-level effects, the effects can become large or amplified when hypoxia is combined with other stressors.
- A prevalent effect of deoxygenation documented in the case studies was changes in fishing locations in response to fine-scale distribution changes of the target species due to hypoxia that then affects the catchability and bio-economics of fishing. Catchabilities are relied upon for effective fisheries management and not including the effects of deoxygenation on catchability can result in ill-informed management analyses and incorrect harvesting advice.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in habitats presently used by fish that support fisheries will result in species-specific reductions in growth, survival, and reproduction of individuals. When sufficient numbers are affected, there will be effects at the population level.	<ul style="list-style-type: none"> • Reduced fishable biomass. • Poor quality of fish (e.g. skinny) in the catch.
Increasing areas of the ocean will experience lower oxygen concentrations that will cause organisms to avoid lethal areas, and in some cases, cause individuals to aggregate around the hypoxia areas or shift their spatial distributions.	<ul style="list-style-type: none"> • Fishing activities will be affected economically (higher costs) by vessels requiring longer trips, and spending less time fishing because they spend more time motoring to access the fishing grounds. • In some situations, fish will become easier to catch (aggregation closer to shore) and more available to local fishers. • In both cases, deoxygenation will affect management (likely being riskier than thought) that relies on relating catch to population abundance (catchability) because catches will no longer adhere to the underlying assumptions about catchability used in stock assessments.
Increasing deoxygenation is occurring worldwide, especially in coastal areas that also provide much of the world's commercial and subsistence fisheries catch.	<ul style="list-style-type: none"> • With the catch of wild fish approaching maximum sustainable levels, the need for accurate management advice is critical. • Management needs to account for the effects of deoxygenation in its stock assessments and deliberations.

10.1 Introduction

Fisheries involve the harvest of individuals from populations or stocks. Fisheries include harvested invertebrates (e.g. shrimp), finfish, sharks, and rays; the terms fish and fisheries are used here to refer to all of these. Fisheries vary in their scale from highly localized activities involving small boats that provide fish for a local community to large vessels and fleets that operate trans-oceanic and enter their catches into world-wide markets. Fisheries also include recreational activities, which are fishing activities that do not serve as a primary source of nutrition and whose catch is not generally sold or otherwise traded (FAO, 2012) (Figure 10.1).

Fisheries play a vital role in the global food system and in nutrition (or food) security and are therefore considered an ecosystem service (Daily et al., 1997; Holmlund & Hammer, 1999). In situations of persistent over-harvesting, or fishing affecting critical habitat, or removals altering the food web and ecosystem function, a fishery becomes a stressor (Chapman, 2017; Worm et al., 2009). Proper management of a fishery involves considering the biology of the species, economic aspects of the harvesting, how the species fits into the broader ecosystem, and consideration of the well-being of the human communities that rely on the catch (Marshall et al., 2018). Fisheries are a source of nutrition for many people, ranging from the primary source in some developing countries and for some local communities to a supplemental, but still important, source in other places (Béné et al., 2015). Insufficient protein in many developing nations leads to human health issues (Golden et al., 2016).

Deoxygenation is anticipated to increase over the coming decades (Chapter 4; Breitburg et al., 2018; Keeling et al., 2010). We consider three types of deoxygenation that affect marine ecosystems: (1) coastal hypoxia (Rabalais et al., 2014), and oxygen minimum zones (OMZs) in

both (2) upwelling and (3) open-ocean systems (Levin, 2018). Upwelling systems are also coastal but their low oxygen is driven by the upward nearshore influxes of low oxygen waters, while coastal hypoxia is fuelled by eutrophication (e.g. nutrients coming in through rivers and land runoff). Low dissolved oxygen affects the habitat quantity and quality for many species of interest, and can have both direct (e.g. reduced growth, spatial displacement) and indirect effects (e.g. slowed growth from low oxygen causing reduced prey) on individuals. Direct and indirect effects can affect a sufficient number of individuals to then influence the abundance, mean size, tissue composition (quality as food), and locations (e.g. displacement due to avoidance) at levels that would affect the catch of fisheries (i.e. population or stock level) or the behaviour or economics of the fishers.

In this chapter, we first summarize the status of fisheries worldwide and discuss possible effects of deoxygenation on fisheries dynamics. Second, the complications arising from oxygen concentrations being correlated with other environmental variables, such as water temperature, and that the species of interest are often actively managed that affects their abundance are discussed. We then present the evidence for deoxygenation effects on fisheries using available correlation-based analyses and using a suite of case studies. Finally, we discuss the implications of deoxygenation on the management of fisheries.

10.2 Current status of fisheries

Annual catches world-wide have levelled off at about 90 million MT, suggesting many stocks are fully exploited and some are over-exploited (Figure 10.2; FAO, 2016). The percentage of fish stocks within biologically sustainable levels has declined from 90% in 1974 to 68% in 2013, and the percentage of stocks fished at unsustainable levels increased rapidly from 10% in 1974 to 26% in 1989 and then at a slower rate to 31% in



Figure 10.1 (A) Artisanal fishing boats Senegal © Juan Vilata / Alamy stock photo (B) Pelagic trawlers tied up in Peterhead harbour, Scotland © Keith Lloyd Davenport / Alamy stock photo (C) Sea angling off rocks at North, Scotland © John M Baxter.

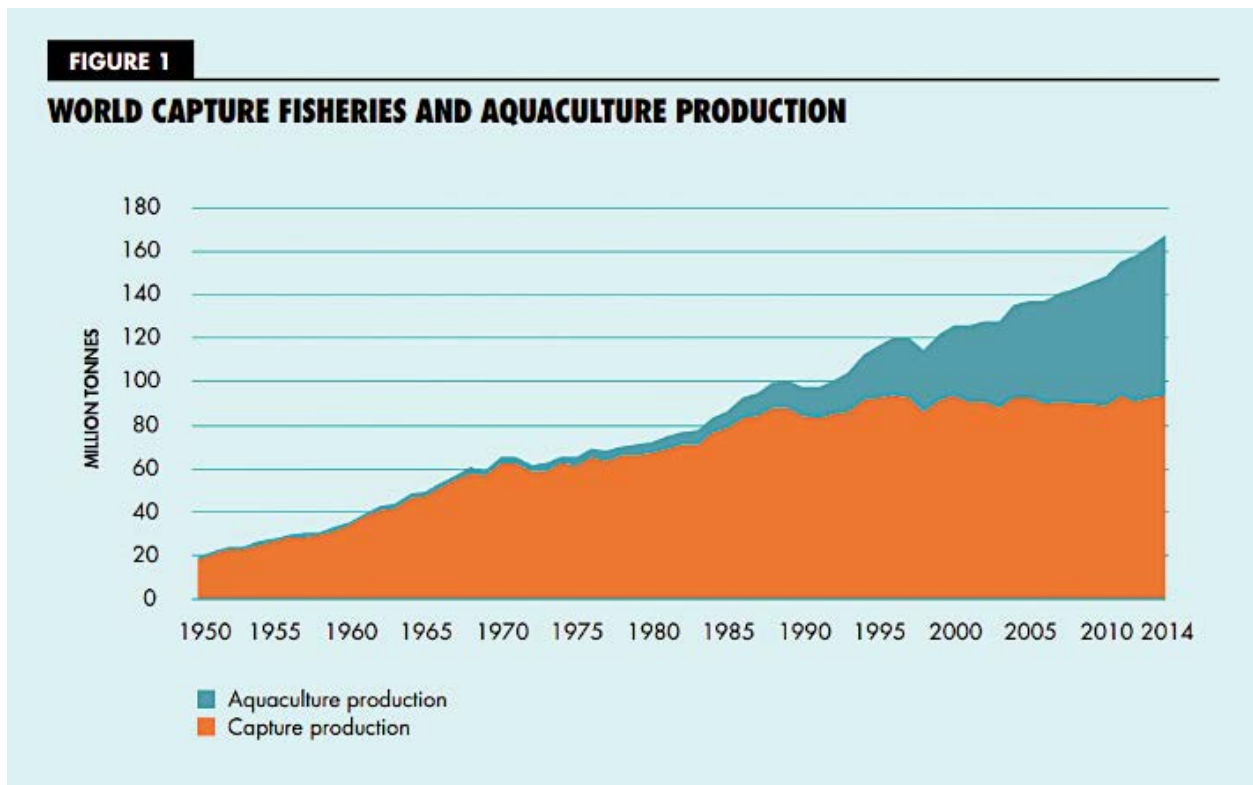


Figure 10.2 Worldwide fisheries and aquaculture production for 1950 to 2014 (FAO, 2016).

2013 (FAO, 2016). The terms overfishing and overfished are rooted in the classical view of a single species management approach and relate to the spawning biomass and fishing rate at maximum sustainable yield (MSY) (Hilborn & Stokes, 2010; Murawski, 2000; Ulltang, 2002). Sound management results in stock biomass being at the biomass associated with MSY, which is often substantially below the biomass that would occur without any fishing. In general, when the current spawning stock size is below the stock size at MSY (i.e. allowing for more stock would increase yield), the stock is considered overfished. Overfishing (as distinct from overfished) occurs when the current fishing rate is above the fishing rate at MSY. In both cases, there can be “safety factors” included to adjust the targets of biomass and fishing at MSY; sometimes referred to as part of the precautionary approach (Darcy & Matlock, 1999; FAO, 1996; Restrepo & Powers, 1999).

The degree of the over-exploitation of fisheries worldwide, and therefore the degree of success of current management practices, is an ongoing debate (Branch et al., 2011; Pauly et al., 2002; Worm et al., 2009). Fisheries management has been challenged in its ability on how to achieve an equitable and sustainable balance between the upper limits imposed by fish production in nature and the ever-increasing demand.

This has led to scrutiny of the status of fisheries stocks worldwide and to debates about the current status of the populations supporting the fisheries and about the effectiveness of fisheries management itself. Some have suggested that additional long-term yield is possible (albeit with large reductions of fishing pressure in the short-term) with better management and effective stock rebuilding efforts (Ye et al., 2013). Regardless, there is no doubt that there is a low likelihood of expanded global yields from capture fisheries, while the demand for fish products will continue to rise into the future (Bell et al., 2016). Rice and Garcia (2011) estimated that an additional 75 million MT will be needed to provide 20% of the protein requirements for the human population expected in 2050. Aquaculture is expected to increase its contribution to worldwide fish harvests, but even with a significant contribution from aquaculture, capture fisheries will continue to be pushed to their limits (FAO, 2016).

Effective management of fisheries is absolutely critical to ensure optimal use of the resource in terms of sustainable harvesting and ensuring ecosystem health and human well-being. Allowing for too much harvest will endanger fisheries yields and ecosystem health in the future. An overly cautious approach, such as greatly reducing harvests to purposely under-exploit many stocks, is also

non-optimal because of the heavy and growing reliance on fisheries for nutrition. With this current status of near-maximum harvesting by fisheries and the urgent need for management to be highly effective, it is critical for us to understand and quantify the effects of stressors such as deoxygenation on fish populations and the dynamics of fisheries.

10.3 Possible deoxygenation effects on fisheries

The effects of low dissolved oxygen on individual organisms are well studied and documented (e.g. Vaquer-Sunyer & Duarte, 2008). Effects on growth, survival, reproduction, and movement are of primary interest to assessing possible effects on fisheries. These effects on individuals and in localized areas can lead to responses at the population and food web levels (Pörtner & Peck, 2010; Rose et al., 2009), which in turn, can change the harvestable stock abundance, body sizes and quality of the tissues of harvested individuals, and where harvestable individuals are vulnerable and feasible to be caught (Breitburg et al., 2009a; Townhill et al., 2017).

Many population processes in fish, such as survival rate, maturity, and fecundity, are size-dependent; thus, effects on growth can lead to changes in population abundance and other attributes that affect fisheries (Rose et al., 2001). Available prey and growth can also affect the composition of the tissues of individuals, which affects their nutritional value and price (e.g. tuna – Carroll et al., 2001; Wessells, 2002). Movement typically also increases with size or age, and a common response of mobile individuals to low DO is for individuals to move away to avoid exposure to very low DO concentrations that could be lethal (Zhang et al., 2009). Movement also results in individuals experiencing different environmental, habitat, and food web (prey and predators) conditions than they would have if they had not avoided the low DO, and this, in turn, affects the growth, survival, and reproduction (fecundity, maturity) of these individuals (Breitburg, 2002; Ekau et al., 2010). Deoxygenation can therefore affect fisheries in two ways: effects on individual fish that result in population changes that affect catch, and effects on the fishers' behaviour and vessel dynamics (e.g. which species to target and where to fish) that affect fishing location and pressure and thus catch. Low DO can reduce growth, survival, and reproduction, of individual fish and thus the abundance of the fishable stock itself (Townhill

et al., 2017). Smaller individuals and altered spatial distributions due to avoidance movement can affect the dynamics of the fishing vessels and the economics of the fishery (e.g. Huang et al., 2012; Langseth et al., 2014).

A key consideration determining potential effects of deoxygenation on fisheries is whether enough individuals are exposed and sufficiently affected to result in meaningful changes in the fishable stock. This moves the analysis from effects on individuals to the effects seen at the population level. Such scaling-up of individual effects to the population level is a common requirement for assessing the ecological effects of many stressors (e.g. Barnthouse et al., 2008; Pastorok et al., 2001) because it puts the effects of the stressor on an ecologically- and publically-relevant scale and, for fisheries, the same biological level (i.e. population) at which management operates (Barnthouse et al., 2008; Hilborn & Walters, 2013).

Documenting and quantifying the effects of deoxygenation on fisheries is necessarily site-specific. This is because the spatial and temporal dynamics of low DO are site-specific depending on local conditions such as bathymetry, nutrient inputs, and biota. Fisheries also are highly site-specific depending on access to the fishable stocks, location of ports, types of vessels used, and because most fisheries are managed locally or regionally. We therefore use case studies to illustrate how deoxygenation affects fisheries.

10.4 Multiple stressors and managed populations

A challenge in the study of deoxygenation effects is to separate oxygen effects from the concomitant changes in other simultaneously changing stressors (Chapman, 2017). Oxygen, temperature, and ocean acidity are all changing, and they interact and affect each other (Bopp et al., 2013; Gruber, 2011). Warmer temperatures and higher acidity are associated with lower dissolved oxygen. Other simultaneous changes will be sea-level rise (and its possible direct or indirect effects on oxygen) and uncertain changes in nutrient loadings that drive hypoxia in coastal ecosystems. Nutrient loadings and low oxygen act in opposite ways on fish: increasing nutrient loadings can positively affect fish stocks (more prey), while the concomitant increase in hypoxia can negatively affect fish stocks (Breitburg et al., 2009a, b). Examination of the role of a single stressor (deoxygenation) when

multiple stressors are varying is challenging (Chapter 6) but also a common situation in the analysis of coastal and marine ecosystems. One result is that the power to isolate the effects of an individual stressor become lower even though the effects of that stressor may be present (Rose et al., 2017c). The effects of the stressor of interest can simply be undetected or inseparable amongst the mix of multiple stressors that co-vary to some degree or because the stressor of interest is important only under certain conditions and has secondary effects under other conditions (e.g. hypoxia effects may be especially important in years of high nutrient loadings and warm summers).

Several modelling studies demonstrated that the effects of deoxygenation alone on fish populations can be small to moderate but, when combined with other stressors, the combined effect can be large. For example, Ainsworth et al. (2011) used Ecosim for five ecosystems in the North-east Pacific and showed that the average change in landings caused by projected climate change factors (primary production, zooplankton size structure, oxygen, and acidification) were individually less than 7% but when combined resulted in a 20% reduction. When range shifts were added to the effects, landings were predicted to be reduced by 77%. Cheung et al. (2016) used coupled physical and ecological models that covered the major large marine ecosystems worldwide and showed that the maximum catch potential (a proxy of MSY) was most sensitive to changes in net primary production and temperature and generally moderately sensitive to deoxygenation alone (low DO assumed to cause reduced productivity). When all effects were combined, they concluded negative impacts would dramatically increase if warming above 1.5 to 2 °C occurred. De Mutsert et al. (2016) used the Ecospace model configured for the Gulf of Mexico and concluded the positive effects of increased nutrient loadings outweighed the negative effects of more hypoxia, although some species showed predicted decreases in their total biomass and projected landings under higher nutrients. Finally, Froehlich et al. (2017) showed increased sensitivity of the Dungeness crab fishery to overfishing when deoxygenation was included with a mix of other stressors (see 10.6.3).

Examining stressor effects on fisheries is also challenging because fisheries are often managed for stability (constrained inter-annual variability in long-term biomass) so that detecting the effects of stressors on the population and catch can be masked by

good management practices. Providing fishers with relatively accurate expectations of future yields enables them to plan, at least in the near term. Management actions occur in response to changes in population dynamics. Thus, a signal of a low oxygen effect would not be in the population abundance itself (which is difficult to measure) but rather in the lowering of the allowable catch that was dictated by management as their response to the lowered population abundance. Detecting a deoxygenation effect in catch can also be difficult because catch reflects how the fishers and fleets respond to other factors, such as fishing effort, price, costs, profitability, dynamics of other species that could be fished, and general environmental conditions. Thus, harvest levels fluctuate due to many factors, not just as a result of the effects due to deoxygenation. Linking deoxygenation effects to fisheries often relies on modelling to separate oxygen effects from the effects of other stressors and management actions.

10.5 Correlation-based analyses

Studies that have utilized cross-system comparisons, considering whole ecosystems and total fisheries landings, have provided two views of the relationship between eutrophication, hypoxia, and fisheries. Analyses and conceptual models by Caddy (1993, 2000) and de Leiva Moreno et al. (2000) suggested that very high nutrient loads resulted in general system degradation, including hypoxia (Caddy, 1993, 2000) or very high chlorophyll-a levels (de Leiva Moreno, 2000), and were associated with reduced fisheries landings and increases in the ratio of planktivore to demersal species (P/D ratio) in the catch. They suggested that hypoxia reduced the availability and quality of the demersal habitat resulting in a decline in demersal species, and in some cases, an increase in pelagic species that benefited from reduced predation, increased food, or reduced competition. In contrast, Nixon and Buckley (2002) examined quantitative relationships among nitrogen loads, primary production, and fisheries landings, and found a positive relationship between nitrogen loads, primary production, and fisheries landings across a very wide range of ecosystems. These analyses did not explicitly consider hypoxia, but do not indicate catch declines in systems where hypoxia would be expected to be problematic.

Cross-system comparisons that have explicitly considered the spatial extent of hypoxia generally support Nixon's model of increasing landings (sum of

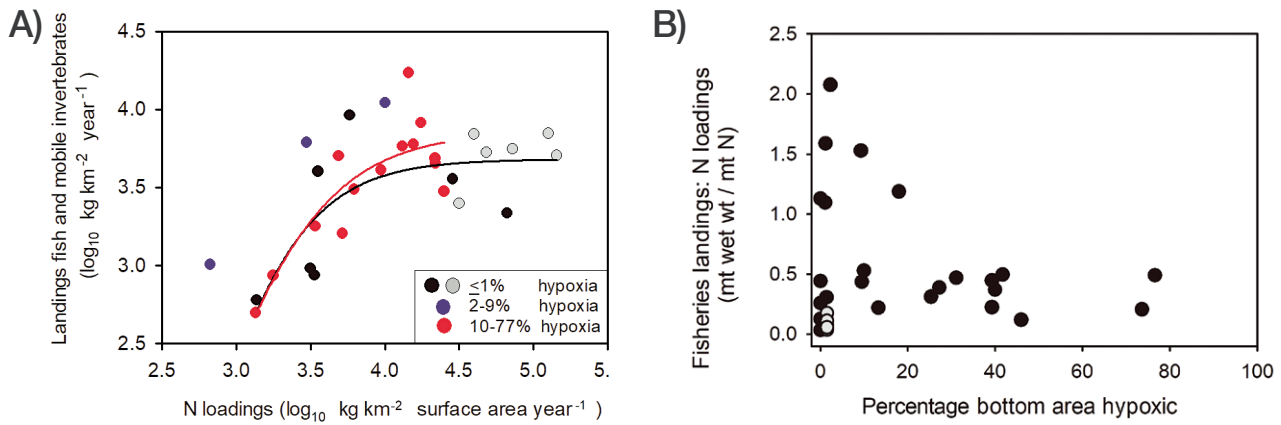


Figure 10.3 Relationship between fisheries landings, nitrogen loadings and hypoxia in estuaries and semi-enclosed seas. (A) fisheries landings versus nitrogen loadings to the basin and (B) landings per unit of nitrogen loadings versus spatial extent of hypoxia (as percentage of total bottom area). (A) shows that the relationship between nitrogen loadings and fishery landings is similar for systems with <1% of the bottom area hypoxic (black regression line; $R^2 = 0.55$) and systems where hypoxic waters can cover as much as with 10–77% of the bottom (red regression line; $R^2 = 0.73$). Both categories are fitted with 4 parameter sigmoid functions. The points in panel (A) are colour coded for the percentage of bottom that is hypoxic. (B) shows a decrease in trophic efficiency (decreasing landings per unit nitrogen) under high hypoxia conditions. Both panels plot small Australian systems in grey. (modified from Breitburg et al., 2009b). Note that landings reflect fishing effort and regulations as well as system production, and that aquaculture production was excluded.

finfish, decapods, and cephalopods) with increasing nitrogen loads (Breitburg et al., 2009 a, b; Hondorp et al., 2010). These analyses included a suite of estuaries, coastal, and semi-enclosed seas that varied sufficiently in physical characteristics that nitrogen loads, and the spatial extent of hypoxia were not significantly correlated to each other, allowing effects of nutrients and hypoxia to be statistically separated. In these analyses, the spatial extent of hypoxia did not affect the relationship between nitrogen loads and total landings (Breitburg et al., 2009b) (Figure 10.3A). Instead, the primary effect of hypoxia was to reduce the efficiency of the transfer from nutrients to secondary production, resulting in a decline in the ratio of fisheries landings to nitrogen loadings with an increasing percentage of bottom area hypoxia (Figure 10.3B). In contrast to predictions from earlier cross-system studies, further analyses of these systems found a negative relationship between total nitrogen load and the P/D ratio in landings (Hondorp et al., 2010). The maximum spatial extent of hypoxia was, nonetheless, positively related to the P/D ratio in this dataset. However, this relationship was largely driven by low landings of pelagics in estuaries where purse seining is not practised or is restricted, and low landings of benthic/demersal species in the Black Sea—a semi-enclosed sea with a deep hypoxic and anoxic basin that covers nearly 80% of its bottom area.

These cross-system analyses do not preclude the possibility that landings of individual species decline, shift in geographic location, or lead to changes in fisher behaviour. Rather the results of cross-system

comparisons suggest the importance of compensatory mechanisms related to fish and fisher behaviour, enhanced fish production, and fisheries practices and regulations that sustain total landings across a broad range of spatial and temporal patterns of hypoxia.

10.6 Case studies

Eight case studies are presented where deoxygenation effects on fisheries have been suggested based on empirical data or have been clearly documented with data or modelling (Table 10.1). These examples involve various combinations of deoxygenation effects on different fisheries types located in ecosystems impacted by coastal hypoxia and OMZs. The exact effects and role of deoxygenation versus other co-varying factors are not always clearly known. However, all of the case studies have at least some evidence or supporting information that deoxygenation played a role. These include several case studies with very strong evidence, mostly because of extensive data and analyses specifically designed to assess deoxygenation effects (i.e. croaker and shrimp in Gulf of Mexico, Dungeness crab in Hood Canal, cod in Baltic Sea). We also include several case studies with suggestive but not always conclusive evidence because they also illustrated features like possible impacts on a major fishery (i.e. anchovy in Peru EEZ), artisanal and traditional fisheries (i.e. Indian oil sardine, white grouper in coastal North-west Africa), and a highly migratory top predator (i.e. billfishes in the eastern tropical Atlantic). Many are model-based because of the challenges of using field data only to detect and isolate the effects

of low oxygen amongst the many factors affecting fish population and fisheries dynamics.

There are multiple examples of analyses examining the effects of global climate change on fisheries that include changes in oxygen as one of the drivers of the response (e.g. Ainsworth et al., 2011; Cheung et al., 2016). However, the role of oxygen changes was not the major focus and so deoxygenation effects were often limited in the analysis and their effects were not

always cleanly isolated from the other drivers, such as temperature. This made it difficult to quantify the role of deoxygenation itself in influencing the predicted effects on fish and fisheries. We therefore selected case studies that focus on deoxygenation effects (Table 10.1), with the knowledge that other case studies, including global change analyses, include deoxygenation but not in a simple way that permits us to say what role oxygen changes played.

Table 10.1 Summary of the characteristics of the eight case studies described in this chapter.

System	Species	Deoxygenation	Fisheries	Oxygen Effects	Fisheries and Management
Gulf of Mexico	Atlantic croaker	Nutrient-driven coastal shelf hypoxia	Past and now limited for use as bait fish	Trade-off between nutrient loadings affecting food (growth) and hypoxia (growth, mortality, reproduction) in opposite directions	An example 25% nutrient reduction would result in sufficient reduction in hypoxia to offset the lowered food effect and likely benefit the population
Gulf of Mexico	Shrimp	Nutrient-driven coastal shelf hypoxia	Major trawl fishery	Growth, mortality, and spatial displacement effects on fleet dynamics and price	Price changes showed decrease in availability of large-sized shrimp
Hood Canal	Dungeness crab	Fjord with nutrient loading	Recreational and commercial	Catchability decreases with shallower depth of hypoxia	Hypoxia magnified the negative effects of other stressors (e.g. illegal harvest) thereby affecting management advice by increasing the sensitivity of the population to overfishing
Baltic Sea	Cod	Nutrient-driven estuarine hypoxia	Major multi-national fishery	Oxygen and salinity determine the effective volume of reproductive habitat; decreased body condition related to hypoxia	While the details are debated, hypoxia has a clear negative effect on recruitment; the negative effects of hypoxia on body condition may also contribute to the lowered cod population
Peruvian EEZ	Anchovy, sardine, jack mackerel, giant squid, demersal species	OMZ	Anchovy is a major biomass contributor to worldwide fisheries	Spatial distribution shifts among pelagic species that leads to effects on the anchovy population; upwelling acts opposite to the effects of hypoxia (more food with worse hypoxia); fishing fleet dynamics	Under small extent/deep hypoxia and intrusion of oceanic waters, sardine, jack mackerel, and predatory species come closer to the coast (more vulnerable and higher catches) and may heavily forage on anchovy (lowered abundance). Warm SST, high primary production, and shallow oxycline allowed anchovy schools to be onshore and vessels to fish near the coast. Opposite conditions resulted in deep and dispersed anchovy that caused fishers to spend more time in transit and searching
Southwest Coast of India	Indian oil sardine	Upwelling and nutrient inputs	Multi-national commercial and local traditional fisheries	Low oxygen into spawning areas	Low oxygen affecting spawning and recruitment as well as the availability of fish to capture
Coastal West Africa	White grouper or "thiof"	Deep and shallow water OMZ	Commercial and artisanal	Exposure of adults to low oxygen, likely causing mortality	White grouper is overexploited and critical to human welfare and economic activities
Eastern Tropical Pacific	Billfishes	Oceanic OMZ	Commercial	Shallowness of low oxygen affects habitat	Increases vulnerability to harvest and confounds estimation of catchabilities in stock assessment

10.6.1 Atlantic croaker in Gulf of Mexico

Atlantic croaker (*Micropogonias undulatus*) in the Gulf of Mexico supported a fishery in the 1950s (about 55,000 MT) and there is a small inshore fishery for croaker as bait fish (including as bycatch from shrimping) for recreational harvesting of other species (VanderKooy, 2017). The Gulf of Mexico exhibits annual summertime hypoxia that started in the 1950s and has slowly but steadily increased in volume since then, with significant interannual variation due to fluctuating nutrient loadings dependent on Mississippi River flows in the spring (Scavia et al., 2017). Croaker is a dominant demersal forage fish in coastal Louisiana (Monk et al., 2015). Rose et al. (2017a, b) simulated the population-level response of croaker to changes in nutrient loadings, which affected both food availability and the extent of hypoxia. While croaker do not presently support a large fishery in the Gulf of Mexico, the croaker analysis is included as a case study because the modelling did project effects at the population-level (relevant scale for fisheries) and included a quantitative tradeoff between the counteracting effects of nutrient loadings affecting food availability and affecting hypoxia (i.e. higher

nutrients can mean more food (positive) but also more hypoxia (negative)).

Model simulations were for 140-years with an average year of seasonally-varying temperatures repeated every year, DO randomly selected each year from one of three years (mild, intermediate, or severe,) and chlorophyll concentrations dependent on the hypoxia year type (higher chlorophyll with more severe hypoxia years since both occur with high nutrient loadings). While the simulated individual croakers were good at avoiding DO less than 2.0 mg L^{-1} , which is considered hypoxia and stressful to aquatic life in many systems, some mortality due to exposure to less than 2.0 mg L^{-1} occurred. More importantly, relatively large growth and fecundity effects occurred on some individuals because those effects occurred at DO above levels that triggered avoidance (i.e. 2.0 to 4.0 mg L^{-1}).

Simulations to examine the tradeoff of how a 25% reduction in nutrient loading negatively affects croaker through reduced food versus positively affects croaker through less hypoxia were undertaken. The simulations used were: (1) unadjusted hypoxia and chlorophyll concentrations (i.e. representing present-day or baseline

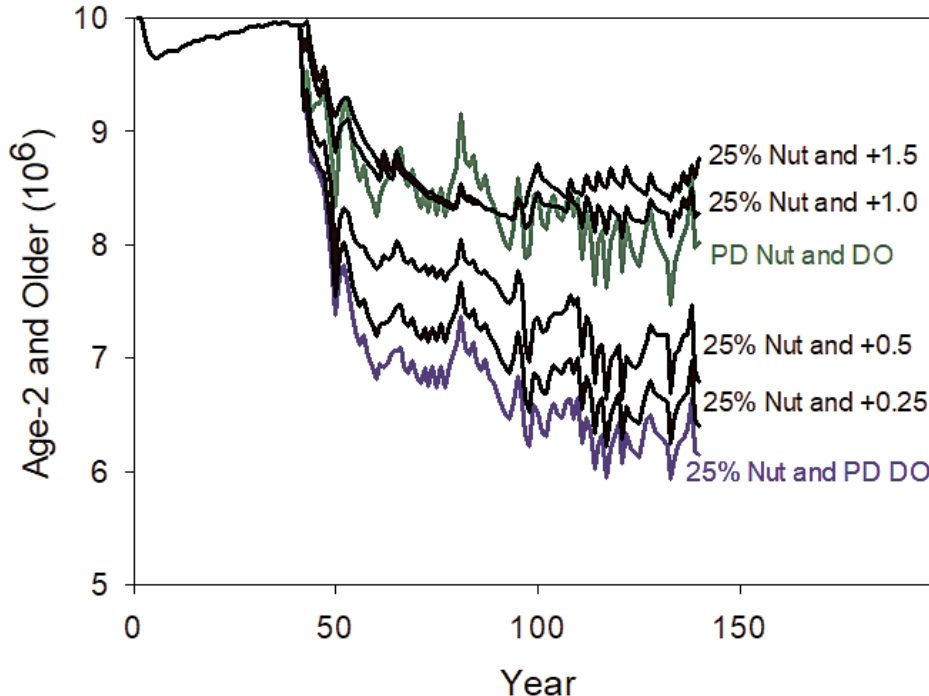


Figure 10.4 Simulated annual age-2 and older croaker abundance for present-day (PD) nutrient loadings (nut) and hypoxia (green), reduced food (25% Nutrients) and present day hypoxia (blue), and reduced food and dissolved oxygen (DO) adjusted by adding $+0.25$, 0.5 , 1.0 , and 1.5 mg L^{-1} to the hourly values. Reduced food was due to the 25% reduction in nutrient loadings. The decrease in population from green to blue is due to the reduced food resulting from reduced nutrient loadings. The progressively higher population abundances from $+0.25$ to $+1.5$ is the effect of improving oxygen (reducing hypoxia). Note the y-axis starts at 5×10^6 . Source Rose et al. (2017b).



Figure 10.5 (A) Shrimp trawler operating in the Gulf of Mexico © Tosh Brown / Alamy stock photo (B) Brown shrimp catch from Gulf of Mexico © Inga Spence / Alamy stock photo (C) White shrimp catch © Frank Bienewald / Alamy stock photo.

conditions), (2) unadjusted hypoxia but reduced food for croaker expected with a 25% reduction in nutrients (lowered chlorophyll due to reduced nutrients), and (3) reduced food and DO manually increased by adding 0.25, 0.5, 1.0, and 1.5 mg L⁻¹ to every hour's value. The first simulation is considered baseline and representative of current conditions. The second simulation is hypothetical – prediction of croaker abundance with reduced food under present-day hypoxia and serves as a measure of the deficit in abundance caused by reduced nutrients leading to lowered food. The third set of simulations then start with the second simulation (reduced food) and adds known concentrations of DO to see how much DO would have to increase to offset the deficit caused by reduced food. A review of the statistical models used to predict summer hypoxia area from nutrient loadings showed that a reduction in hypoxia equivalent to a 0.5 mg L⁻¹ addition was reasonable to expect under a 25% reduction in nutrient loadings but that the larger increase of 1.0 mg L⁻¹ was unlikely to be achieved.

The addition of 0.5 to 1.0 mg L⁻¹ of oxygen offset the negative effects of lowered food that would result from a 25% reduction in nutrient loadings (25% Nut and +0.5 and +1.0 lines bracket the green line in Figure 10.4). Other models show that it is feasible that a 25% reduction in nutrients would result in a 0.5 to 1.0 mg L⁻¹ increase in DO. Thus, reduced nutrient loadings would not reduce, and may increase, the croaker population abundance. Moving towards an integrated modelling approach that can simultaneously look at how reduced nutrient loadings affect croaker food availability and hypoxia is now underway.

10.6.2 Shrimp in the Gulf of Mexico

The Gulf of Mexico shrimp fishery is a bottom trawl fishery that operates in estuarine and coastal shelf waters from southern Florida to the Texas-Mexico border. The fishery primarily targets two penaeid shrimp

species: brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) (Figure 10.5). As recently as 2000, brown shrimp generated the highest revenue of any US single-species fishery. Brown shrimp, like a number of other demersal species, avoid low oxygen water on the Louisiana shelf and aggregate at high densities near the edges (< 5 km) of the hypoxic zone (Craig, 2012; Craig & Crowder, 2005; Craig et al., 2005). Increased susceptibility to the Gulf shrimp trawl fishery, which peaks during the summer when hypoxia is most severe, is a potential indirect effect of hypoxia-induced aggregation of the shrimp (Purcell et al., 2017). If shrimpers are able to locate these high-density aggregations of shrimp, then catchability, or the harvest efficiency of a given unit of shrimping effort, could increase.

Huang et al. (2010), in an analysis of the North Carolina shrimp trawl fishery and oxygen conditions in the Neuse-Pamlico estuarine system, determined that hypoxia had reduced catch by about 10-15% with an annual value loss of US\$1.25 million relative to pristine (normoxic) conditions. The Neuse-Pamlico system supports harvest within its waters and also contributes shrimp to the Pamlico Sound where much of the state-wide harvest comes from. This economic loss was much reduced in subsequent analyses that allowed the fishers to dynamically respond to the changing economic (e.g. price) incentives (Huang et al., 2012). Here, we focus on spatial bio-economic models of the brown shrimp fishery in the Gulf of Mexico that included the same researchers (Smith et al., 2014, 2017).

Smith et al. (2017) analysed 20 years of monthly brown shrimp price data in the Gulf of Mexico and found that the severity of hypoxia measured by the spatial extent of low DO water was related to short-run deviations from long-run prices. More severe hypoxia caused short-run increases in the price of large shrimp relative to small shrimp. Based on model estimates, about a 1000 km² increase in the spatial extent of hypoxia (a 6% increase

from the long-term mean) triggers a 1% increase in the relative price of large brown shrimp. The interpretation is that in years when hypoxia is severe, there are more, small brown shrimp caught due to some combination of increased aggregation of smaller shrimp early in the season, impaired growth, and reduced survival that had a larger effect on the abundance of large shrimp than on small shrimp. As a result, there are fewer large shrimp available to be harvested later in the season. Severe hypoxia thus results in increased catch when shrimp are smaller (and of lower monetary value) and reduced catch of the more valuable larger shrimp later in the season. The smaller sized shrimp captured earlier in the season, with their lower prices, make up most of the harvest and thus severe hypoxia imposed an economic cost on the fishery. This effect was not detectable in the catch data itself because the fleet is highly mobile and integrates catches across hypoxic and non-hypoxic areas. Price data could be used because the shrimp markets are highly integrated and the relative prices of different sized shrimp in the Gulf of Mexico have been remarkably consistent over time. These analyses demonstrate that hypoxia can have important (albeit complex) economic effects on fisheries that would be very difficult to detect in traditional fisheries data.

10.6.3 Dungeness crab in Hood Canal

The Dungeness crab (*Metacarcinus* or *Cancer magister*) is one of the most valued and heavily exploited species on the west coast of North America (Figure 10.6), with some estimates that 90% or more of the legal-sized males are harvested by stationary traps during the fishing season (Armstrong et al., 2003, 2010; Gotshall, 1978; Pauley et al., 1986; Smith & Jamieson, 1991). Both recreational (open-access) and commercial (limited entry) fishing are regulated by a quota system with additional restrictions on the size and sex of crab that can be harvested during certain seasons (Armstrong et al., 2003).

Hood Canal (110 km) is a seasonally hypoxic, fjordic estuary in Puget Sound, Washington State, USA (Figure 10.7), where hundreds of thousands of Dungeness crab are landed by recreational and tribal fisheries every year (Washington Department of Fish and Wildlife (WDFW) unpublished data). The narrow sill at the mouth of the estuary and the deep bathymetry (maximum depth ca. 200 m) reduce tidal and exchange rates (turnover ≥ 1 year) that set up the deoxygenated conditions that expand through the water column over the summer

months, particularly in the southern reaches (Cope & Roberts, 2013; Newton et al., 2007; Warner et al., 2001). Oxygen conditions appear to be worsening, in part, due to climate change and nutrient loading (Cope & Roberts, 2013; Fagergren et al., 2004; Newton et al., 1995, 2007). Importantly, Dungeness crabs – even with their relatively high tolerance to hypoxia (Bernatis et al., 2007; Froehlich et al., 2015) – appear to shoal, similar to other demersal species, into shallower depths in order to avoid the lower, deoxygenated extremes (Froehlich et al., 2014) (Figure 10.8).

A management strategy evaluation (MSE) was performed to examine the indirect effects of hypoxia on the performance of management practices and the long-term sustainability of the Hood Canal Dungeness crab fisheries. Based on an age-structured population and fishery model of the system, the MSE revealed that hypoxia effects can erode the effectiveness of the management system when other fishing-related pressures are included (Froehlich et al., 2017). Hypoxia was included by specifying that catchability increased with decreasing minimum hypoxic depth (higher catchability when hypoxia is near the surface). Simulations showed that changes in catchability due to hypoxia alone did not significantly reduce catch or crab abundance ('base-case' scenario in Figure 10.9C and F with all other pressures at zero). However, the effects of other stressors associated with fishing, including increased fishing effort, illegal crabbing, incidental mortality of captured non-harvested crabs (i.e. bycatch or discards), and impaired reproduction ability due to fishing were all magnified by hypoxia-induced behavioural shifts that affected catchability. This is seen in Figure 10.9 by the black lines increasingly lower than the grey lines for the population (10.9A



Figure 10.6 Dungeness crabs for sale at Seattle's Pike Place market © The Old Major / Shutterstock.com.



Figure 10.7 Hood Canal, Seabeck, Washington looking towards the Olympic Mountains © Don Paulson / Alamy stock photo.

and B) and landings (10.9D and E) as other stressors (illegal crabbing, incidental mortality) were increased in intensity, and by black bars being lower than grey bars for impaired reproduction (10.9C and F) that only had two levels (off and on) of intensity. In addition to the effects on average population abundance and legal catch, the presence of hypoxia also affected the year-to-year variability of catch. The presence of hypoxia resulted in patterns of significantly higher catch variability and lower minimum catch returns (Froehlich et al., 2017). Thus, non-lethal environmental forcing from hypoxia increased the sensitivity of the fishery to other pressures and increased its susceptibility to overfishing.

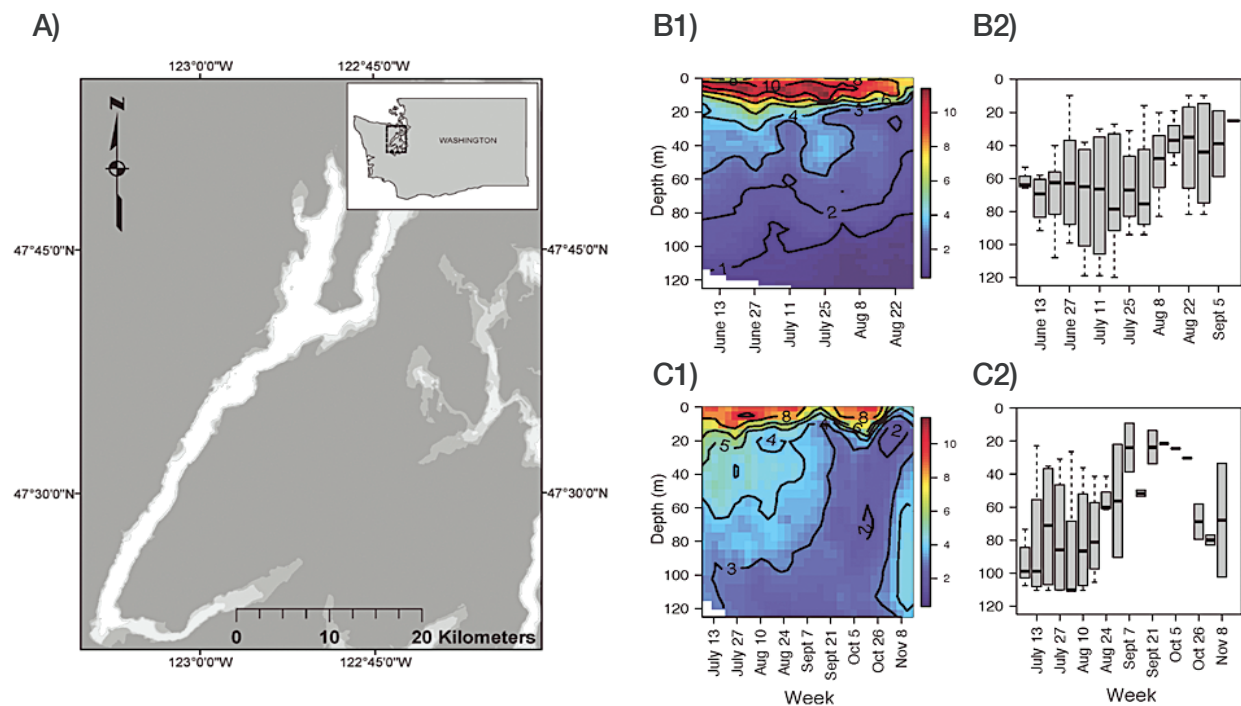


Figure 10.8 A) Hood canal; B1) and C1) Interpolated dissolved oxygen (DO, mg L⁻¹) in Hood canal and B2) and C2) maximum depth (metres) ranges of acoustically-tagged Dungeness crab for (B) July to August in 2010 and (C) July to November in 2009 (from Froehlich et al., 2014). Note low DO concentrations are shown in darker blue colours. Comparison of oxygen with depths of crabs shows that crabs move towards the surface to avoid shoaling low oxygen.

10.6.4 Cod in Baltic Sea

The biomass of fish in the Baltic is dominated by three species: cod (*Gadus morhua*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) (Ojaveer et al., 2010). Total marine fisheries landings for the nine coastal countries bordering the Baltic Sea was conservatively estimated as 41.3 to 53.5 million tonnes for the period between 1950 and 2007 (Zeller et al., 2010, 2011). When the cod population size was high, large amounts of cod were landed in the northern areas of the Baltic Sea, while landings shifted to the southern region when population size was low (Bartolino et al., 2017).

The Baltic Sea is the largest anthropogenically-induced hypoxic area in the world (Conley et al., 2009). The dramatic increase in hypoxia area in the Baltic Sea over the last 115 years is primarily linked to increased inputs of nutrients from land, although increased respiration due to warmer temperatures during the last two decades has also contributed (Figure 10.10A). Reducing anthropogenic nutrient inputs is a major policy goal for restoring good environmental status of coastal marine ecosystems. However, it is unclear to what extent reducing nutrients would also lower fish production and thus fisheries yield (MacKenzie et al., 2007). The strongest factor influencing the biodiversity of benthic communities is the increased prevalence of

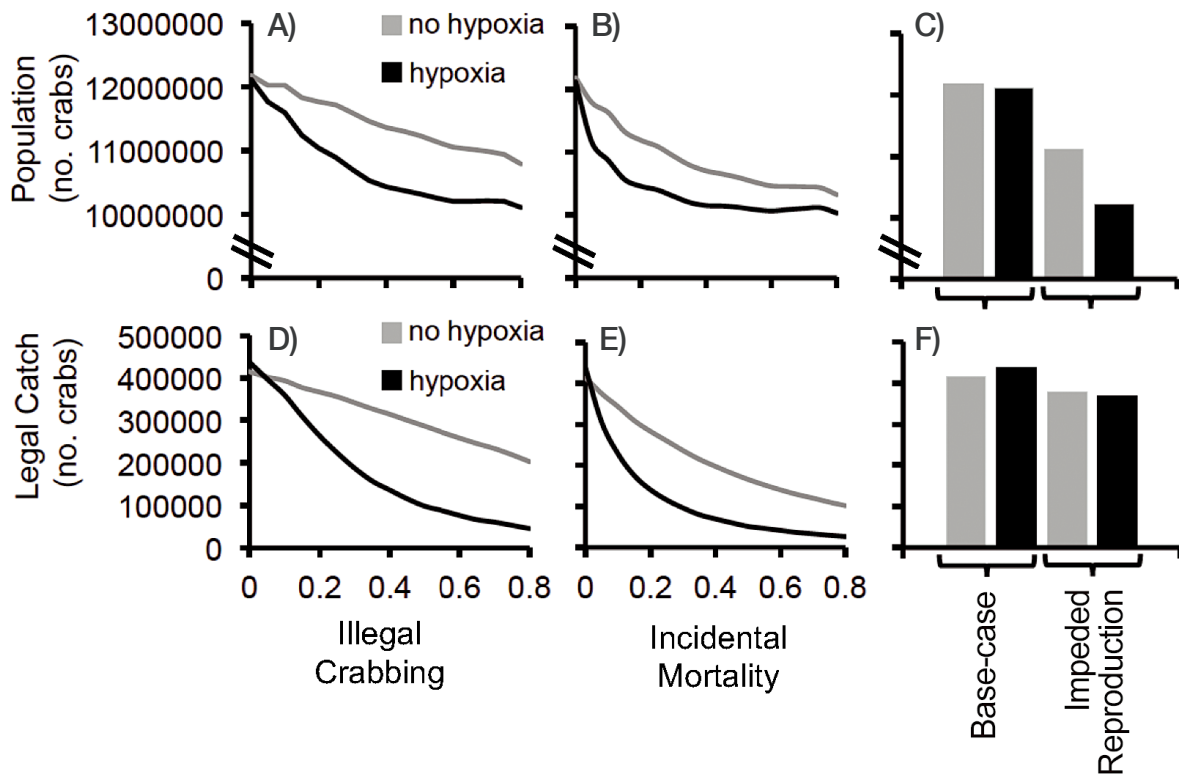


Figure 10.9 Simulated equilibrium (average over 50 years) population abundance (A-C) and catch (D-F) of Dungeness crab in Hood Canal under high fishing effort (20,000 pots/week) and increasing levels of three stressors (illegal crabbing incidental mortality, and impeded reproduction). Mean values are shown for no hypoxia effects (grey) and with hypoxia effects (black). Panels (A) and (D) show the mean values for increasing intensity of illegal crabbing. Panels (B) and (E) show the predictions for increasing intensity of incidental mortality. Panels (C) and (F) show the predicted abundance and catch for the base-case (all stressors set to zero) and for the third stressor of impeded reproduction that only had two intensities (off or on). The effect of hypoxia alone is small (grey and black bars similar in Base-case) but hypoxia effects amplify the negative effects of the other stressors (black lines and bars below grey lines and bars). Source: Froehlich et al. (2017).

oxygen-depleted bottom water, which has resulted in habitat loss and the elimination of benthic macrofauna over vast areas (Figure 10.10B) and severely disrupted benthic food webs (Conley et al., 2009).

Cod in the Baltic Sea live in an estuarine environment whose salinity and oxygen conditions impose physiological stresses on spawning success including egg fertilization and survival (Hinrichsen et al., 2016). Earlier field and laboratory studies have shown that spawning success and egg survival is greatly reduced at salinities less than 11 and oxygen content less than 2 ml L⁻¹. Reproductive habitat, estimated as the volume of the water column conducive for successful reproduction based on salinity and oxygen, has been quantified by numerous authors (e.g. Bartolino et al., 2017; Eero et al., 2015; MacKenzie et al., 2000) and has been shown to be a key driver of cod recruitment success (e.g. Jarre-Teichmann et al., 2000; Koster et al., 2005; Margonski et al., 2010). The mean and variance of the reproductive volume time series changed after 1983, due primarily

to a reduction in the frequency of large reproductive volume years (Carstensen et al., 2014). As a result, the mean and range of reproduction volume has declined, reducing egg survival and resulting in lower cod recruitment. Reproductive volume, and similar measures of reproductive habitat, were used to affect cod recruitment in an Ecosim model and was important in enabling the Ecosim model to better fit to stock biomasses estimated from stock assessments (Harvey et al., 2003). Hansson et al. (2007) used a version of the same model and showed, among other things, that cod catch would increase if the reproductive volume was increased as estimated under an oligotrophic Baltic Sea (i.e. as expected by reduced nutrient loadings); however, if primary production (food) was also reduced, catch of cod showed a net decrease. They also showed that in some oligotrophic conditions, lowering fishing intensity results in higher biomasses of key stocks and higher cod catches. This suggests that fisheries management targets need to be adjusted based on the productivity of the ecosystem.

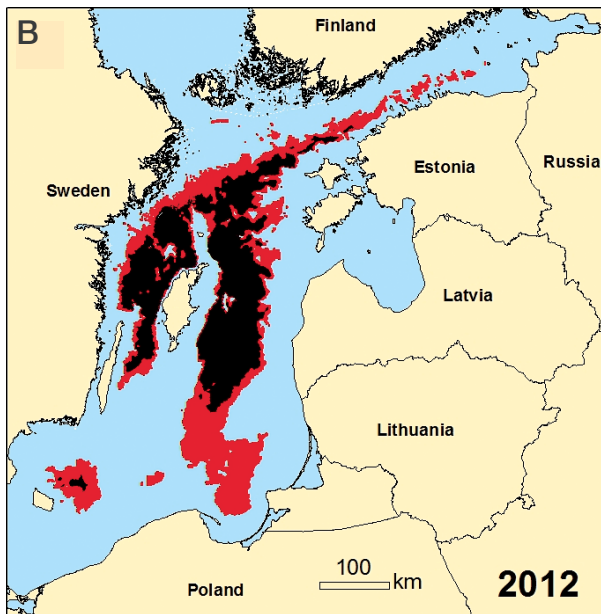
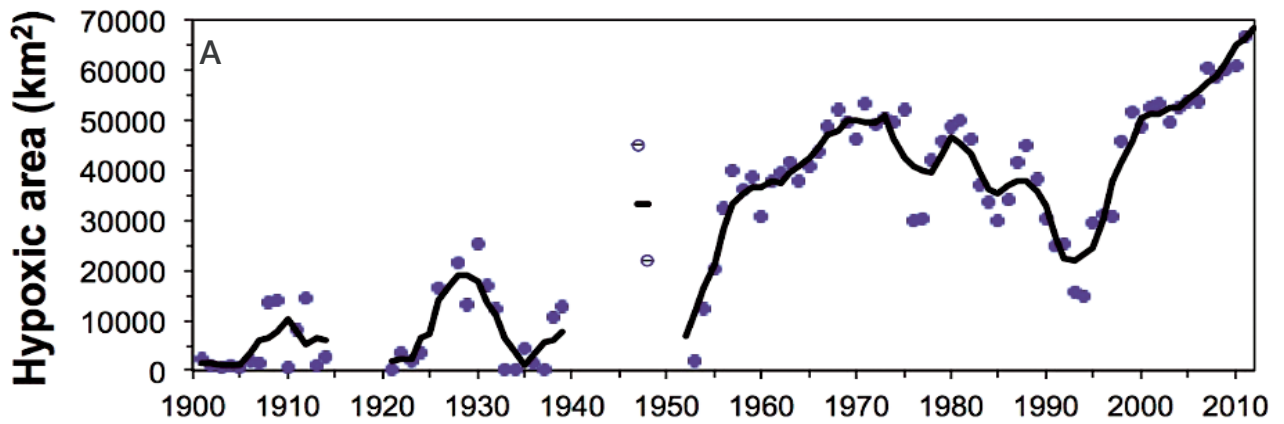


Figure 10.10 (A) Annual average hypoxic area with oxygen concentrations $<2 \text{ mg L}^{-1}$ in the Baltic Proper (redrawn from Carstensen et al., 2014). (B) Red are hypoxic areas with oxygen concentrations $<2 \text{ mg L}^{-1}$ and black areas are anoxic $<0 \text{ mg L}^{-1}$ in the Baltic Sea (from Carstensen et al., 2014). The increasing hypoxic area is primarily due to increased nutrient loadings. The spatial extent of the hypoxia causes widespread habitat loss and mortality of the benthos and distribution of the benthic food web.

In addition to low oxygen affecting reproductive success, the increasing areal extent of hypoxic waters was also related to a decrease in the condition of cod, leading to a major decline in condition over the last 10 - 20 years (Casini et al., 2016; Limburg & Casini, 2018). Fish condition was quantified by the weight compared to length cubed of individuals and indicates degree of girth or how streamlined a fish is; “fatter” fish are considered healthier. The effects of such a decline on population dynamics are presently unclear, but low condition cod in other regions usually produce fewer eggs and eggs of lower quality (e.g. lipid content, developmental ability). Consequently, it is possible that hypoxia may be having effects on Baltic cod populations in addition to those

directly associated with abiotic effects through reduced egg survival and hatch success (Wieland et al., 1994).

10.6.5 Peruvian fisheries

Fisheries in the Peruvian EEZ account for around 10% of the world's marine fish landings. This area also experiences low oxygen related to the OMZ that characterizes the tropical South-eastern Pacific (Codispoti et al., 1989; Helly & Levin, 2004). The main fishery resource is the Peruvian anchovy (*Engraulis ringens*) (Figure 10.11) with jack mackerel (*Trachurus murphyi*) also being important off Chile; recently, the jumbo squid has become an important contributor (Gutiérrez et al., 2016). Peruvian hake (*Merluccius gayi peruanus*) is the main demersal fishery but demersal fish harvest is limited due to the strong oxygen deficiency that characterizes the subsurface waters, particularly south of 7°S (Bertrand et al., 2011). It has been proposed that one factor that contributes to the exceptional pelagic fish productivity is that low oxygen compresses the epipelagic habitat in the region and that compression results in a highly efficient trophic transfer of the high rates of upwelled nutrients to the upper food web levels (Bertrand et al., 2011).

The relatively higher tolerance to hypoxia of the Peruvian anchovy is evidenced by its more coastal distribution than other pelagic species. Onshore surface oxygen content can decrease to 40% saturation, with the oxycline being located shallower ($\sim 30 \text{ m}$) than offshore ($\sim 100 \text{ m}$) (Bertrand et al., 2011). By contrast, the distribution of sardine, jack mackerel, and the giant squid (Alegre et al., 2015; Bertrand et al., 2016) are restricted to offshore, more oxygenated waters. Recent studies of coastal sediment records have revealed significant natural variability of abundance indicators of the main fish populations at multidecadal to millennial



Figure 10.11 Peruvian fishermen unloading their catch of Peruvian anchovy © Mark Bowler – MBSI / Alamy stock photo.

time-scales (Gutiérrez et al., 2009; Salvatelli et al., 2017). Periods of higher overall abundances coincide with enhanced coastal upwelling and productivity, but also increased oxygen deficiency (less DO) in the water column. From the late 1970s to the early 1990s, warmer conditions developed off the Peruvian coast and coastal upwelling was reduced, along with the positive phase of the Pacific Decadal Oscillation (Alheit & Niquen, 2004; Chavez et al., 2003; Purca et al., 2010). At the same time, highly oxygenated surface waters (saturation >80%) approached onshore and the oxycline was deepened (Bertrand et al., 2011). These changes allowed the increase of the populations of sardine, jack mackerel, and other predatory species nearer to the coast, where anchovies were negatively impacted due to the increased predation, and lower macro-zooplankton abundances (prey) were triggered by the environmental changes (Ayón et al., 2008; Bertrand et al., 2011). The higher availability of sardine and jack mackerel was reflected in the increase of their fisheries (Bertrand et al., 2011, 2016). The habitat compression of the pelagic, anchovy-dominated system by the shallow oxycline enhanced prey accessibility to predatory birds and fishers (Barbraud et al., 2017; Joo et al., 2014; Passuni et al., 2016).

Joo et al. (2014) identified four scenarios from the analyses of concomitant satellite, acoustic survey, and extensive Vessel Monitoring System data for the

2000 – 2009 period off Peru. The favourable scenarios for the fishing activity were characterized by relatively high SST, high primary production, and a shallow oxycline. In these scenarios, relatively more time was spent on fishing rather than on cruising, and in cases when anchovy patches were located closer to the coast, the vessels did not need to go as far in order to catch fish. In contrast, the unfavourable scenarios were characterized by relatively low SST, low primary production, and a deep oxycline. Under these conditions, anchovy was scarce, concentrated in very few spots, and the schools were deep. Fishermen went far from the coast and made fishing trips that lasted longer; more time was spent cruising and relatively less time searching and fishing, resulting in a non-efficient activity budget.

10.6.6 South-west coast of India

The coastal shallow waters of south-west coast of the Indian sub-continent experience low oxygen conditions of varying intensities during upwelling. Observations of the dissolved oxygen levels in the coastal waters along the south-west coast have clearly indicated the occurrence of short spells of low oxygen conditions (<1.0 ml L⁻¹) (Johannessen et al., 1987; Murty & Vishnudatta, 1976; Pillai et al., 2000; Ramamritham & Jayaraman, 1960; Rao et al., 1973).

The Indian oil sardine (*Sardinella longiceps*) supports a commercial fishery in India, Iran, Oman, Pakistan, United Arab Emirates and Yemen (FAO, 2017). India has been the major contributor in all the six decades (1956 to 2015) and, among the 10 maritime Indian states, the major contribution of sardine landings is from Kerala where sardines have been the major target species for thousands of traditional fishers (Nair & Chidambaram, 1951; Shyam et al., 2015) (Figure 10.12). The major sardine habitat and fishing areas are the coastal waters with depths from 5 to about 30 m. This region is influenced by upwelling and also by river runoff during the monsoon (Johannessen et al., 1987; Longhurst & Wooster, 1990; Madhupratap et al., 1994). Historically, sardine would abandon its coastal habitat for several years and these lean periods negatively affected the economy of the coastal communities (ICAR, 1971; Nair & Chidambaram, 1951). The fishery for oil sardine typically starts in June to July with the entry of spawners that were spawned during the previous year. Spawning then occurs during June to September, and adults and large shoals of juveniles spawned earlier in the same year are vulnerable to harvest within the 30 m depth zone. The fishery for oil sardine has shown wide fluctuations on seasonal, annual, and decadal scales (Pillai et al., 2003) and has experienced recent (1994 and 2015 - 2016) dramatic drops in landings (Figure 10.13).

Low oxygen waters usually spread into the coastal fishing area during or soon after the monsoon season. Negative effects can also occur pre-monsoon when intense upwelling occurs during early and low oxygen conditions prevent sardines from moving towards their preferred nearshore coastal waters for spawning. This upwelling the low oxygen pre-monsoon effect can be seen in the fishery in the following year (Kripa et al., 2015). Recruitment can be affected when the low oxygen occurs very close to the shore (5 to 20 m depth zone) during late or post-monsoon, and this affects catch in the same year. Length frequency studies and observations on gonad maturity and spawning have clearly shown that spawning of sardine occurs with the onset of monsoon and recruitment to the fishery starts by August (Antony Raja, 1964, 1969). Kripa et al. (2015, 2018) noted that the two rapid declines in landings (Figure 10.13) were coincident with low oxygen conditions in the shallow waters during late or post-monsoon. Correlation analysis between monthly catch rates of different size classes of Indian oil sardine and environmental data, which included the 2015 - 2016 decline, showed that low oxygen waters, especially inshore, had both positive and negative relationships with catch rates, suggesting low DO has effects both on spawning success and early life stage abundance (recruitment) as well as on the availability of fish to capture (Kripa et al., 2018).



Figure 10.12 A catch of Indian oil sardines being spread out to dry in the sun © Minden Pictures / Alamy stock photo.

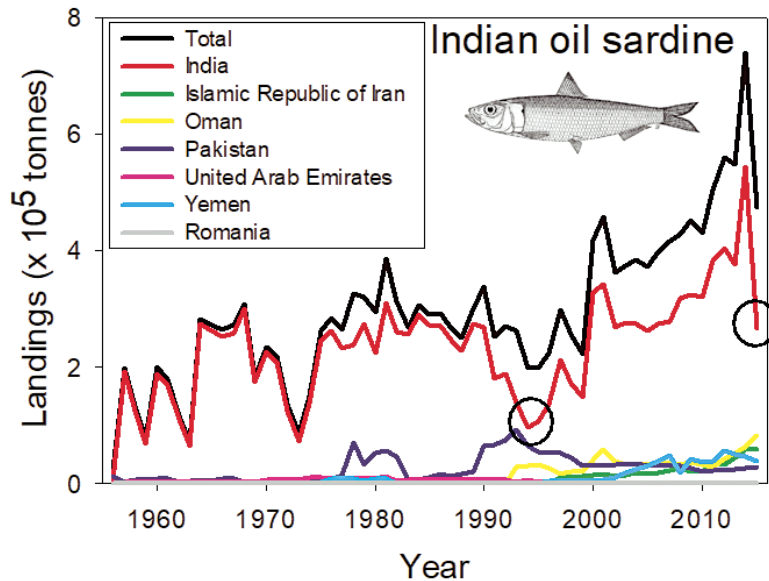


Figure 10.13 Annual landings ($\times 10^5$ tonnes) of Indian oil sardine by country and total for 1956 to 2015. Note the rapid drops in Indian and total landings in 1994 and 2015–2016 (circles).

10.6.7 North-west African fisheries

Fishing is a major socio-economic consideration for coastal countries in West Africa, as it represents more than US\$1.5 billion in fish annually legally captured, employs over 3 million individuals in the West African industry, and generates substantial export revenues (World Bank, 2009). For example, the fisheries sector in Senegal report a catch of over 350,000 tons that provides 70% of the protein intake, employs about

600,000 people, and contributes 37% of the total export revenues. The North-west African upwelling area is known to be the richest fishing ground in West Africa (Aristegui et al., 2009; Cury & Roy, 1988) and sustains a large variety of demersal and pelagic commercial fish species (Cury & Roy, 1989; Demarcq & Faure, 2000; Guénette et al., 2001; Ribeiro et al., 2004). The North-west upwelling is dynamically linked to the OMZ that is part of the Eastern Tropical North Atlantic (ETNA), which is composed of a deep OMZ at about 400 m depth

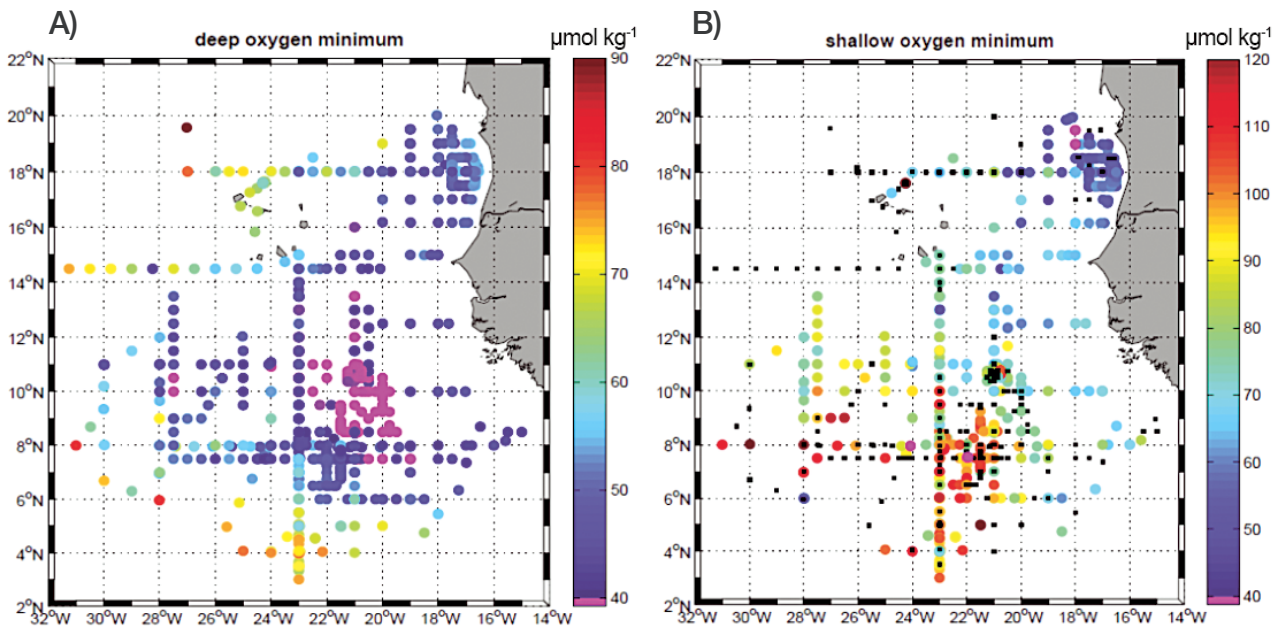


Figure 10.14 Oxygen concentrations illustrating the (A) deep oxygen minimum (>200 m depth) and (B) shallow oxygen minimum (<200 m depth) zones in the Eastern Tropical North Atlantic (source: Brandt et al., 2015). The data are CTD station data during 2006–2013. Purple dots show locations with oxygen less than $40 \mu\text{mol kg}^{-1}$ and black dots in (B) show vertical profiles without a shallow oxygen minimum (i.e. minimum occurred at the lower boundary of 200 m).



Figure 10.15 White grouper *Epinephelus aeneus* © Paulo Oliveira / Alamy stock photo.

offshore and a shallow OMZ at about 100 m depth (Figure 10.14; Brandt et al., 2010, 2015).

In this West Africa coastal region, unusually high mortality rates of demersal Serranidae were observed in the late 1980s, mainly for the most important commercial fish *Epinephelus aeneus* (white grouper) locally known as “thiof” (Figure 10.15). Commercial catches from industrial, and mostly artisanal, fisheries decreased from about 4000t in 1987 to less than 1000t by 2007 (Figure 10.16, Ndiaye et al., 2013). The mortality of the “thiof” was related to low bottom DO concentration (Caveriviere & Toure, 1990). While the evidence is not conclusive, similar episodes of high Serranidae mortality with their abdomen distended have been reported along the Senegalese coast by local fishers and investigators of the Senegalese National Research Center in Oceanography (CRODT). The Senegalese-Mauritanian sub-region is the only one within the North-west African upwelling

with hypoxic conditions (Karstensen et al., 2008). The “thiof” stock harvested by the Senegalese is considered over-exploited (Ndiaye et al., 2013; Thiao et al., 2012), and given its importance to the welfare and economics of the area, determining the role of deoxygenation on the population is critical.

10.6.8 Tropical pelagic billfishes

The OMZs in the eastern tropical Pacific and Atlantic oceans overlaps with where valuable commercial fisheries for tunas and billfishes, and recreational and bycatch fisheries for sailfish and blue marlin occur. Harvested tunas and billfishes include swordfish, skipjack tuna, and yellowfin tuna (Figure 10.17). These fishes require oxygen-rich environments and typically have high hypoxic thresholds (3.5 mg L^{-1}) below which they experience respiratory distress. Furthermore, billfishes prefer the warmest water available that typically occurs at the surface (Hoolihan et al., 2011). Suitable physical habitat for tropical pelagic fishes becomes compressed into a narrow surface mixed layer while the cold, hypoxic water below limits vertical distribution and diving behaviour (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011). The amount of the surface ocean layer (measured as depth) that is above 3.5 mg L^{-1} has been decreasing at a rate of one metre per year in the tropical North-east Atlantic, resulting in a loss of 15% of the volume of the usable vertical habitat in the upper 200 m for billfishes in this region since the 1960s. Habitat compression is evident from depth distributions of blue marlin (Figure 10.18) and sailfish monitored with

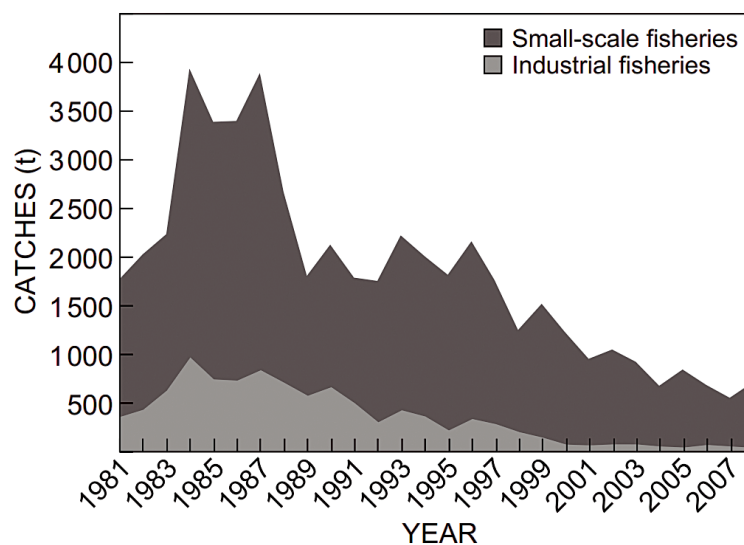


Figure 10.16 Total annual landings of *Epinephelus aeneus* by small-scale and industrial fisheries in Senegal between 1981 and 2008. (Source: Ndiaye et al., 2010).



Figure 10.17 Yellowfin tuna *Thunnus albacares* © David Fleetham / Alamy stock photo.

pop-up satellite archival tags. Comparisons of tagged fish between the Western North Atlantic (WNA), which lacks a vast OMZ, with fish tagged in the Eastern Tropical Pacific (ETP), which has one of the most extensive OMZs in the world, show striking differences in vertical habitat use (Prince & Goodyear, 2006). While the fish primarily occupy the upper 50 m of the water column in both oceans, Atlantic billfishes spent 25-35% of their time below 50 m while Pacific billfishes only spent 1-5% of their time below 50 m. Sailfish and blue marlin also spent more time in surface waters in the Eastern Tropical Atlantic (ETA) than the WNA, suggesting the OMZ in the ETA region, like that in the ETP, compresses available habitat to near surface waters as well (Prince et al., 2010).

The shallowing depth of suitable surface habitat has been hypothesized to increase the vulnerability of pelagic predators to surface fishing gear, such as longlines and purse seines (Prince & Goodyear, 2006; Prince et al., 2010; Section 8.2). Many billfish and related stocks are considered overfished, mostly due to bycatch mortality from fisheries targeting swordfish and tunas, suggesting expansion of OMZs could potentially exacerbate overfishing for these and related species. High catch rates in habitat-compressed areas can lead to overly optimistic estimates of population status and potentially biased management advice from stock assessment models. If catch data used to develop abundance indices are simply pooled for samples inside and outside of OMZ regions, then estimates of catchability will be biased (Prince et al., 2010). Increases in catchability due to habitat compression that are not accounted for in stock assessment models will often lead to overestimates of harvestable biomass and underestimates of fishing mortality, so that management advice based on these models may be less conservative than intended.

10.7 Management implications

Deoxygenation has complicated effects on fish populations and fisheries that can be difficult to isolate and quantify. Deoxygenation in all ecosystems often occurs with changes in other environmental conditions. When deoxygenation occurs in coastal systems influenced by riverine inputs, there are the competing effects of more food occurring with greater hypoxia (both are fuelled by nutrient loadings). This view of a food versus hypoxia tradeoff presumes that the increase in food quantity can at least partially compensate for the habitat lost to hypoxia, reduced food quality, and other negative effects of eutrophication, such as plankton community shifts and harmful algal blooms (Cloern, 2001; Rabalais et al., 2009). Under global climate change, warming and increased acidification is expected to co-vary with worsening hypoxia (Gruber, 2011).

Fish populations are often managed for sustainable yield and certain population sizes, and so management can reduce allowable catch to compensate for a lowered population resulting in no decline in the population itself but rather a lowered catch. Thus, data on population abundance trends can disguise a deoxygenation effect. Multiple stressors and managed fisheries make isolation of the effects of deoxygenation difficult; however, our difficulties in quantifying deoxygenation effects does not mean that the effects are necessarily small or unimportant. Most analyses that attempted to isolate the effects of hypoxia determined that deoxygenation itself has small to moderate effects on fish populations and food webs (like many of the other factors looked at one-at-a-time), but when hypoxia is combined with the other co-varying factors, large effects are predicted (e.g. Ainsworth et al., 2011).

The various case studies illustrate the complicated effects of deoxygenation on fisheries (Table 10.1); under continued and likely accelerating deoxygenation, these effects will intensify at the same time that demand for fish for nutrition will rise. We described effects on the populations themselves that then affected the fisheries. These included low oxygen dynamics affecting croaker recruitment and abundance in the Gulf of Mexico, cod recruitment and adult condition in the Baltic Sea, and possibly white croaker or “thiof” mortality in West Africa, and the sudden drop in landings of Indian oil sardine off the south-west coast of India. Other case studies showed how hypoxia affected the spatial distributions of the population that then determined the availability of



Figure 10.18 Blue marlin *Makaira nigricans* © Waterframe / Alamy stock photo.

individuals to harvest and had cascading effects through the fishery. Habitat compression led to changes in the availability of billfishes to harvest in the Eastern Tropical Pacific. The key fisheries species in the Peruvian EEZ illustrated a multi-species response to low oxygen; overlap of sardine and jack mackerel can affect predation pressure on anchovy and the availability of all three species to harvest. Prices of brown shrimp in the fishery in the Gulf of Mexico showed the effects of hypoxia causing a lessening of large shrimp relative to smaller shrimp. From a management viewpoint, the Dungeness crab in Hood Canal case study demonstrated how hypoxia can negatively affect fisheries management performance (e.g. sensitivity to overfishing), especially when hypoxia is combined with other stressors.

Fisheries management is under intense scrutiny about whether it is sufficiently effective, adequately protective of the resource (sustainability), and equitable. There is also great pressure to move towards an ecosystem-based fisheries management approach (Essington et al., 2016). Deoxygenation is part of the mix of stressors that, when combined, have population-level effects on abundance and spatial distributions that affect the fisheries. There are multiple examples of hypoxia affecting the catchability of the fish. Altered catchability can have profound effects on how abundance indices

from monitoring data are interpreted and the accuracy of the population dynamics models that underlie stock assessment. Almost all management analyses rely on indices derived from field data (catch, fishery-independent) at some level. Most fisheries management analyses are not detailed in space and so the effects of deoxygenation, which are localized within the spatial area used for management, are difficult to quantify and incorporate into the analyses. The effects of hypoxia on catchability are therefore not considered, which can result in misleading management advice. This applies to data-limited and well-studied species, and to artisanal and commercial and recreational fisheries.

The effects of deoxygenation on fisheries can, at times, be difficult to truly isolate and quantify, but nevertheless are important. Effects manifest themselves through the dynamics of the populations and the fishery, and often co-vary with other environmental variables. Furthermore, oxygen and fisheries dynamics are both dependent on local conditions, making most analyses complicated and dependent on extensive data and modelling to account for the site-specific conditions.

Further understanding and incorporating the role of deoxygenation on fisheries can increase the effectiveness of management by providing better information on

the temporal and spatial dynamics of the populations and how fisheries respond. This will enable proper interpretation of population fluctuations (e.g. growth, recruitment), the vulnerability of individuals to harvest (e.g. catchability), and population indices derived from monitoring data that are used to determine stock status and trends and also used to tune assessment models. There is little room for management miscalculations and offering misguided advice; too many people depend on effective management of fisheries to ensure sustainable harvests and healthy ecosystems.

10.8 References

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