



# Ocean deoxygenation: Everyone's problem

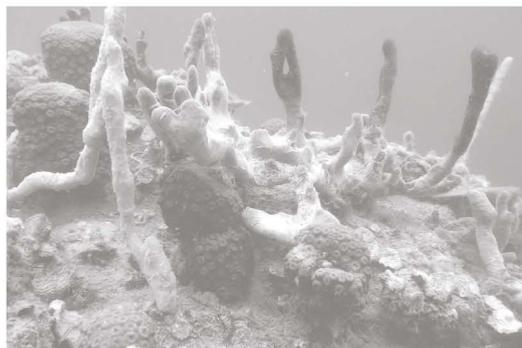
Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



## 8.9 The significance of ocean deoxygenation for Elasmobranchs

David W. Sims



IUCN GLOBAL MARINE AND POLAR PROGRAMME





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### Summary

- All of the >1000 species of sharks, skates and rays are obligate water-breathers with comparatively high absolute oxygen demands being relatively large-bodied, active predators. With broad distributions across aquatic habitats exhibiting large variations in physico-chemical variables including oxygen concentration indicates elasmobranch physiology, behaviour and ecology to be strongly influenced by oxygen depletion.
- Many elasmobranchs show rapid behavioural responses to hypoxic water by increased activity associated with avoidance. Nonetheless, elasmobranchs also appear capable of withstanding mild hypoxia with circulatory and/or ventilatory responses, perhaps even for extended periods. However, such strategies may be insufficient to endure moderate, progressive or prolonged hypoxia or anoxia.
- As water temperatures rise with climate warming most elasmobranchs (as ectotherms) will exhibit elevated metabolic rates and will be increasingly less able to tolerate the effects of even mild hypoxia associated with ocean deoxygenation. Thus, sustained hypoxia in warmer coastal waters is likely to lead to shifts in elasmobranch distributions.
- Expansion of oxygen minimum zones (OMZs) of the open ocean in particular are predicted to have significant population-level implications for pelagic elasmobranchs as they become habitat compressed into surface layers by shoaling hypoxic water.
- Surface layers overlying OMZs appear to be space use hotspots of pelagic sharks that may be increasingly likely to undergo significant 'habitat compression' (reduced habitat volumes) with expanding OMZs, potentially increasing their susceptibility to surface fisheries, e.g. long-lining, leading to further risks of over-exploitation especially of threatened species such as shortfin mako (*Isurus oxyrinchus*).
- A priority for conservation is to mitigate ocean deoxygenation effects on elasmobranchs, such that future catch rates are controlled in the light of climate change rather than for exploitation to be exacerbated by ocean oxygen losses.

Ocean hypoxia effect	Potential consequences
Large-scale transport of oxygen depleted water, or eutrophication-induced hypoxia, in shallow water ecosystems may overlap entire movement ranges of individuals of less active species.	<ul style="list-style-type: none"> <li>Leads to mortality of individuals from species with limited daily range (limited daily movement distances) or those exhibiting pronounced fidelity to particular locations, e.g. home range, spawning grounds.</li> </ul>
Declining oxygen concentrations in current habitats may result in species-specific shifts in distribution and abundance patterns as well as changes to vertical niche.	<ul style="list-style-type: none"> <li>Shifts in upper-trophic level relationships between elasmobranch predators and their prey, altering food web structure and stability.</li> <li>Spatial redistribution of coastal and open-ocean elasmobranchs both horizontally and vertically changing the location and intensity of interactions with fisheries with consequences for catch rates and management.</li> </ul>
Shoaling hypoxic layers may result in species-specific vertical movement constraints and compression of vertical habitat into surface waters.	<ul style="list-style-type: none"> <li>Altered geographic and vertical overlap with prey distributions that establish more persistent space-use hotspots of pelagic elasmobranchs closer to the surface</li> <li>Increased susceptibility to capture by surface fishing gears, e.g. long-lining.</li> </ul>
The North Atlantic Ocean is projected to undergo large decreases in oxygen content within the upper water column, and in intermediate waters (100 – 1000 m) associated with OMZs.	<ul style="list-style-type: none"> <li>Species occurring in this region, including currently overfished as well as internationally protected sharks, are predicted to undergo exposure to large declines in oxygen and pronounced shoaling of hypoxic layers of OMZs.</li> </ul>

### 8.9.1 Introduction

The elasmobranchs (sharks, skates and rays; Subclass Elasmobranchii, literally “plate gills”) are cartilaginous fishes that, like the majority of all other fish, are obligate water-breathers reliant upon extracting oxygen from the surrounding water to meet metabolic demands. There are over 1,000 extant species of elasmobranch that arose sometime during *c.* 400 million years of independent evolution, with the main living families having first appeared sometime between the Permian and Jurassic Periods (~250–150 million years ago) (Young, 1981). Over that time elasmobranchs have evolved to occupy a very broad range of habitats within aquatic ecosystems worldwide: they are distributed in freshwater and estuarine systems and in the oceanic pelagic realm and the deep sea (to at least 4,500 m depth; Kyne & Simpfendorfer, 2010), and from polar Arctic seas (but not the Antarctic) in water temperatures of ~2 °C (Watanabe et al., 2012) through to low latitude coral reefs circumglobally (~30 °C). This broad distribution across aquatic habitats that exhibit large spatial and temporal variations in physico-chemical variables, including oxygen concentration, coupled with the relatively large body size and active predatory lifestyle of elasmobranchs indicates the physiology,

behaviour and ecology of sharks, skates and rays are likely to be strongly influenced by oxygen depletion.

Understanding how elasmobranchs will be affected by ocean deoxygenation is important not only for assessing the potential for altered distributions and abundance in relation to climate-driven changes (Deutsch et al., 2015), but also in determining how such environmentally induced changes may interact with commercial fisheries potentially to exacerbate exploitation rates. Life-history traits such as slow growth, late maturity and low fecundity make elasmobranchs less resilient to fishing pressure than bony fishes (Field et al., 2009). Many sharks, skates and rays are highly valued worldwide by fisheries and over-harvesting in some regions has led to declines in the population levels of numerous species (Baum et al., 2003; Ferretti et al., 2010; Worm et al., 2013) (Table 8.9.1). There is particular concern that target- and by-catch fisheries are depleting populations below sustainable levels where recovery may not be possible, or at best may be very slow, even if fishing pressure is removed (Field et al., 2009; Sims et al., 2018). An increasing number of elasmobranchs are being listed on the International Union for the Conservation of Nature (IUCN) Red List of threatened species, with some larger species of greater economic value now being listed on the Convention of International Trade in

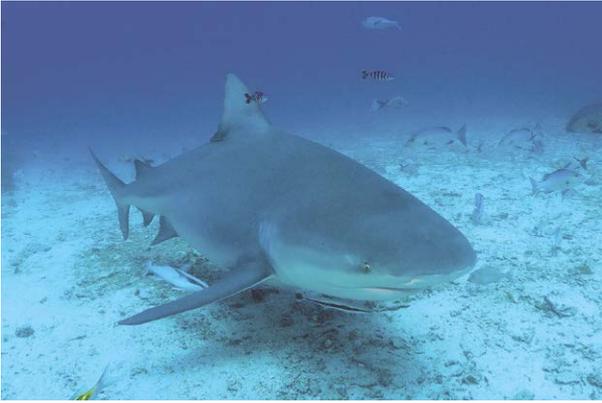


Figure 8.9.1 Bull shark *Carcharhinus leucas*. © James Lea.

Endangered Species (CITES) (Dulvy et al., 2014) (Table 8.9.1). The conservation of elasmobranch populations may become increasingly difficult in the face of multiple pressures such as the expansion of industrialized fisheries, climate-driven changes in the ocean such as deoxygenation and, for many species, little or no sustainable management of stocks (Sims et al., 2018; Sims & Queiroz, 2016; Sims & Simpson, 2015).

Levels of dissolved oxygen in open ocean and coastal waters have been decreasing since at least the middle of the 20th century (Breitburg et al., 2018). Models predict climate-driven ocean warming and reduced ventilation of the deep ocean will lower levels of dissolved oxygen (DO) in the ocean by 1–7% by 2100, with *in situ* observations suggesting reductions of >2% since 1960 (Breitburg et al., 2018; Schmidtko et al., 2017). Permanent oxygen minimum zones (OMZ) across the world's ocean are increasing in area and volume as a result, with unknown consequences for ecosystems and biodiversity (Gilly et al., 2013; Mora et al., 2013; Stramma et al., 2008). Potential impacts may be particularly significant for large, active oceanic predators with high absolute oxygen demands because available habitats will become reduced, concentrating them further in surface waters where they may be more vulnerable to fisheries (Gilly et al., 2013; Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011).

The effects of ocean deoxygenation on sharks, skates and rays is examined by considering what is known about their spatial overlap with hypoxic regions of the open ocean, including the so-called oxygen minimum zones, their physiological and behavioural responses to low oxygen concentrations, and how such responses may affect their vulnerability to open ocean fisheries.

### 8.9.2 Elasmobranchs and ocean deoxygenation

Dissolved oxygen (DO) has a major role in shaping marine ecosystems by determining the spatio-temporal distributions of all water-breathing marine organisms including fish (Gilly et al., 2013; Levin & Bris, 2015). Elasmobranchs are principally a marine taxon (only ~5% of species occur in fresh water) with the majority of species having range distributions associated with estuarine, coastal and shelf ecosystems. In shelf environments, naturally occurring processes such as seasonally high temperatures reducing oxygen solubility of water, and seasonal upwelling transporting oxygen-poor waters into shallow areas where respiration may further reduce DO, can both lead to chronic, episodic or prolonged hypoxia or anoxia in inner-shelf waters (<50 m depth) (Chan et al., 2008; Grantham et al., 2004) and estuarine habitats (Heithaus et al., 2009). Oxygen depleted water in shallow-water systems can also occur due to eutrophication-induced hypoxia (Breitburg et al., 2018; Diaz & Rosenberg, 2008). Both natural and anthropogenic-induced hypoxia have been recorded to change the distribution and abundance of fishes (Breitburg et al., 2018; Chan et al., 2008; Diaz & Rosenberg, 2008). Hypoxic waters occurring in shallow shelf areas have important consequences for major fisheries since some fish appear to respond by 'escaping' oxygen-poor environments, for example disappearance of rockfish (*Sebastes* species) from rocky reefs in the north-east Pacific Ocean during an anoxia event (Chan et al., 2008). OMZs intercepting shelf slopes in deeper water (>600 m) and oceanic seamounts far from continental landmasses can also result in dramatic changes in benthic and demersal fish vertical distributions (Chan et al., 2008; Wishner et al., 1990). However, hypoxic waters affecting the distributions, behaviour and ecology of sharks, skates and rays *in situ* are poorly documented by comparison, despite such events potentially overlapping the range distributions of many species. It is possible that large-scale coastal deoxygenation could result in mortalities of individuals of less active or wide-ranging elasmobranch species that are unable to move beyond the affected area, as has been observed for bony fish exposed to upwelling-driven nearshore hypoxia (Grantham et al., 2004). Nevertheless, the few studies that have been undertaken indicate large, active sharks appear to select habitats that are generally not oxygen depleted. For example, a comprehensive survey of bull sharks (*Carcharhinus leucas*) (Figure 8.9.1) in a subtropical

Table 8.9.1. Examples of threatened species of pelagic sharks with geographic distributions known to occur in waters above OMZs or in other areas projected to undergo oxygen losses over the coming decades. CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora; CITES 'II' denotes Appendix II listing with the year it was effective from. Data were accessed from the website of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (<<http://www.iucnredlist.org/>>; accessed May 2018).

Scientific name (common name)	Global IUCN Red List classification	Year of IUCN assessment	Population trend	Management measures	CITES listing effective from
<b>Carcharhiniformes</b>					
<i>Carcharhinus falciformis</i> (Silky shark)	Vulnerable A2bd	2017	Decreasing	Retention bans and live release are in place for all vessels operating under ICCAT and WCPFC management. IATTC and IOTC has prohibited retention of Silky Sharks on purse seine vessels, limited longline vessel bycatch.	II (2017)
<i>Carcharhinus galapagensis</i> (Galapagos shark)	Near Threatened	2003	Unknown	No management known to be in place.	
<i>Carcharhinus leucas</i> (Bull shark)	Near Threatened	2009	Unknown	No specific management programmes known. Managed in the U.S. east coast shark fisheries as part of the "large coastal" groups of species.	
<i>Carcharhinus longimanus</i> (Oceanic whitetip shark)	Vulnerable A2ad+3d+4ad	2015	Decreasing	Subject to protections under all the world's tuna-focused Regional Fishery Management Organisations (RFMOs). EEZs: Listed on U.S. Endangered Species Act. Protected in New Zealand.	II (2013)
<i>Galeocerdo cuvier</i> (Tiger shark)	Near Threatened	2009	Unknown	No specific conservation or management measures in place. EEZs: US Atlantic and Gulf of Mexico this species is managed under a Fisheries Management Programme.	
<i>Prionace glauca</i> (Blue shark)	Near Threatened	2009	Unknown	No species-specific catch limits or other protections in place in international waters for this species. Managed in EEZs of Canada, Mexico, USA (Atlantic, Gulf of Mexico) and New Zealand waters.	
<i>Sphyrna lewini</i> (Scalloped hammerhead)	Endangered A2bd+4bd	2007	Unknown	EEZs: Included in U.S. Large Coastal Shark complex management unit.	II (2014)
<i>Sphyrna mokarran</i> (Great hammerhead)	Endangered A2bd+4bd	2007	Decreasing	No known species-specific conservation measures in place. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)
<i>Sphyrna zygaena</i> (Smooth hammerhead)	Vulnerable A2bd+3bd+4bd	2005	Decreasing	ICCAT region: Banned retention, trans-shipment, landing, storage, and sale of species in the family Sphyrnidae. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)
<b>Lamniformes</b>					
<i>Alopias pelagicus</i> (Pelagic thresher)	Vulnerable A2d+4d	2009	Decreasing	IND: Prohibited to retain, transship or land in IOTC waters.	II (2017)
<i>Alopias vulpinus</i> (Common thresher)	Vulnerable A2bd+3bd+4bd	2009	Decreasing	ATL: Prohibited to target in ICCAT waters. IND: Prohibited to retain, transship or land in IOTC waters.	II (2017)
<i>Carcharodon carcharias</i> (Great white shark)	Vulnerable A2cd+3cd	2009	Unknown	EEZs: Protection in waters of Australia, EU, South Africa, Namibia, Israel, New Zealand, Malta and USA.	II (2005)
<i>Isurus oxyrinchus</i> (Shortfin mako)	Vulnerable A2abd+3bd+4abd	2009	Decreasing	N ATL: ICCAT 2017 Shortfin Mako Stock Assessment concludes "overfished and undergoing overfishing" and recommends zero TAC. Starting 2018 in NATL ICCAT waters can only retain if brought alongside dead (hence 'live release'). MED: Retention, transshipment, landing, display or sale prohibited. EEZs: Management in Australia, Canada, Chile, EU, New Zealand, USA.	
<i>Isurus paucus</i> (Longfin mako)	Vulnerable A2bd+3d+4bd	2006	Decreasing	No management measures in place for this species.	
<i>Lamna nasus</i> (Porbeagle)	Endangered A1abd	2006	Decreasing	EEZs: Management plans in waters of Canada and USA. Managed by quotas in New Zealand.	II (2014)

estuary in Florida, USA, showed they were highly responsive to reduced DO, being much more frequently caught in waters where DO was  $>2.50 \text{ ml O}_2 \text{ L}^{-1}$  (Heithaus et al., 2009). Furthermore, Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) show little tolerance to hypoxia and move away from warm ( $22 - 24 \text{ }^\circ\text{C}$ ) waters with reduced oxygen concentration ( $\sim 2.86 \text{ ml O}_2 \text{ L}^{-1}$ ) seasonally in the north central Gulf of Mexico (Parsons & Hoffmayer, 2005).

Among large predators such as the majority of elasmobranchs, how variations in oxygen concentrations may alter behaviour and structure distributions in shelf seas has not been the subject of extensive studies (Heithaus et al., 2009). The impacts of ocean deoxygenation on elasmobranchs urgently requires more research given the environmental changes projected (Levin, 2018), and in addition to the high levels of exploitation of sharks, skates and rays in fisheries spanning coasts to the open ocean (Dulvy et al., 2014; Worm et al., 2013). In this context, the effects of expanding OMZs on pelagic shark and ray ecology and exploitation rates is emerging as a critical issue needing to be addressed given the potential for widespread population impacts that may already be occurring (Queiroz et al., 2016).

### 8.9.3 Ocean oxygen minimum zones

Global climate change has led to declines in DO in the ocean interior (ocean deoxygenation) that are predicted to continue (Keeling et al., 2010; Schmidtko et al., 2017). Therefore, the effects on marine biota are likely to be profound in regions projected to have significant oxygen concentration changes, such as in permanent OMZs where long-term DO declines are acute (Gilly et al., 2013) (Figure 8.9.2). Vast expanses of the world's ocean show strong vertical changes in oxygen levels (oxyclines), where DO initially decreases to low levels before rising again at greater depths (Gilly et al., 2013; Schmidtko et al., 2017). This reduction in DO delimits the OMZ, typically defined by concentrations of  $20\text{--}90 \mu\text{mol O}_2 \text{ kg}^{-1}$  ( $<0.47\text{--}2.11 \text{ ml O}_2 \text{ L}^{-1}$ ) and lower, and located in the depth range 200–800 m (Gilly et al., 2013). OMZs are globally distributed and comprise  $\sim 5\%$  of ocean volume ( $\sim 10$  million  $\text{km}^3$ ). They are associated with lower  $\text{O}_2$  ventilation, increasing surface stratification and high primary production coupled with enhanced mesopelagic (200–1000 m) decomposition (Diaz & Rosenberg, 2008). However, as core oxygen values in the OMZ decline with ocean deoxygenation, the vertical

extent of the hypoxic layer thickens, that have resulted in geographic and vertical OMZ expansions over the past 50 years (Gilly et al., 2013; Stewart et al., 2014; Stramma et al., 2008).

Low-oxygen concentration water characterizing OMZs is seriously hypoxic for the vast majority of marine organisms (Vacquer-Sunyer & Duarte, 2008) prompting an urgent need to understand responses of marine biota to OMZ geographic and vertical expansions (Rosa & Seibel, 2008). Effects may include alteration of microbial processes that are key to nutrient cycling and gas fluxes (Levin & Bris, 2015), changing predator-prey dynamics (Stewart et al., 2013), and shifts in distributions, abundance and vulnerability of ecologically and commercially important fish species (Deutsch et al., 2015; Gilly et al., 2013; Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011). OMZ expansion is accompanied by shoaling of the upper boundaries of the OMZs (Stramma et al., 2008) and this, in particular, is hypothesized to hold significant implications for fish ecology and fisheries (Gilly et al., 2013; Stramma et al., 2011), including, presumably, oceanic elasmobranchs. As OMZs shoal, acute oxygen gradients are expected to compress the habitat of pelagic fish against the layer of hypoxic water (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011) (Figure 8.9.2). This raises an important question: will expanding volumes of oxygen-depleted water, such as expanding OMZs, 'compress' oceanic sharks and rays in surface layers above expanding hypoxic waters, reducing their habitat space and potentially increasing their susceptibility to surface fisheries? Furthermore, if surface waters above OMZs are preferred habitats for pelagic elasmobranch foraging, given that prey species may be similarly habitat compressed, will these waters act as a 'habitat trap', further exacerbating interactions with surface fisheries?

Ocean deoxygenation occurring in oceanic regions away from continental landmasses will affect fewer elasmobranch species because only about 2.5% are oceanic (Compagno, 2008). However, if the preferred habitats of oceanic species such as the blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and giant manta ray (*Manta birostris*) (Figure 8.9.3), for example, are centred in areas where ocean deoxygenation occurs, then impacts may be significant for these threatened species. Oceanic sharks and rays are large-bodied predators that are also of high value to commercial, high-seas fisheries for their fins, meat and, in the case of *M. birostris*, their gill rakers. Hence, given

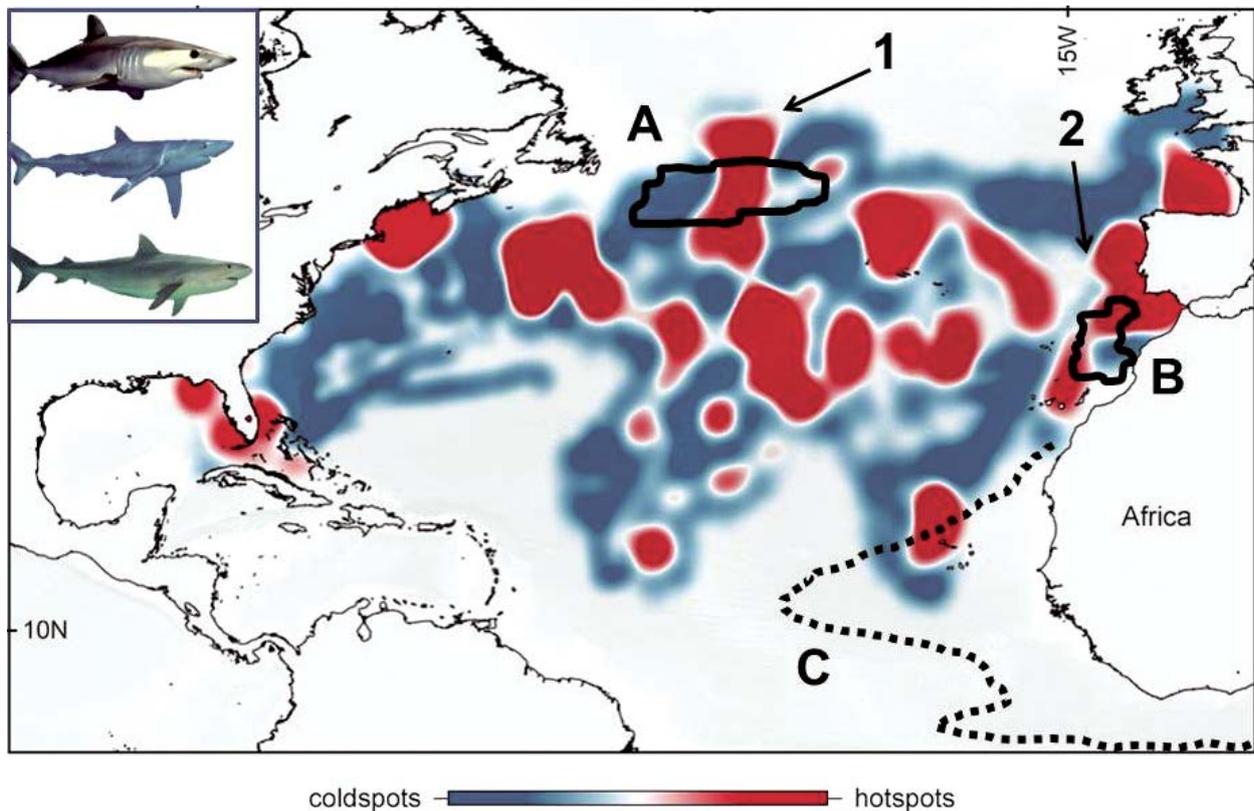


Figure 8.9.2 Oceanic space use hotspots of satellite-tracked pelagic sharks (shortfin mako, blue, tiger – shown in inset panel) overlapping with example areas of significant ocean deoxygenation in the North Atlantic. (A) Area projected from models to have  $O_2$  losses of  $>45 \mu\text{mol L}^{-1}$  (black lines), and (B) with losses of  $30\text{--}40 \mu\text{mol L}^{-1}$ , by 2090–99 compared to 1990–99 levels (mapped from Bopp et al., 2013). (C) Spatial extent of the eastern tropical Atlantic (ETA) OMZ as represented by the  $3.5 \text{ ml O}_2 \text{ L}^{-1}$  at 100m contour (dashed black line). Shark hotspot map redrawn from Queiroz et al. (2016) where a higher cluster density (Z score) signifies a space-use hotspot. Shark images provided by Jeremy Stafford-Deitsch (mako, blue) and James Lea (tiger).

the relatively slow life-history traits, commercial value and significant catch rates of oceanic elasmobranchs, these are species for which there is particular conservation concern. But what evidence is there that preferred habitats of oceanic shark and ray overlap hypoxic zones in the open ocean?

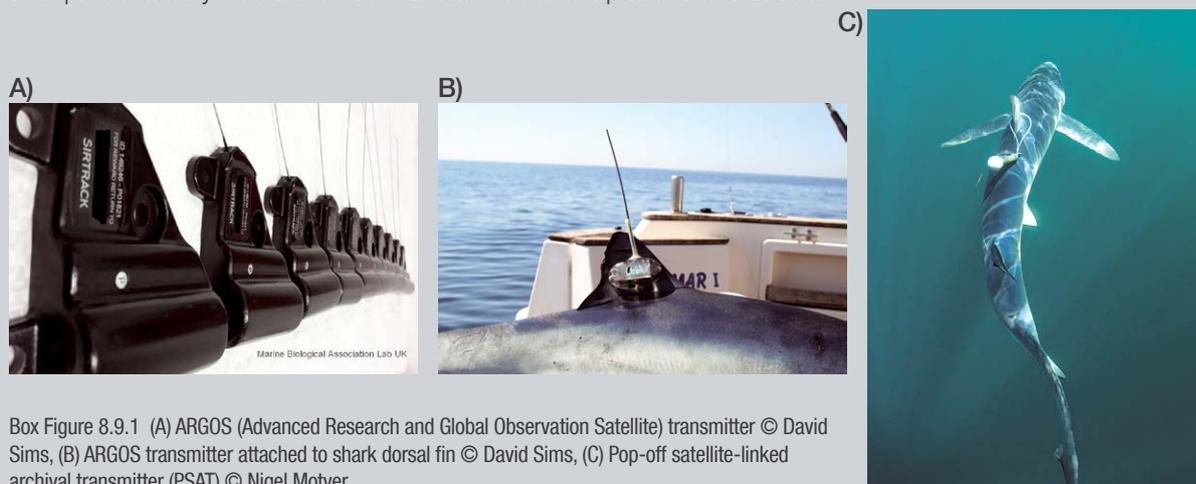
Only with the recent advances in miniaturized electronic tags for tracking fish at sea (Sims, 2010) have ocean-basin scale distributions of large oceanic sharks been possible to resolve at the fine-scale for multiple species over long-time periods (Block et al., 2011; Queiroz et al., 2016). Before then, elasmobranch distributions were generally understood only from fisheries-dependent catch data, which may not accurately represent actual population distributions. Satellite tracking of horizontal and vertical movements of large numbers of oceanic elasmobranchs has transformed understanding of spatial distributions over time, enabling the potential for impacts from ocean deoxygenation to be examined for the first time. For example, a recent study in the north Atlantic Ocean tagged over 100 individual pelagic sharks from six species (*P. glauca*; *I. oxyrinchus*; longfin

mako *I. paucus*; tiger shark, *Galeocerdo cuvier*; great and scalloped hammerheads, *Sphyrna* spp.) in both shelf and oceanic tagging locations and satellite tracked their movements for over 8,000 days (Queiroz et al., 2016). It showed that pelagic sharks occupy predictable habitat hotspots of high space use (Figure 8.9.2) that are persistent over years and characterized by strong sea-surface temperature gradients; movement modelling demonstrated these were preferred over other available habitats (Queiroz et al., 2016). Several of these multi-species hotspots of space-use overlap large-scale ocean areas with OMZs, in addition to areas that are projected to have among the highest rates of oxygen loss over the next century. For instance, a key pelagic shark hotspot in the North Atlantic occurs where the Gulf Stream flows into the North Atlantic Current and converges with the cold Labrador Current (arrowed 1; Figure 8.9.2). It appears to be an important foraging area for large sharks that undertake deep dives ( $>1000 \text{ m}$ ) apparently to feed on deep-water cephalopods (Sims, 2017). Ocean modelling projects that a large-scale area of the North Atlantic overlapping this important pelagic shark space use hotspot (area A; Figure 8.9.2) will have

**Box 8.9.1****Tracking elasmobranchs**

Two types of electronic tag are used to track long-distance movements of sharks and other marine vertebrates. The first is an ARGOS (Advanced Research and Global Observation Satellite) transmitter (Box Figure 8.9.1A) that emits ultra-high frequency radio signals when the tag and antenna attached to a shark's first dorsal fin breaks the sea surface (Box Figure 8.9.1B), with these signals being detected by Argos receivers on polar-orbiting satellites that relay the data to ground stations. Geographic positions of the tag are computed in near-real time and are available to researchers via a web portal.

The second is a pop-off satellite-linked archival transmitter (PSAT) that is attached to the fin or body (Box Figure 8.9.1C) which records swimming depth, water temperature and light intensity, before releasing from the shark at a pre-programmed time, floating to the surface and relaying data to overpassing ARGOS receivers. Data are then processed by researchers to estimate movement paths and activities.



Box Figure 8.9.1 (A) ARGOS (Advanced Research and Global Observation Satellite) transmitter © David Sims, (B) ARGOS transmitter attached to shark dorsal fin © David Sims, (C) Pop-off satellite-linked archival transmitter (PSAT) © Nigel Motyer.

Tags are small, weighing only about 50 – 160 g depending on battery size, and can be attached rapidly, within a couple of minutes. Tagging procedures require institutional, and in some countries governmental, training and approval to reduce the potential of injury to tagged animals.

one of the most dramatic oxygen losses for the North Atlantic of  $>45 \mu\text{mol O}_2 \text{ L}^{-1}$  ( $>1.03 \text{ ml O}_2 \text{ L}^{-1}$ ) by 2090-99, compared to 1990-99 levels (Bopp et al., 2013). This is not the only pelagic shark hotspot likely to be exposed to deoxygenation; for example, a hotspot between the Iberian Peninsula and north-west Africa (arrowed 2; Figure 8.9.2) occurs in an area projected to lose 30 – 40  $\mu\text{mol O}_2 \text{ L}^{-1}$  by 2090-99 (area B; Figure 8.9.2). Oxygen loss in large-scale ecosystems of the open ocean away from OMZs, are proposed to be driven by multiple contributing factors, including increased warming of surface waters, increased stratification, enhanced productivity and increased microbial respiration rates (Levin, 2018). Furthermore, a shark space use hotspot overlaps the eastern tropical Atlantic (ETA) OMZ (area C; Figure 8.9.2). Although the  $\text{O}_2$  concentration in the ETA OMZ is significantly higher than in Pacific and Indian Ocean OMZs where the  $\text{O}_2$  level can approach zero (Gilly et al., 2013), the decline in  $\text{O}_2$  content has been

most intense in the ETA OMZ where OMZ thickening (leading to shoaling) has been relatively fast, increasing by 85% in 40 years, which may have the potential for large increases in the area of hypoxic regions (Stramma et al., 2008). The co-occurrence of pelagic shark space use hotspots in areas of high projected oxygen loss has, at present, unknown consequences for sharks given the paucity of specific studies.

Despite few specific studies to date on large pelagic fish and OMZs (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011), those that have been undertaken provide a background to assess how sharks may respond to ocean deoxygenation. It is suggested that a DO concentration of  $\sim 3.5 \text{ ml O}_2 \text{ L}^{-1}$  represents a hypoxic threshold that induces stress in tropical pelagic fish such as tunas and billfishes, whereas levels  $< 1.5 \text{ ml O}_2 \text{ L}^{-1}$  probably represent a below lethal threshold for continuous exposure in istiophorid

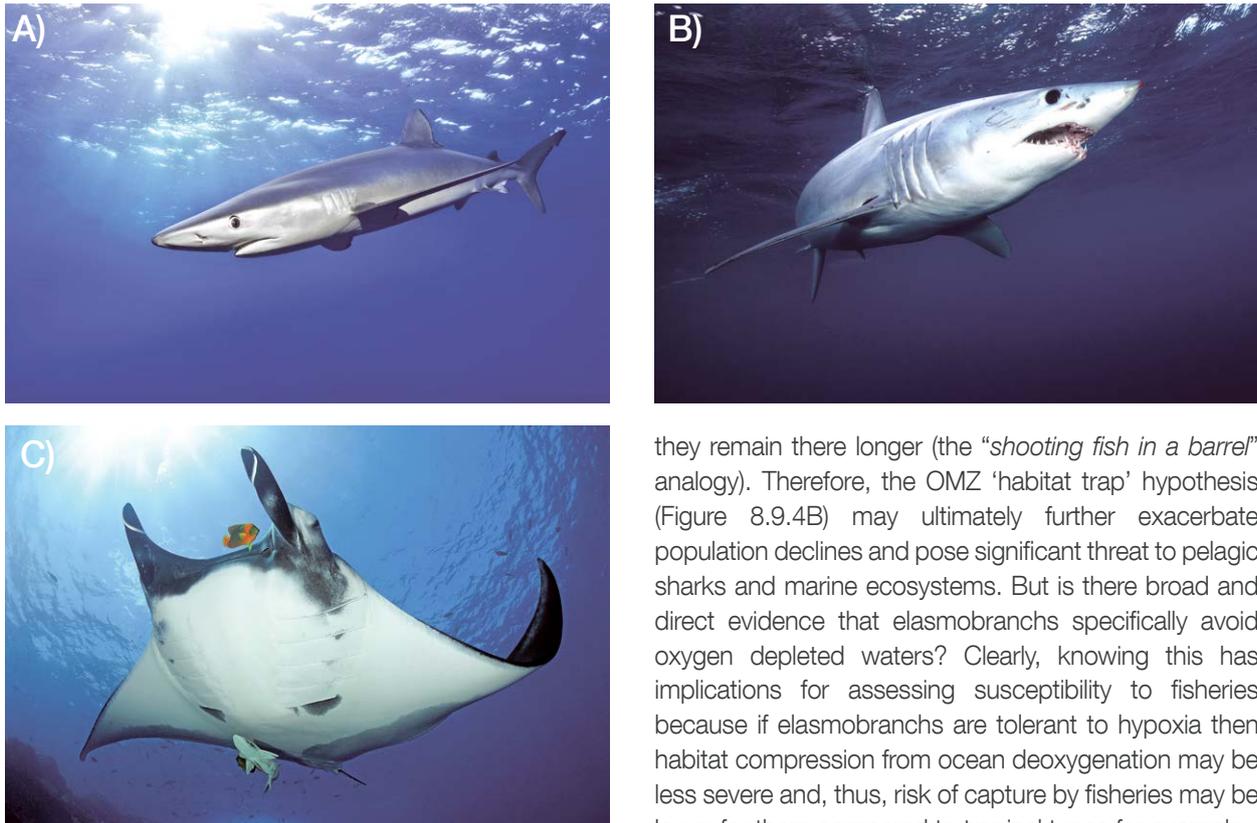


Figure 8.9.3 (A) Blue shark *Prionace glauca* off the Azores; (B) shortfin mako off New Zealand; (C) giant manta ray with shark suckers *Remora remora* and clarion angelfish *Holocanthus clarionensis*. (A) © Broker / Alamy stock photo; (B) © Richard Robinson / Alamy stock photo; (C) © Helmut Corneli / Alamy stock photo.

billfishes (Prince & Goodyear, 2006). A principal result of studies using electronic tags to track horizontal and vertical movements of tropical pelagic fish such as blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) associated with OMZs has been that they undergo 'habitat compression' (Figure 8.9.4A) through restriction in depth distribution generally to layers above  $3.5 \text{ ml O}_2 \text{ L}^{-1}$ , to about 50 - 100 m depth in the ETA OMZ (Prince et al., 2010; Stramma et al., 2011). If large pelagic elasmobranchs are similarly restricted by low DO levels then habitat compression is likely to occur for them also as OMZs expand with continued ocean deoxygenation. In this way, expanding OMZs could act as a 'habitat trap': sharks and rays may benefit from increased habitat compression that may also act on hypoxia-intolerant prey species (e.g. small pelagic fish, epipelagic cephalopods) that become increasingly aggregated in surface waters by shoaling hypoxic water (Gilly et al., 2013), potentially increasing feeding opportunities for elasmobranchs (Figure 8.9.4B). Thus, sharks and rays showing preferences to aggregate for enhanced foraging opportunities in reduced habitat volumes above OMZs may be more vulnerable to capture by fishers because

they remain there longer (the "shooting fish in a barrel" analogy). Therefore, the OMZ 'habitat trap' hypothesis (Figure 8.9.4B) may ultimately further exacerbate population declines and pose significant threat to pelagic sharks and marine ecosystems. But is there broad and direct evidence that elasmobranchs specifically avoid oxygen depleted waters? Clearly, knowing this has implications for assessing susceptibility to fisheries because if elasmobranchs are tolerant to hypoxia then habitat compression from ocean deoxygenation may be less severe and, thus, risk of capture by fisheries may be lower for them compared to tropical tunas for example.

#### 8.9.4. Physiological responses

Pelagic sharks have relatively high oxygen demands so encountering oxygen depleted waters of the open ocean may lead to metabolic stress. Among vertebrates, elasmobranchs are relatively large bodied, which confers on them higher absolute oxygen requirements than smaller bodied taxa (Payne et al., 2015; Sims, 1996). Elasmobranchs are also generally highly mobile predators and scavengers, predominating as upper-trophic-level predators in the ecosystems in which they occur. They have a key role in the structure and functioning of such systems, for example by regulating the abundance of prey populations that acts to stabilize trophic interactions across complex marine foodwebs (Heithaus et al., 2008). Naturally, the capacity for movement and activity among elasmobranchs varies with individual lifestyle, extending from slower-moving, ectothermic benthic species such as catsharks (e.g. *Scyliorhinus* spp.) and skates (*Raja* spp.) (Figure 8.9.5) that can lie motionless on the sea bed for many hours each day (Wearmouth et al., 2014), to the highly active, oceanic pelagic sharks such as the shortfin mako (Figure 8.9.3B) that swim at high speed, can traverse ocean basins and possess morphological adaptations such

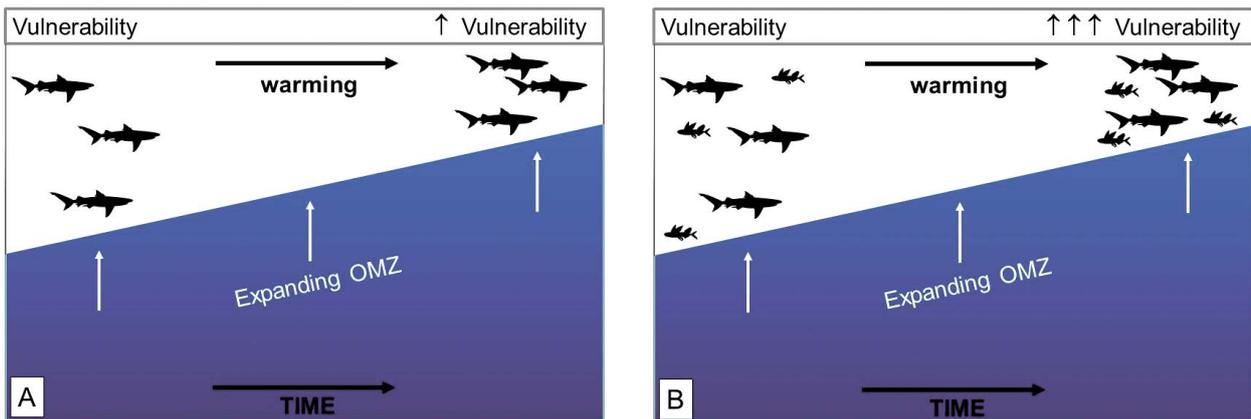


Figure 8.9.4 Scenarios of how ocean deoxygenation in oxygen minimum zones will potentially affect pelagic sharks. Schematic of the habitat trap hypothesis. (A) The concept of fish habitat compression from expanding OMZs increasing vulnerability leads to (B) the 'habitat trap' hypothesis, whereby habitat compression combined with predator and prey aggregation increases predator relative vulnerability to fisheries capture as predators remain in above-OMZ for extended periods. Shark and fish silhouettes from [www.iconspng.com](http://www.iconspng.com).

as endothermy, where body temperature is maintained some 4–6 °C above ambient (Bernal et al., 2010).

For elasmobranchs exposed to hypoxia that are unable to move due to physical environmental constraints, e.g. hypoxic water overlaps their entire preferred habitat or activity space, then physiological mechanisms must be employed to compensate for oxygen limitation (Jensen et al., 1994). Direct measurements of ventilatory responses of fishes indicates they can be considered oxygen regulators, that are able to maintain or even increase oxygen uptake in hypoxic conditions, or oxygen conformers, that immediately reduce their oxygen uptake as oxygen levels decline (Fritsche & Nilsson, 1994). It has been proposed that bony fishes are mainly oxyregulators, whereas most elasmobranchs are oxyconformers (Fritsche & Nilsson, 1994). However, elasmobranch ventilatory responses to hypoxia appear varied, including having been shown to increase upon exposure to low oxygen concentrations (Di Santo et al., 2016; Metcalfe & Butler, 1984). Little skate (*Leucoraja erinacea*) embryos for example, that develop within immobile egg-cases attached to substrata associated with the sea bed, maintain constant levels of oxygen uptake above  $\sim 2.90 \text{ ml O}_2 \text{ L}^{-1}$  ( $\sim 45\%$  air saturation in water at 15 °C) that are driven by increased tail-beat frequency that pumps more water through the egg-case (Di Santo et al., 2016). However, below this critical threshold oxygen consumption declines abruptly with increasing levels of hypoxia despite maintenance of elevated tail-beat frequency. Furthermore, temperature has a profound effect on the responses of the relatively inactive elasmobranch species (Butler & Metcalfe, 1988). For instance, at the lower temperature of 7 °C hypoxia has little effect on the lesser-spotted catshark

*Scyliorhinus canicula* of temperate north-east Atlantic shelf seas (Figure 8.9.5A), whereas at 12 °C it exhibits reductions in oxygen uptake and heart rate that are even more severe at higher temperatures (Butler & Metcalfe, 1988; Butler & Taylor, 1975). In general, therefore, relatively inactive elasmobranchs from temperate waters are considered to regulate oxygen uptake during hypoxia at low ambient temperatures (oxyregulation). At higher temperatures, that induce higher metabolic rates in ectotherms (decreasing aerobic scope), they exhibit an oxyconformity response, with lowered oxygen uptake matching hypoxic conditions (Butler & Metcalfe, 1988) and perhaps a progressively greater reliance on anaerobic metabolism (Di Santo et al., 2016). This suggests that as water temperatures rise with climate warming, many elasmobranchs may be less able to tolerate the effects of progressive hypoxia associated with ocean deoxygenation.

An obvious response of mobile aquatic animals exposed to hypoxia should be to avoid it and move to normoxic waters (Jensen et al., 1994). However, hypoxia can inhibit spontaneous activity in catshark (*S. canicula*), indicating that this species responds to hypoxia by reducing the demand for oxygen when it is at low ambient levels (Metcalfe & Butler, 1984). Reduction in activity when exposed to hypoxia also occurs in the Florida smoothhound shark (*Mustelus norrisi*) that is capable of ventilating while resting motionless, like other bottom-living elasmobranchs (Carlson & Parsons, 2001). Induced inactivity in response to hypoxia will lower oxygen consumption rate, thereby reducing oxygen demand and compensating for low ambient oxygen concentrations during hypoxia (Jensen et al., 1994). However, that some elasmobranchs may not

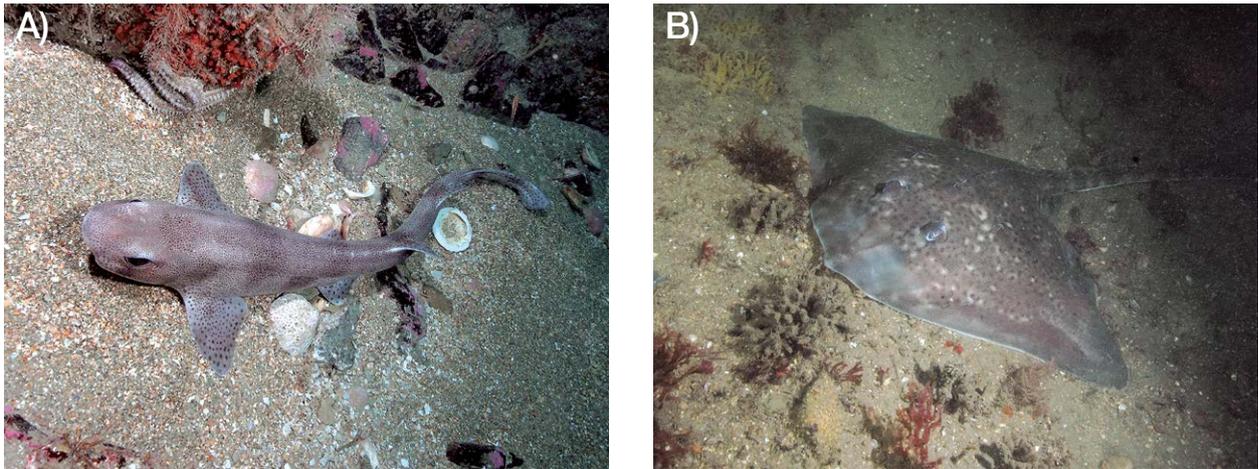


Figure 8.9.5 Distributions of smaller bodied elasmobranchs may be shifted by ocean deoxygenation in coastal waters. (A) the small spotted catshark, *Scyliorhinus canicula*, is common in north-east Atlantic and Mediterranean shelf seas and reaches a maximum length of 0.7 m. It has been shown to be an oxyregulator when exposed to mild hypoxia, but an oxyconformer with increasing hypoxia, indicating it will move to avoid moderate and strongly hypoxic waters resulting in potential distributions shifts. (B) a thornback ray, *Raja clavata*, occurs in the north-east Atlantic, Mediterranean and off north Africa growing to a maximum length of 1.3 m. It utilizes a broad range of habitats from estuaries to open ocean that may become more prone to deoxygenation in the future. © Keith Hiscock.

necessarily move away from hypoxia and developing embryos in egg-cases on the sea bed are unable to, implies compensatory mechanisms should be present to maintain critical oxygen uptake.

Among small-bodied, less active sharks such mechanisms appear to be present as physiological responses to severe oxygen stress. For the less active, temperate elasmobranchs that have been studied in detail, hypoxia causes a general circulatory response (Satchell, 1961) elicited, in *S. canicula*, by externally located  $O_2$  receptors apparently distributed diffusely in the branchial (gill) cavities and innervated by cranial nerves (Butler et al., 1977). The circulatory response in general comprises an increase in the ventilation volume of water passed across the gills accompanied by a reduction in heart rate (bradycardia) and by an increase in cardiac stroke volume (volume of blood pumped from the ventricle per beat) (Butler & Metcalfe, 1988). During moderate hypoxia the ventilation volume is increased by up to 50% (Metcalfe & Butler, 1984). Nonetheless, it appears that this increase is insufficient to maintain partial pressures of oxygen in arterial blood as the inspired oxygen partial pressures decline (Butler & Taylor, 1975). Similarly, bradycardia and increased stroke volume only act to maintain overall cardiac output such that once a reduction in the venous concentration of oxygen no longer matches the decrease in arterial oxygen concentration, oxygen uptake falls (Butler & Metcalfe, 1988; Butler & Taylor, 1975). Butler et al. (1979) found that *S. canicula* were unable to survive prolonged exposure to severe hypoxia ( $<2.30 \text{ ml } O_2 \text{ L}^{-1}$ ) whereas

developing embryos within egg-cases recovered after variable periods of hypoxia and up to 12 h anoxia (Diez & Davenport, 1987). Similarly, the sluggish, bottom-dwelling electric ray (*Torpedo marmorata*) (Figure 8.9.6) that is found in European shelf seas shows a significant increase in ventilation frequency and amplitude during hypoxia, and similar to catsharks, extreme hypoxia can be endured for many hours (Fritsche & Nilsson, 1994; Hughes, 1978). These studies indicate many inactive elasmobranchs from temperate waters are capable of withstanding mild hypoxia with circulatory responses, perhaps even for extended periods, however, such strategies may be insufficient to endure moderate, progressive or prolonged hypoxia or anoxia for periods greater than a day. Collectively, these observations suggest that deoxygenation occurring in temperate, coastal waters is highly likely to result in shifts in



Figure 8.9.6 Torpedo ray *Torpedo marmorata*. © Martin Habelnetzel / Alamy stock photo.

distributions of elasmobranchs arising from avoidance movements away from persistent hypoxic habitats. In the absence of avoidance, however, and where oxygen depleted waters entirely overlap the daily movement ranges of less active species it is possible mortalities could occur.

In tropical waters, the epaulette shark (*Hemiscyllium ocellatum*) is one of the few elasmobranchs that appears able to tolerate extreme hypoxic conditions for long periods in its natural habitat of shallow coral reefs (Nilsson & Renshaw, 2004). This shark tolerates repeated exposure to severe hypoxia (5% of normoxia) and even anoxia at 25 – 30 °C (Wise et al., 1998) during tidal fluctuations that at low tide cut-off the warm, shallow reef platform water (where it forages) from the surrounding ocean. In the isolated reef platform water at low tide the respiration of organisms trapped in this fixed volume of water lowers oxygen concentration to <20% air saturation (<1.3 ml O<sub>2</sub> L<sup>-1</sup>) (Nilsson & Renshaw, 2004). A comparative study demonstrated that the critical oxygen tension,  $P_{crit}$ , at which an animal transitions from being an oxyregulator to an oxyconformer, was much lower for the hypoxia-tolerant epaulette shark than a hypoxia-sensitive shovel-nose ray (*Aptychotrema rostrata*), probably due to a significantly greater haemoglobin O<sub>2</sub> binding affinity in the shark (Speers-Roesch et al., 2012a). In addition, among elasmobranchs it was evident that the variation in hypoxia tolerance was not solely determined by differences in O<sub>2</sub> uptake and transport, but also by tissue-specific metabolic responses, such as metabolic depression associated with lower tissue lactate concentrations, for example (Nilsson & Renshaw, 2004; Speers-Roesch et al., 2012b). In contrast, exposure of the spurdog shark (*Squalus acanthias*) to severe hypoxia (5% air O<sub>2</sub> saturation for 4 h; ~0.30 ml O<sub>2</sub> L<sup>-1</sup>) leads to reduction in active gill homeostatic processes, such as urea retention, ionoregulation, and an osmoregulatory compromise due to increased functional gill surface area (Zimmer & Wood, 2014). Overall therefore, it appears that most elasmobranchs can be considered to be only weak oxyregulators, principally elicited via circulatory responses, and across a relatively narrow range of temperatures. However, in a few species, like the epaulette shark, severe hypoxia may be regularly tolerated for extended periods, with oxyregulation persisting down to very low oxygen tensions through physiological adaptations in cardiovascular function and metabolic responses of the heart and other tissues.

There appear to be few studies documenting anaerobiosis (respiration without oxygen) in elasmobranchs exposed to hypoxia, even though it is feasible that sharks and rays may enter OMZs for instance, to feed on slow-moving, hypoxia-tolerant prey species, such as deep-water cephalopods (Rosa & Seibel, 2008; Seibel, 2011; Seibel et al., 2014), and which would be possible through use of anaerobic metabolic pathways. Interestingly, the hearts of the few elasmobranchs so far studied in this context have been identified to be well equipped biochemically for sustained periods of anaerobiosis (Sidell & Driedzic, 1985; Tota, 1999), with the catshark *Scyliorhinus stellaris* showing little cardiac ultrastructural damage even during periods of anoxia (Helle et al., 1983; Tota, 1999).

In the context of open ocean deoxygenation such as that observed in permanent OMZs, an important question is whether threatened pelagic sharks vulnerable to commercial exploitation are tolerant of hypoxia, or even short-term anoxia. Expanding midwater OMZs are likely to have the most pronounced effects on species with high metabolic oxygen demands. Oceanic sharks in the family Lamnidae are large, fast-swimming apex predators with high oxygen demands arising from cardiovascular and respiratory specializations (e.g. large gill surface areas, high mitochondrial densities, larger heart mass, increased muscle capillary density and myoglobin concentration) and swimming muscle physiology (red muscle endothermy) that maintain body temperatures above ambient, potentially expanding both horizontal and vertical niches (Bernal et al., 2010). These adaptations for a high O<sub>2</sub> uptake lifestyle suggest endothermic mako sharks may be intolerant of hypoxia, but it remains an open question how high-performance fish like this may be affected by hypoxic waters in the absence of experimental physiological studies of the type undertaken on smaller, less active elasmobranchs (Payne et al., 2015). However, behavioural responses of smaller bodied coastal pelagic sharks have been measured under controlled laboratory conditions in response to hypoxia. For large sharks that have not been studied under experimental conditions, DO has been measured or estimated in habitats through which shark movements have been tracked. Both these approaches provide insight into how pelagic sharks may respond to low oxygen, and thereby how they may interact with OMZs and other deoxygenated habitats that may influence their ecology and risk of capture.

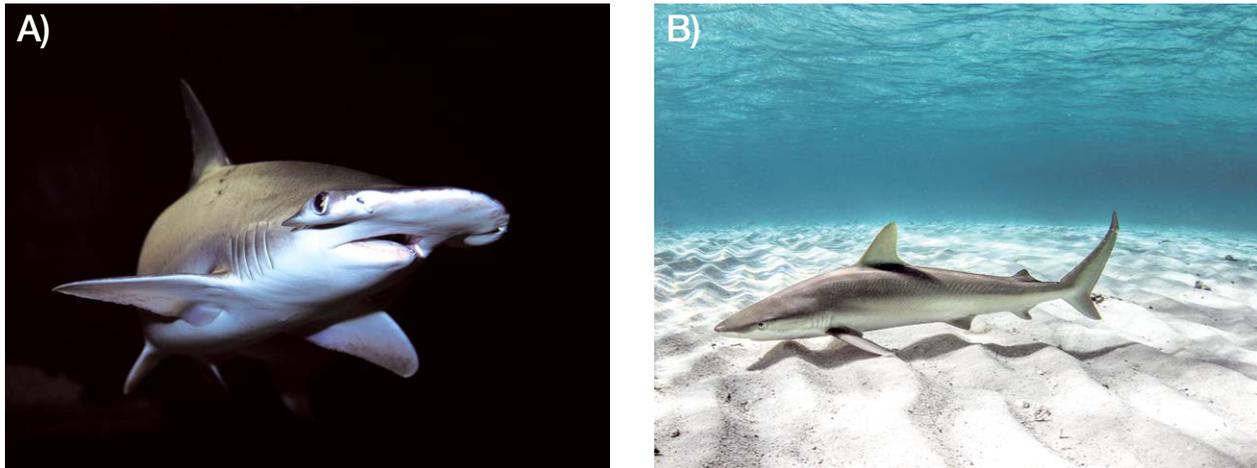


Figure 8.9.7 Ram ventilating sharks – (A) bonnethead *Sphyrna tiburo* and (B) blacknose *Carcharhinus acronotus*. © (A) Mark Conlin / Alamy stock photo; (B) Ken Kiefer / Alamy stock photo.

### 8.9.5 Behavioural responses

Many pelagic sharks and rays are obligate ram-ventilators that extract oxygen from water by swimming forwards with an open mouth to pass water across the gills. Under conditions of hypoxia therefore, elasmobranchs must increase mouth gape, swimming speed, or both, to increase ventilation volume and maintain oxygen uptake rate (Carlson & Parsons, 2001). Coastal ram-ventilating bonnethead (*Sphyrna tiburo*) and blacknose (*Carcharhinus acronotus*) sharks (Figure 8.9.7) exposed to hypoxic conditions ( $\sim 1.80 - 2.43$  ml  $O_2$   $L^{-1}$ ) in laboratory respirometers have been observed to increase swimming speed, mouth gape and oxygen consumption rate (Carlson & Parsons, 2001). These were responses similar to those seen in other ram-ventilating species of fish such as skipjack and yellowfin tunas. In sharks, the behavioural response of increased mouth gape during hypoxia has been proposed as a mechanism for maintaining oxygen delivery (Carlson & Parsons, 2001), which is supported by measurements for *S. tiburo* showing changes in oxygen content of water during swim trials caused no significant changes in either blood oxygen content or haematocrit (the ratio of the volume of red blood cells to the total volume of blood) (Carlson & Parsons, 2003). This suggests obligate ram-ventilating pelagic sharks may be able to tolerate minor or perhaps moderate levels of hypoxia.

That open-ocean pelagic sharks may be capable of withstanding moderate hypoxia, at least for short periods, is suggested by tracking studies where spatial movements have been related to modelled DO data that are estimated for the surface and at-depth environments visited by the sharks. For example, tracking shortfin

mako sharks in the eastern tropical Pacific (ETP), the world's largest OMZ, indicated those individuals generally remained in waters with  $>3.0$  ml  $O_2$   $L^{-1}$ , rarely encountering water with  $<2.0$  ml  $O_2$   $L^{-1}$ , although on very deep dives they may have reached water with  $1.25$  ml  $O_2$   $L^{-1}$  (Abascal et al., 2011; Vetter et al., 2008). In another study, great white sharks *Carcharodon carcharias* offshore in the ETP were typically associated with dissolved oxygen concentrations of  $>3$  ml  $O_2$   $L^{-1}$  with an estimated minimum  $O_2$  level of  $0.3$  ml  $O_2$   $L^{-1}$  during occasional dives to near 1000 m (Nasby-Lucas et al., 2009). Similarly, the dive profile of a single scalloped hammerhead shark *Sphyrna lewini* in Baja California indicated it may have entered depths where modelled oxygen indicated waters were extremely hypoxic ( $<0.5$  ml  $O_2$   $L^{-1}$ ) (Jorgensen et al., 2009).

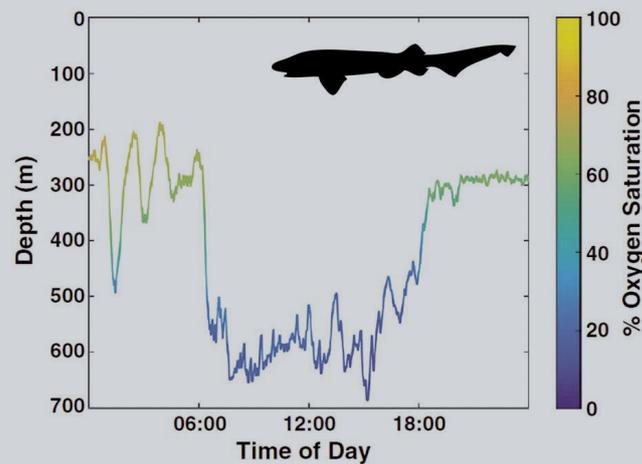
The studies discussed above were limited to using modelled DO data from oceanographic datasets to assess potential oxygen levels along paths taken by tracked sharks. Hence, actual DO in the habitats



Figure 8.9.8 Great white shark *Carcharodon carcharias*. © Wilyam Bradberry / Shutterstock.com.

**Box 8.9.2****Measuring ocean oxygen with shark ‘oceanographers’**

Dissolved oxygen (DO) data can now be measured along the paths of elasmobranchs. DO-depth-temperature recording tags with the potential capability for data retrieval via ARGOS satellites have been developed and trialled on sharks and seals (Baillleul et al., 2015; Coffey & Holland, 2015). Box Figure 8.9.2 shows the tag-recorded swimming depth of a six-gill shark, *Hexanchus griseus*, and the dissolved oxygen concentration of water encountered over a 24 hr period (from Coffey & Holland, 2015). The trace illustrates that during daylight hours the shark was in deep waters between about 450 and 700 m depth and oxygen saturation of ~10–50%.



Box Figure 8.9.2 Swimming depth of a tagged six-gill shark and the environmental dissolved oxygen concentration recorded by the tag along its track. Figure credit (Coffey & Holland, 2015) available under the terms of the Creative Commons Attribution 4.0 International Licence ([www.creativecommons.org/licenses/by/4.0/](http://www.creativecommons.org/licenses/by/4.0/)). The six-gill shark silhouette has been added to original made available by phylopic.com with credit to Tony Ayling (vectorized by T. Michael Keeseey) under the terms of the Creative Commons Licence ([www.creativecommons.org/licenses/by-sa/3.0/](http://www.creativecommons.org/licenses/by-sa/3.0/)).

As DO sensing tags become readily available, in the future they will no doubt improve our understanding of how elasmobranchs respond to climate-driven warming and deoxygenation occurring in the ocean. They will also make elasmobranchs ‘animal oceanographers’ with the tags they carry collecting very large quantities of DO data during horizontal and vertical excursions over huge areas. These data can be provided to oceanographic databases to help improve predictions of climate changes generated by atmosphere-ocean system models.

selected by sharks could be different to the values supposed. Direct measurements are needed to assess more accurately how pelagic sharks will respond to hypoxia. Important recent developments are data-logging tags capable of measuring dissolved oxygen and swimming depth for recording directly the DO levels experienced by free-ranging marine predators (e.g. Baillleul et al., 2015), including sharks (Coffey & Holland, 2015). The new tag used to track sharks provided DO concentration measurements highly correlated with vertical profiles obtained simultaneously from ship-borne instruments. Deployment on two bluntnose sixgill sharks (*Hexanchus griseus*) off Hawaii, Pacific Ocean, recorded oxygen saturations as low as 9.4% of normoxia for short durations (few mins) during dives to

nearly 700 m depth (Coffey & Holland, 2015). Although *H. griseus* (Figure 8.9.9) are large, generally slow moving sharks with lower metabolic rates than the high oxygen demand pelagic sharks, the new tag results confirm that moderate to extreme hypoxia may not necessarily be a barrier to space use of large sharks, although the time spent in those zones may be limited to short excursions.

### **8.9.6 Population impacts of deoxygenation and fishing**

A major concern is how ocean warming, deoxygenation and fisheries exploitation may interact to impact elasmobranch populations. The available evidence indicates that elasmobranchs are well equipped

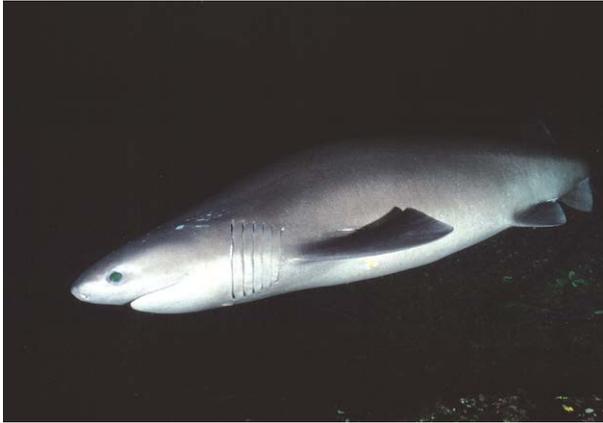


Figure 8.9.9 Bluntnose sixgill shark *Hexanchus griseus*. © Kelvin Aitken / WWPics / Alamy stock photo.

physiologically to detect hypoxia and, being mobile species, will generally be able to avoid them and move to normoxic waters. If, however, 'escape' to normoxic waters is less feasible (i.e. it is too far away for instance) or is not desired (e.g. greater foraging opportunities occur in a hypoxic zone), then elasmobranchs can exhibit behavioural and physiological responses to hypoxia. Where large-scale hypoxic zones occur and persist in shallow water systems, the habitat space of

smaller-bodied species such as benthic sharks and skates (Figure 8.9.5A, B) may be overlapped significantly by hypoxic waters that may result in movements and distribution shifts for affected species. This is largely because elasmobranchs are only weak oxyregulators that show oxyconformity responses with increasing levels of hypoxia and at the higher temperatures that are predicted in the future, with few species being tolerant to progressive or prolonged severe hypoxia. For shelf fisheries it seems likely, therefore, that expanding deoxygenation coupled with rising sea temperatures may result in periodic shifts in elasmobranch distributions which, if shifted to areas with higher fishing intensity, may result in exposure of populations to greater risks of capture.

The available studies indicate that pelagic sharks generally spend much of the time above stress thresholds of hypoxia, but behavioural responses to hypoxia and directly measured and modelled DO data along shark tracks suggest periodic entry into hypoxic zones may occur for some species. This supports the hypothesis that expanding OMZs will cause 'habitat

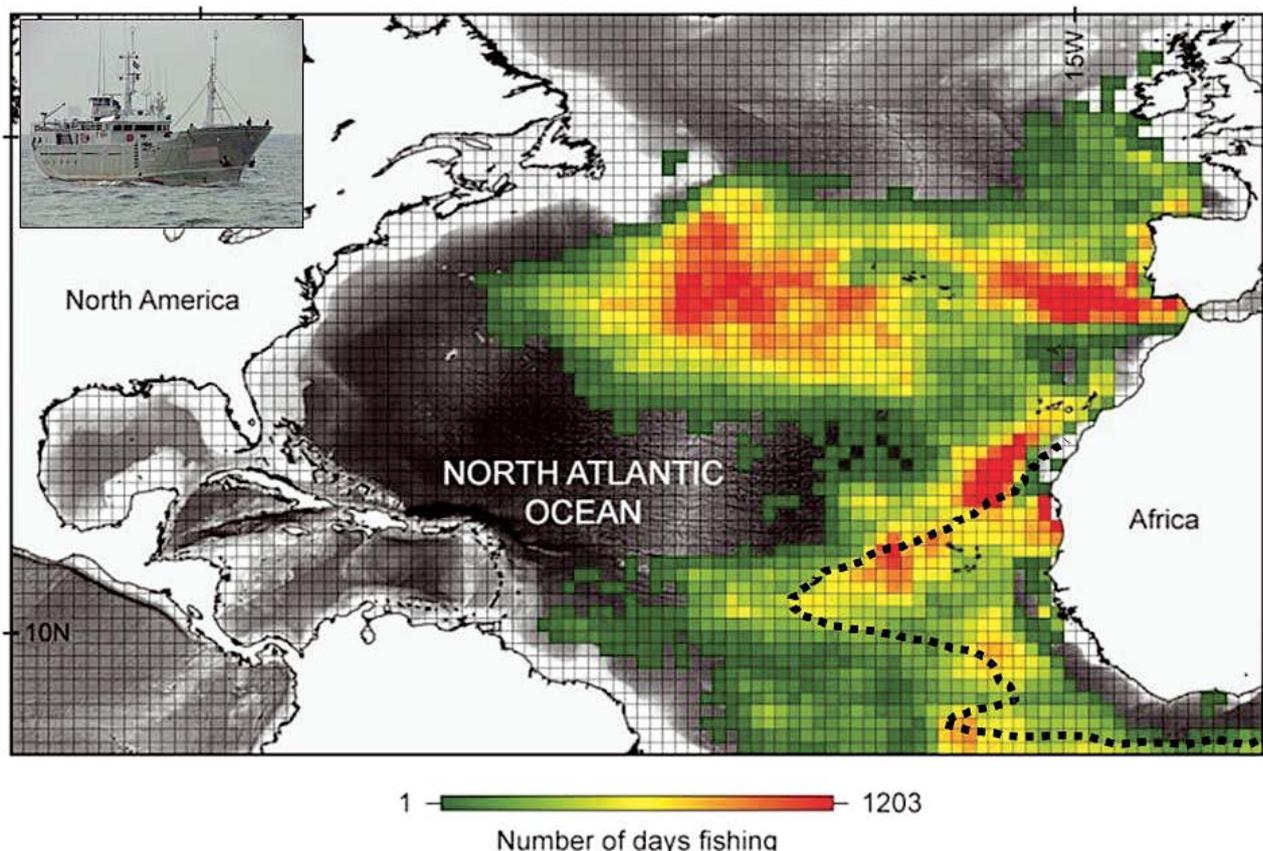


Figure 8.9.10 Exploitation hotspots of the Spanish and Portuguese surface-longline fleets shows co-occurrence of persistent, year-round hotspots covering a major part of the eastern tropical Atlantic (ETA) OMZ. Dashed black line represents the  $3.5 \text{ ml O}_2 \text{ L}^{-1}$  at 100m as an indicator of the spatial extent of the ETA OMZ. Note the fishing hotspots located along the OMZ. Fishing effort map redrawn from Queiroz et al. (2016) where warmer colours denote greater effort (days) per grid cell.

compression' of pelagic sharks by generally limiting vertical range to surface layers above  $\sim 3.5 \text{ ml O}_2 \text{ L}^{-1}$  for example (Figure 8.9.4A). Similarly, there is evidence that pelagic sharks show habitat preferences for surface waters above intermediate-depth OMZ areas (100 – 1000 m) (Queiroz et al., 2016). Shark space use hotspots in such areas (Figure 8.9.2) may characterize preferred foraging areas for sharks because hypoxia-intolerant prey may also be restricted to surface layers with reduced vertical space use (Sims, 2017). This supposes that expanding OMZs could be considered as 'habitat traps' for pelagic sharks (Figure 8.9.4B). Research on this topic is needed because habitat compression into surface layers together with habitat trapping of pelagic sharks, will potentially increase their risk of capture by surface fisheries such as pelagic longlines. This is because habitat compression and trapping will result in reduced habitat volumes and persistent higher densities of sharks in surface waters above OMZs, theoretically leading to greater spatial overlap of sharks with surface fishing gear such as longlines. A recent study identified a fishing hotspot of the Spanish and Portuguese longline fleets above the eastern tropical Atlantic OMZ that was persistent for most of the year (Queiroz et al., 2016) (Figure 8.9.10). The spatial co-occurrence of a pelagic shark hotspot and a fishing hotspot in surface waters above an OMZ suggests greater catches are possible compared to many adjacent normoxic areas. This argues the need for specific management of elasmobranch populations occurring in areas where OMZs and other deoxygenated habitats occur. Where these are also subjected to intense fishing exploitation indicates risks of overfishing are likely to become more marked as OMZs expand in the future and further compress pelagic elasmobranch habitats.

The degree to which hypoxic waters are entered by pelagic sharks will also likely vary species by species and will need to be considered in the context of the management and conservation of pelagic sharks (Sims et al., 2018). Understanding the responses of different shark species to OMZs for example is important because predictions about future habitable space available to an endothermic species may be inappropriate to extrapolate to ectothermic species. For instance, the cardiovascular and respiratory specializations of the warm-bodied shortfin mako shark contrasts with the blue shark, which is ectothermic and lacks some of these adaptations, suggesting their responses to low DO may be different. As a warm-bodied, fast swimming shark, the shortfin mako may be an elasmobranch

that is most likely to become habitat compressed above OMZs, where it is possible they may remain for extended periods feeding on a greater abundance of habitat compressed prey.

Many elasmobranch species are in decline as a result of overexploitation by fisheries (Baum et al., 2003; Dulvy et al., 2014; Ferretti et al., 2010; Worm et al., 2013), particularly from fleets operating in open ocean areas such as the high seas which remain largely unregulated with regards to shark catches (Campana, 2016; Queiroz et al., 2016). The effects of ocean deoxygenation on species is only likely to add to the impacts on already threatened populations. For example, the shortfin mako shark occurs broadly in areas currently undergoing ocean deoxygenation (Queiroz et al., 2016) and in areas projected to undergo significant oxygen loss over the next 50 – 100 years (Bopp et al., 2013; Levin, 2018) (Figure 8.9.2). However, in the North Atlantic where significant oxygen losses are predicted, shortfin mako is already being overfished (ICCAT, 2017a), with little or no management in place that will halt the decline and promote stock rebuilding (ICCAT, 2017b; Sims et al., 2018). Therefore, there is the potential for widespread habitat compression to occur through ocean deoxygenation that will likely exacerbate population decline by potentially increasing interactions between sharks and fishing gear (Figure 8.9.4). Moreover, the shortfin mako is unlikely to be an isolated example. Many other pelagic shark species form space use hotspots in the same ocean areas as makos (Queiroz et al., 2016) and are similarly classified as threatened according to IUCN criteria (Table 8.9.1). For instance, in the North Atlantic blue, tiger, silky (*Carcharhinus falciformis*), oceanic whitetip (*C. longimanus*) and smooth hammerhead (*Sphyrna zygaena*) sharks which are already threatened by fisheries overexploitation (Queiroz et al., 2016) overlap with existing OMZs or other areas projected to undergo oxygen loss. (Figure 8.9.2) (Table 8.9.1). This suggests that the interaction of ocean deoxygenation effects and shark fisheries will be broad across both species and regions.

A priority for both scientific research and policy will be to understand how expanding hypoxia affects the most threatened elasmobranchs, and to identify the conservation measures needed to mitigate ocean deoxygenation effects on elasmobranchs, such that future catch rates are controlled in the light of climate change rather than for exploitation to be exacerbated by ocean oxygen losses.

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