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Ocean deoxygenation: Everyone’s problem

Causes, impacts, consequences and solutions

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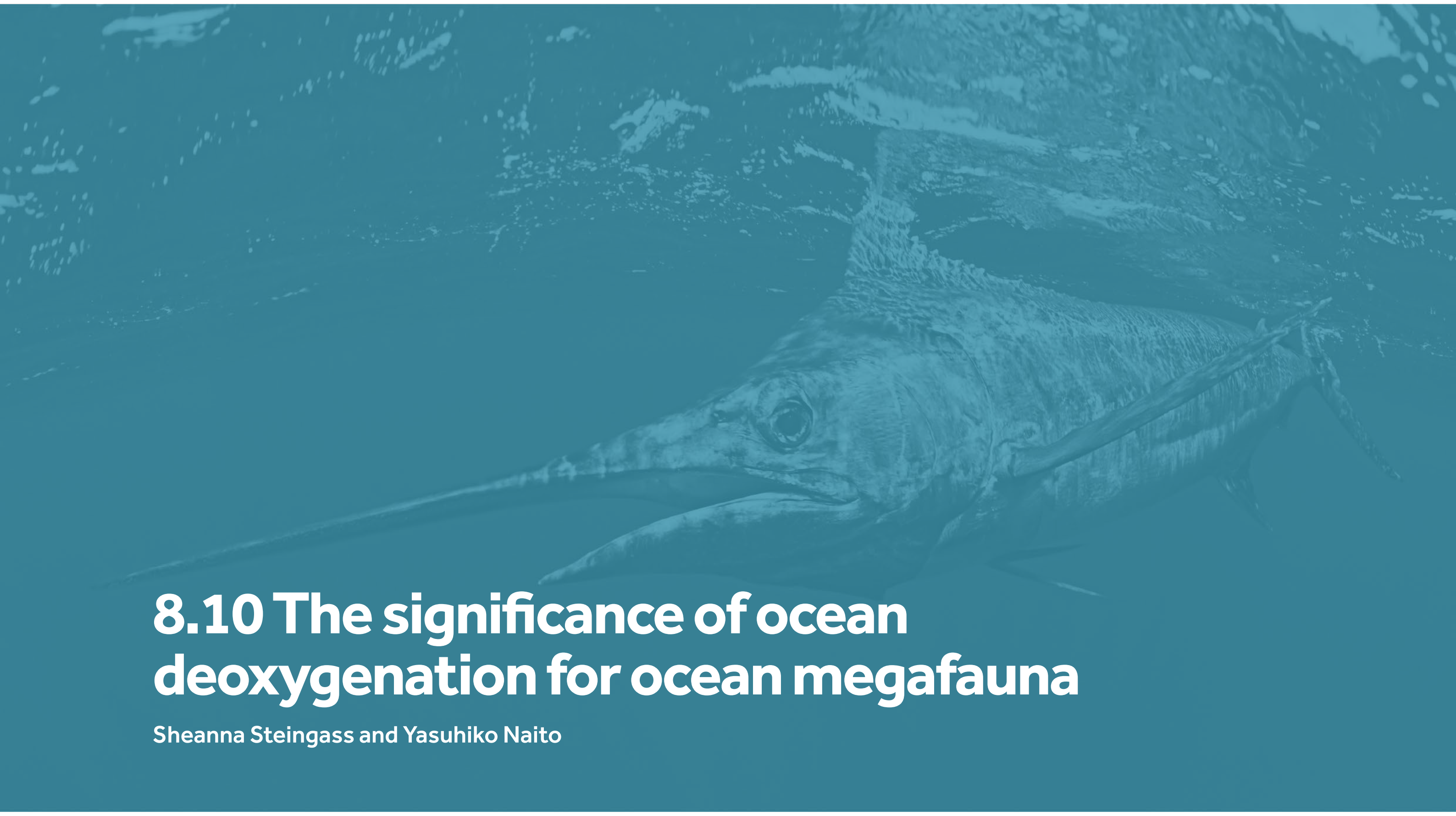
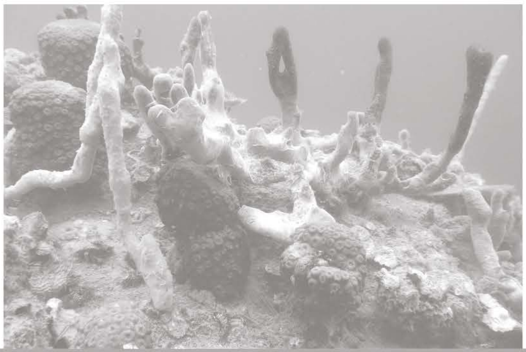


8.10 The significance of ocean deoxygenation for ocean megafauna

Sheanna Steingass and Yasuhiko Naito



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8.10 The significance of ocean deoxygenation for ocean megafauna

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Summary

- Marine mammal distribution is primarily driven by prey availability. Therefore, community-wide impacts on gilled species affect the behaviour of marine mammals. Coastal hypoxia is increasing in areas of critical marine mammal habitat. There are approximately 48 species of marine mammal in the hypoxia-affected regions of the Northern California Current System, Black Sea, Baltic Sea, and Gulf of Mexico.
- Coastal hypoxia events lead to shifts in distribution, mobility, predator avoidance, and mortality of gilled animals. Severe or prolonged hypoxia can lead to shifts in food webs, with the potential for impacting foraging success of marine mammals. Increased ocean warming, and the resultant decreases in oxygen availability suggest an imminent pattern of worsening hypoxia worldwide.
- These patterns may lead to increased pressure for marine mammal species that are already threatened or endangered. Conversely, increased rates of predation on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals. Direct links between coastal hypoxia and marine mammals may be difficult to quantify, but abundant nearshore marine mammals are excellent potential study species to begin understanding the various implications.
- Ocean deoxygenation drives offshore oxygen minimum zone (OMZ) expansion and shoaling. This expansion may positively affect the foraging efficiency of northern elephant seals, due to (1) their increased ability to feed on inactive prey, (2) decrease of diving costs in terms of both time and energy expenditure, and subsequent increased prey search time in the bottom phase of foraging dives, and (3) elevated prey density related to the compression of vertical prey distribution. Increased dependency on the prey in the OMZ (about 40% of total their prey) may lead to species composition changes within the mesopelagic community. Increased foraging efficiency by elephant seals may lead to further population increases, potentially resulting in large disturbance and shifts in the functioning of the mesopelagic ecosystem through top-down and trophic cascade effects.
- Sperm and beaked whales, typical deep divers in the mesopelagic zone, foraging on squids which inhabit the upper mesopelagic zone and often rest in the OMZ. Although foraging and vertical migration of squids remain unclearly defined, it is suggested that future shoaling of the OMZ will cause the vertical compression of this ‘resting zone’, consequently giving a foraging advantage to sperm whales and beaked whales feeding on squid.
- Increased foraging efficiency in habitats where the OMZ shoaling occurs will enhance the role of deep diving mammals in nutrient cycling, via altered nutrient pumping to surface waters from the OMZ, leading to increased productivity and nutrient flux to depths. This increased flux could ultimately affect oxygen consumption as a result of microbial respiration and nitrification in the oxygen limited zone, leading to further expansion of the OMZ.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in nearshore region produce community-wide impacts on gilled species.	• Altered foraging behaviour and spatial habitat use of marine mammals. There are approximately 48 species of marine mammals in the hypoxia-affected regions of the Northern California Current System, the Black Sea, the Baltic Sea, and the Gulf of Mexico. • Shifts in distribution, mobility, predator avoidance, schooling behaviour, and mortality of gilled animals. Severe or prolonged hypoxia can lead to shifting marine community composition, and may potentially impact foraging success of marine mammals. • Increased pressure for marine mammal species, that are already threatened or endangered, to adapt to a changing regime. Conversely, increased predation success on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals.
Decreasing oxygen concentrations and shoaling in offshore regions impact resting zones of mesopelagic prey.	• Increased shoaling may positively affect the foraging efficiency of marine mammals due to (1) their increased ability to successfully feed on inactive or incapacitated prey, (2) decreased diving costs (shallower dives) and increased allotment of search time in the bottom phase of foraging dives, and (3) elevated prey densities related to the vertical and horizontal compression of prey fields. • Increased dependency on the prey in the OMZ (northern elephant seals: about 40%) may lead to species composition and functional changes within the mesopelagic community. • Increased foraging efficiency may lead to population increases (i.e. northern elephant seal), potentially resulting in large functional shifts within the mesopelagic ecosystem. • Future shoaling of the OMZ may provide foraging advantages to sperm whales and beaked whales feeding on squid within these zones. • Increased foraging efficiency will enhance the role of deep-diving mammals in the nutrient cycling of the OMZ via nutrient pumping, leading to increased productivity and nutrient influx to depths. This increased flux could ultimately increase oxygen consumption via microbial respiration and nitrification in the oxygen limited zone, leading to further expansion of the OMZ.

8.10.1 Introduction

Loss of oxygen in the water column may not physiologically affect air-breathing marine mammals, but these animals respond to changes in prey availability as driven by oceanographic factors, including ocean deoxygenation, which makes the threat of increased global deoxygenation to marine mammals as yet unclear. The extent of ocean deoxygenation varies temporally and spatially according to the variability of the environment. Deoxygenation in nearshore areas is very complex due to the influence of land-based inputs and human activities. Severe deoxygenation in the environment has the capacity to affect marine mammals due to changes in prey abundance caused by hypoxic conditions (Chan et al., 2008; Diaz & Rosenberg, 2008; Steingass & Horning, 2017). Offshore deoxygenation occurs with vertical shoaling of the oxygen minimum zone (OMZ) at a decadal scale as a consequence of global warming (Bograd et al., 2008; Emerson et al., 2004; Ito et al., 2016; Keeling et al., 2010; Stramma et al., 2010, 2012), and this may gradually affect the foraging behaviour of marine mammals.

Although it is difficult to provide a detailed explanation of the relationships between ocean deoxygenation and marine mammals, it is possible to provide (1) the general status of nearshore marine mammals in relation to deoxygenation, and (2) provide a scenario of how pelagic deep diving marine mammals could react to ocean deoxygenation adopting the elephant seal, (*Mirounga angustirostris*) (Figure 8.10.1A) and sperm whales, (*Physeter macrocephalus)* (Figure 8.10.1B) as models of offshore marine mammals.

8.10.2 Nearshore deoxygenation

In recent years, coastal hypoxia has increased in spatial extent, prevalence, and duration on a global scale (Diaz & Rosenberg, 2008). Nearshore coastal ecosystems represent a large percentage of fisheries productivity (Chan et al., 2008). However, ecosystem-scale consequences of coastal hypoxia are just beginning to be examined. Little is known regarding the impacts of deoxygenation events on marine predators, particularly mammals. While not directly reliant on the oxygen in the water column, marine mammals are susceptible to alterations in distribution, availability, behaviour, and mortality of their gilled prey. These effects have been initially examined through conceptual models simulating marine mammal foraging during hypoxia, (Steingass & Horning, 2017), ecosystem monitoring (Craig et al., 2001), and modelling mammal behaviour during related oceanographic studies (Hazen et al., 2013). However, these effects have not been well-studied in the wild.

There are an estimated 48 species of marine mammal (Table 8.10.1) in the hypoxia-affected regions of the Northern California Current System, Black Sea, Baltic Sea, and Gulf of Mexico that may be vulnerable to impacts from ocean deoxygenation.

8.10.2.1 Trends and impacts - nearshore

Marine mammal distribution is primarily driven by prey availability. Therefore, community-wide impacts on gilled species affect the behaviour of marine mammals. Coastal hypoxia is increasing in areas of critical marine mammal habitat (Chan et al., 2008; Conley et al., 2011; Rabalais et al., 2009; Zaitsev, 1992). The severity of these events varies seasonally, but events have recently reached anoxia (<0.5 ml O_2 L^{-1}) or near-complete loss of oxygen, to the point of being unable to sustain gilled animals. In such cases, mass mortality of prey could reduce the ability of mammals to find food.

Coastal hypoxia events lead to shifts in distribution, mobility, predator avoidance, and increased mortality of gilled animals. Severe or prolonged hypoxia can lead to shifts in food web function (Rabalais et al., 2009), with the potential for impacting foraging success of marine mammals. These effects are predicted to increase in the future (Checkley Jr. & Barth, 2009; Gilbert et al., 2010; Grantham et al., 2004; Pierce et al., 2012; Rabalais et al., 2009; Steingass & Horning, 2017).

Table 8.10.1 Marine mammal species (n = 48) inhabiting areas impacted by major hypoxic zones. (Barlow et al., 2010; Becker et al., 2012; Carretta et al., 2017; Ciesielski et al., 2004; Das et al., 2003; Klinowska, 1991; Koschinski, 2001; Natoli et al., 2008; Van de Vijver et al., 2007; Verfuß et al., 2007; Viaud-Martinez et al., 2008; Wells & Scott, 1999; Würsig, 2017) GoM = Gulf of Mexico; CCS = California Current System; BLT = Baltic Sea; BLK = Black Sea

Scientific Name	Common Name	Classification	Region
Balaenoptera acutorostrata	Minke whale	Cetacea	CCS GoM
Balaenoptera borealis	Sei whale	Cetacea	CCS GoM
Balaenoptera edeni	Bryde's whale	Cetacea	CCS GoM
Balaenoptera musculus	Blue whale	Cetacea	CCS GoM
Balaenoptera physalus	Fin whale	Cetacea	CCS GoM
Berardus bairdii	Baird's beaked whale	Cetacea	CCS
Delphinus capensis	Long-beaked common dolphin	Cetacea	CCS GoM
Delphinus delphis	Short-beaked common dolphin	Cetacea	BLK CCS GoM
Eschrictius robustus	Gray whale	Cetacea	CCS
Eubalaena glacialis	Northern Atlantic right whale	Cetacea	GoM
Feresa attenuata	Pygmy killer whale	Cetacea	GoM
Globicephala macrorhynchus (not confirmed)	Short-finned pilot whale	Cetacea	CCS GoM
Globicephala melas	Long-finned pilot whale	Cetacea	GoM

SECTION 8.10

Grampus griseus	Risso's dolphin	Cetacea	CCS GoM
Kogia breviceps	Pygmy beaked whale	Cetacea	CCS GoM
Kogia sima	Dwarf sperm whale	Cetacea	CCS GoM
Lagenodelphis hosei	Fraser's dolphin	Cetacea	GoM
Lagenorhychus obliquidens	Pacific white-sided dolphin	Cetacea	CCS
Lissodelphis borealis	Northern right whale dolphin	Cetacea	CCS
Megaptera novaeangliae	Humpback whale	Cetacea	CCS GoM
Mesoplodon	Mesoplodont beaked whales	Cetacea	CCS
Mesoplodon bidens	Sowerby's beaked whale	Cetacea	GoM
Mesoplodon densirostris	Blainville's beaked whale	Cetacea	GoM
Mesoplodon europaeus	Gervai's beaked whale	Cetacea	GoM
Orcinus orca	Killer whale	Cetacea	CCS GoM
Peponocephala electra	Melon-headed whale	Cetacea	GoM
Phocoena phocoena *Phocoena phocoena relicta* *Phocoena phocoena vomerina*	Harbour porpoise	Cetacea	BLT BLK CCS
Phocoenoides dalli	Dall's porpoise	Cetacea	CCS
Physeter macrocephalus	Sperm whale	Cetacea	CCS GoM
Pseudorca crassidens	False killer whale	Cetacea	GoM
Stenella attenuata	Pantropical spotted dolphin	Cetacea	GoM
Stenella clymene	Clymene dolphin	Cetacea	GoM
Stenella coeruleoalba	Striped dolphin	Cetacea	CCS GoM
Stenella frontalis	Atlantic spotted dolphin	Cetacea	GoM
Stenella longirostris	Spinner dolphin	Cetacea	GoM
Steno bredanensis	Rough-toothed dolphin	Cetacea	GoM
Tursiops truncatus	Common bottlenose dolphin	Cetacea	BLK CCS GoM
Ziphius cavirostris	Cuvier's beaked whale	Cetacea	CCS GoM
Arctocephalus townsendi	Guadelupe fur seal	Pinnipedia	CCS
Callorhinus ursinus	Northern fur seal	Pinnipedia	CCS
Eumatopias jubatus	Steller sea lion	Pinnipedia	CCS
Halichoerus grypus	Grey seal	Pinnipedia	BLT
Mirounga angustirostris	Northern elephant seal	Pinnipedia	CCS
Phoca hispida	Ringed seal	Pinnipedia	BLT
Phoca vitulina	Harbour seal	Pinnipedia	BLT CCS
Zalophus californianus	California sea lion	Pinnipedia	CCS
Enhydra lutris	Sea otter	Mustelidae	CCS
Trichecus manatus	West Indian manatee	Sirenia	GoM

Figure 8.10.1 (A) Elephant seal (*Mirounga angustirostris*). © MZPHOTO.CZ / Shutterstock.com; (B) Sperm whale (*Physeter macrocephalus*). © wildest animal /Shutterstock.com.

8.10.2.2 Ecosystem consequences – nearshore

A number of fish species consumed by marine mammals, and affected by hypoxia, are also important fisheries species. Domenici et al. (2000, 2002) showed that swim speeds, schooling behaviour, and predator avoidance of Atlantic herring (*Clupea harengus*) (Figure 8.10.2) are all affected by hypoxia. During the most severe oxygen depletion, swim speed decreased until schooling was completely disrupted, leading to decreased predator avoidance capabilities. In lesser sandeel (*Ammodytes tobianus*), moderate hypoxia increased burrowing. As hypoxia continued to increase, the number of fish in the water column doubled, and diel burrowing cycles were disrupted by severe hypoxia (Behrens & Steffensen, 2007; Behrens et al., 2010). All of these behavioural modifications point to increased susceptibility to predation.

Greater understanding of the effects of coastal hypoxia on marine mammals can be obtained through rigorous monitoring of diet, behaviour, spatial distribution and abundance. Direct links between coastal hypoxia and marine mammals remain difficult to quantify, but abundant nearshore marine mammals are likely excellent study species to begin unravelling this issue.

8.10.2.3 Implications of continuing ocean deoxygenation

Increased ocean warming, and the resultant decreases in oxygen retention ability of sea water suggest an imminent pattern of worsening hypoxia worldwide. This pattern may lead to increased pressure on marine mammals that are already threatened or endangered. Conversely, increased rates of predation on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals. While initially beneficial for opportunistic or generalist species of mammals, hypoxia-driven ecosystem shifts or faunal collapse may result in irreversible trends limiting marine mammal distribution and populations growth and resilience.

8.10.3 Offshore deoxygenation

8.10.3.1 Deoxygenation and foraging behaviour of offshore marine mammals

The capacity of sea water to retain dissolved oxygen universally decreases with increasing temperature (Keeling et al., 2010). Ocean warming simultaneously reduces the water density and stratifies the upper water column; this leads to decreased oxygen transport to subsurface waters and subsequent reduction in the flux of oxygen into the interior ocean (Keeling et al., 2010). These mechanisms suggest offshore deoxygenation may not directly affect offshore marine mammals foraging in shallow waters, such as baleen whales. However, decadal climatic changes have caused deoxygenation events which present as shoaling of the upper boundary of the OMZ or OMZ expansion, in global marine systems, including the North Pacific, Atlantic, eastern tropical Pacific, and Arabian Sea regions (Andreev & Watanabe, 2002; Bograd et al., 2008; Emerson et al., 2004; Gilly et al., 2013; Ito et al., 2016; Keeling et al., 2010; Stramma et al., 2010, 2012). Although the definition of OMZ varies with the physiological tolerance of organisms and ecosystems to hypoxia (e.g. <20 µmol O_2 kg^{-1} or 0.5 ml O_2 L^{-1} in the Pacific region), OMZs have generally expanded globally in the last 50 years (Gilly et al., 2013). Furthermore oxygen levels continue to decline, for example Stramma et al. (2008) describe a

Figure 8.10.2 Large adult male killer whale stalking herring in shallow water off Norway. © Nature Picture Library / Alamy stock photo.

rate of decline ranging from 0.09 - 0.34 µmol O_2 kg^{-1} $year^{-1}$ within the 300 - 700 m depth range in the tropical ocean regions of the eastern Atlantic and the equatorial Pacific.

While there are limited qualitative and quantitative data regarding how marine mammals react to changes in prey conditions in relation to OMZ expansion, there have been consistent changes in mesopelagic foraging behaviour of the northern elephant seal in the eastern North Pacific where the OMZ has expanded (shoaled) (Andreev & Watanabe, 2002), showing evidence that OMZ expansion enhances foraging efficiency of an air-breathing predator. There is also evidence of changes in the diving behaviour of squid-feeding beaked and sperm whales, species that may act as model species to provide simple predictions of how these whales may react to ocean deoxygenation through squid feeding.

8.10.4 Ecological and biogeochemical consequences for northern elephant seals from ocean deoxygenation

Northern elephant seals migrate twice a year, undertaking post-breeding and post-moulting migrations to the north-eastern Pacific (from 38° to 60° N and from the coast to 172.5° E; Le Boeuf et al., 2000; Robinson et al., 2012), during which they dive to depths of 400 - 600 m (maximum depth:1735 m; Robinson et al., 2010). Elephant seals dive continuously both day and night, diving to shallower depths at night and deeper depths during the daytime, showing an apparently diel pattern (Figure 8.10.3).

Daytime foraging in the OMZ and OLZ (oxygen limited zone; 20 - 60 µmol; Gilly et al., 2006) accounts for about 40% of their total feeding, as measured by jaw motion suggesting the importance of daytime foraging despite increased dive depths and thereby reduced foraging efficiency. The high dependency of elephant seals on prey found within the OMZ and OLZ during the day may relate to increased efficiency of capturing prey residing in the OMZ and OLZ at >600 m depth in order to avoid predation pressure in the oxygen rich zone. Gilled animals within the OMZ demonstrate lower metabolic rates making their capture easier (Childress & Seibel, 1998; Naito et al., 2013; Seibel, 2011). Although the mechanistic details are not fully understood, marine hypoxia allows seals to consume large amounts of prey in the OMZ and OLZ due to increased foraging efficiency (roughly estimated total and daytime amounts (i.e. from OMZ): 210,000 t $year^{-1}$ and 84,000 t $year^{-1}$

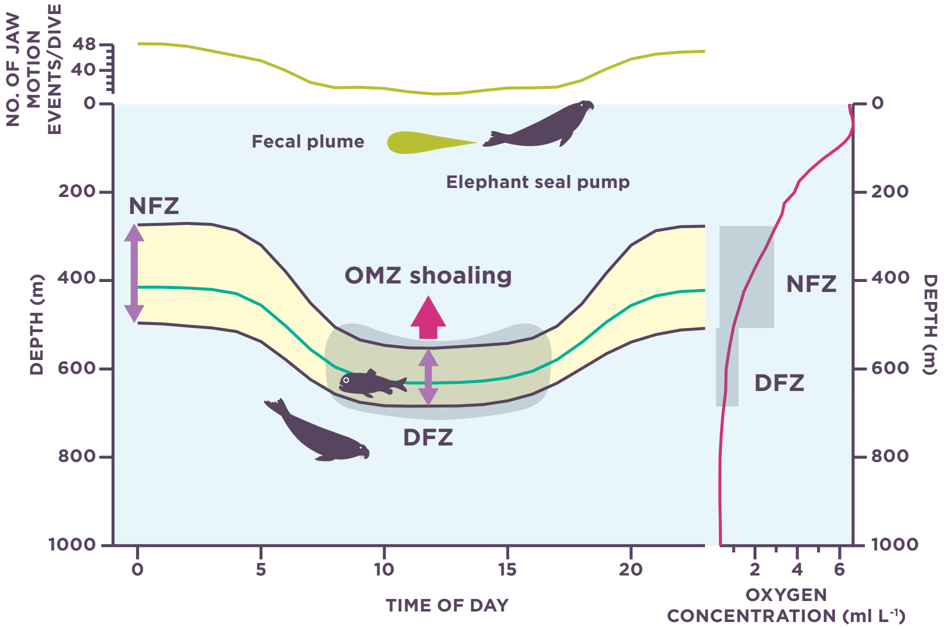

Figure 8.10.3 Typical diel pattern of diving and foraging behaviour based on jaw motion activity of northern elephant seal in the north-eastern Pacific, and typical vertical distribution of oxygen in the region. NFZ and DFZ denote the Night-time Foraging Zone and the Daytime Foraging Zone respectively. These zones of foraging were determined by the depth ranges between average minimum and maximum depth of jaw motion events in every hour during post breeding migration of a seal (Total no. of foraging dives: 6408, Seal ID: PB-1015). Boxes in the vertical oxygen distribution profile indicates depth and oxygen content ranges of NFZ and DFZ.

respectively based on the daily consumption rate: 3% of body mass (Naito et al., 2013), average body mass: 200 kg (assumed value), estimated number of foraging days: 200 (Le Boeuf et al., 2000), approximate population size: 175,000 (Weber et al., 2000)) which underlies the important role of seals in structuring the mesopelagic ecosystem. Further shoaling of the OMZ and OLZ in the future may enhance seal foraging efficiency due to (1) increase of inactive prey, (2) decreased diving cost enabling an increase of prey search time during the dive bottom phase, and (3) increased prey density due to vertically-compressed oxygenated habitat (Gilly et al., 2013). These may further increase the dependency of feeding in the expanded OMZ during the day as compared to night-time foraging, which as a result may decrease. A large modification of the day/night dependency ratio (i.e. from the present approximate day to night ratio of 4:6) may trigger an ecological disturbance, ultimately changing the species composition of the deep-sea community as prey composition may differ between day and night (Naito et al., 2017). Enhanced foraging efficiency could elevate the population fitness and breeding rate of elephant seals, leading to a potential long-term increase in population and thereby top-down modification of their terrestrial breeding habitats. However, any future increase of this population in relation to ocean deoxygenation is uncertain, as carrying capacity at breeding sites may also limit population trends. While long term population increases of elephant seals has been reported (6% increase year^{-1}; Weber et al., 2000), how this increase relates to ocean deoxygenation remains to be confirmed.

The unexpectedly high dependency of elephant seals on prey in the OMZ may have an unprecedented effect on nutrient cycling in relation to OMZ expansion. While an important function of nutrient pumping to the surface water by baleen whales has been reported (Lavery et al., 2010; Roman & McCarthy, 2010), no biological pump information from the OMZ has been reported. Elephant seals, as deep-water foragers, may serve a similar

Figure 8.10.4 Dall's porpoise *Phocoenoides dalli* in south-east Alaska. © Minden Pictures / Alamy stock photo.

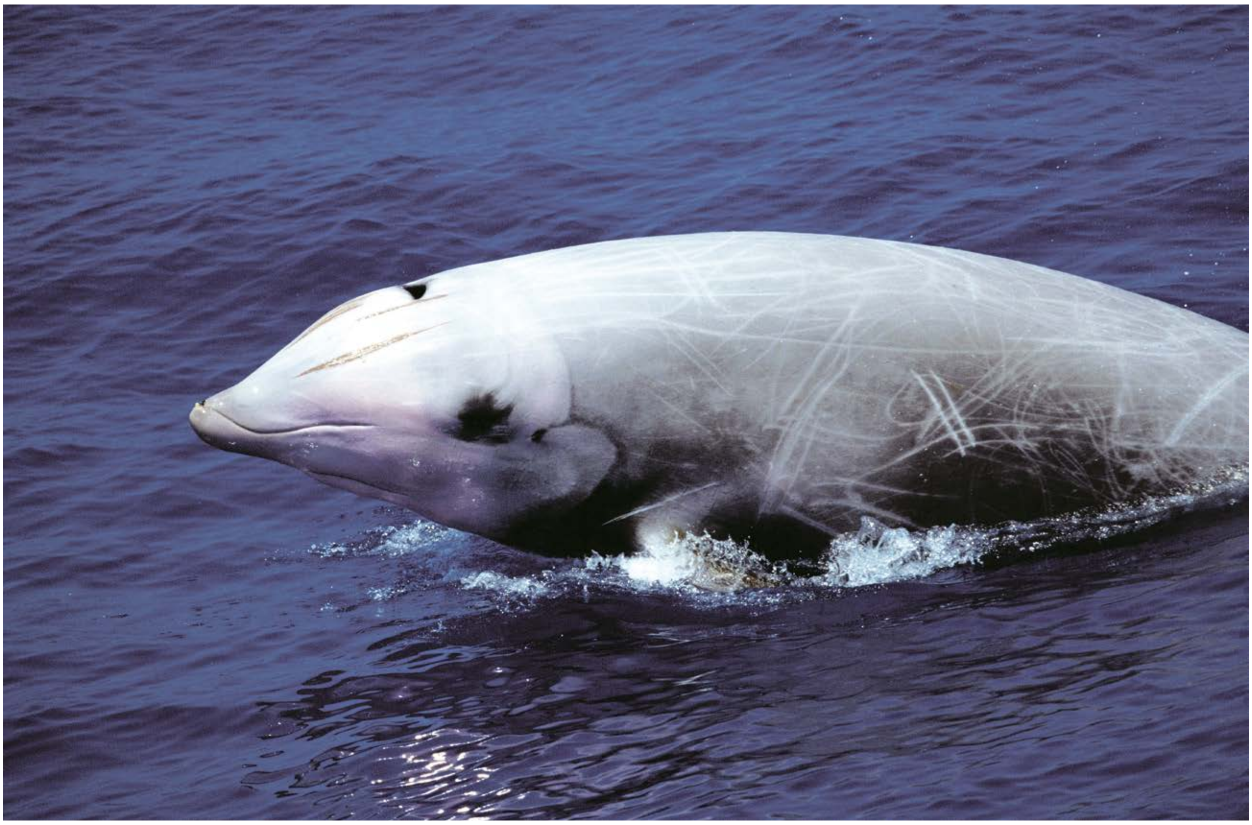

Figure 8.10.5 Cuvier's beaked whale (*Ziphius cavirostris*). © Nature Picture Library / Alamy stock photo.

function as nutrient cyclers. Foraging within the OMZ is particularly important in biogeochemical cycling, since prey extraction from the OMZ and subsequent nutrient delivery to the surface in the form of a faecal plume and urine is relatively large allowing seals to play a driving role in this cycle. The pump effect of feeding by elephant seals and other marine mammals enhances the productivity of surface waters (Lavery et al., 2010). Although the quantitative details are not known, it is predicted that increased future productivity will lead to an increase in the export of organic matter to subsurface waters, as a result of deoxygenation in subsurface waters (Gilly et al., 2013) driven by an increase in oxygen consumption by microbial respiration and nitrification, combined with the stratification and surface water warming effects.

8.10.5 Deoxygenation and foraging behaviour of toothed whales

Toothed whales (odontocetes) are dependent upon the mesopelagic zone as their major foraging zone (Belta, 2015); pelagic porpoises and dolphins (small Delphinidae) (Figure 8.10.4) tend to forage in the upper part of the mesopelagic zone, while whales of the Physeteridae, Ziphiidae and large Delphinidae (Figure 8.10.5) dive very deep to forage in the lower part of the mesopelagic zone (Aoki et al., 2007; Belta, 2015; Clarke, 1996; Miller et al., 2004; Ohizumi et al., 2003; Tyack et al., 2006). Among toothed whales, diving and foraging behaviour of sperm whales and some beaked whales have been investigated extensively, and the results indicate that they hunt and consume squids using an echolocation system in the lower part of the mesopelagic zone, often foraging at deeper depths than elephant seals (Aoki et al., 2007; Blanco & Raga, 2000; Clarke ,1996; Kawakami ,1980; Miller et al., 2004; Ohizumi et al., 2003; Santos et al., 2000; Tyack et al., 2006). This suggests that a key to understanding sperm whale response to ocean deoxygenation is through quantitative understanding of squid behaviour in relation to the OMZ. Although squid forage in the euphotic zone, they are well-adapted to the low oxygen environment and utilize the OMZ to forage and rest (Gilly et al., 2006). These resting squid may give whales a large advantage in foraging. Davis et al. (2006) monitored diving behaviour of sperm whales and the jumbo squid, *Dosidicus gigas*, which rests in the upper boundary of the OMZ (>300 m depth) after feeding on myctophid fish in warmer shallow waters in the Gulf of California. Consistent dive depths of sperm whales foraging for jumbo squid suggested that the OMZ expansion compresses the distributional range of squids allowing whales to forage upon them more efficiently. Compared to sperm whales within the shallow OMZ in the Gulf of California, other populations of sperm whales often dive to deeper depths (400-1000 m) in zones with no apparent OMZ, including the North Atlantic, Gulf of Mexico, Ligurian Sea, Kumano coast of Japan, and Ogasawara Islands (Aoki et al., 2017; Watwood, 2006). These differences in foraging depth suggest that sperm whales and beaked whales may in fact experience a large advantage to foraging within areas of OMZ shoaling, due to greater efficiency in feeding upon squid. As with elephant seals, increased efficiency of foraging by toothed whales could lead to significant disturbance and disruption to the marine ecosystem through top-down effects leading to a trophic cascade (Estes & Palmisano, 1974) of ecosystem function in the future.

Toothed whales may have a similar deep biological pump function which affects biogeochemical cycling as in the case of the northern elephant seal, but the details of this pump function are as yet not clearly understood. Further investigations detailing the relationship between marine mammals and mesopelagic deoxygenation are necessary to enable a clear understanding of how ocean warming is affecting the deep sea ecosystem.

8.10.6 References

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