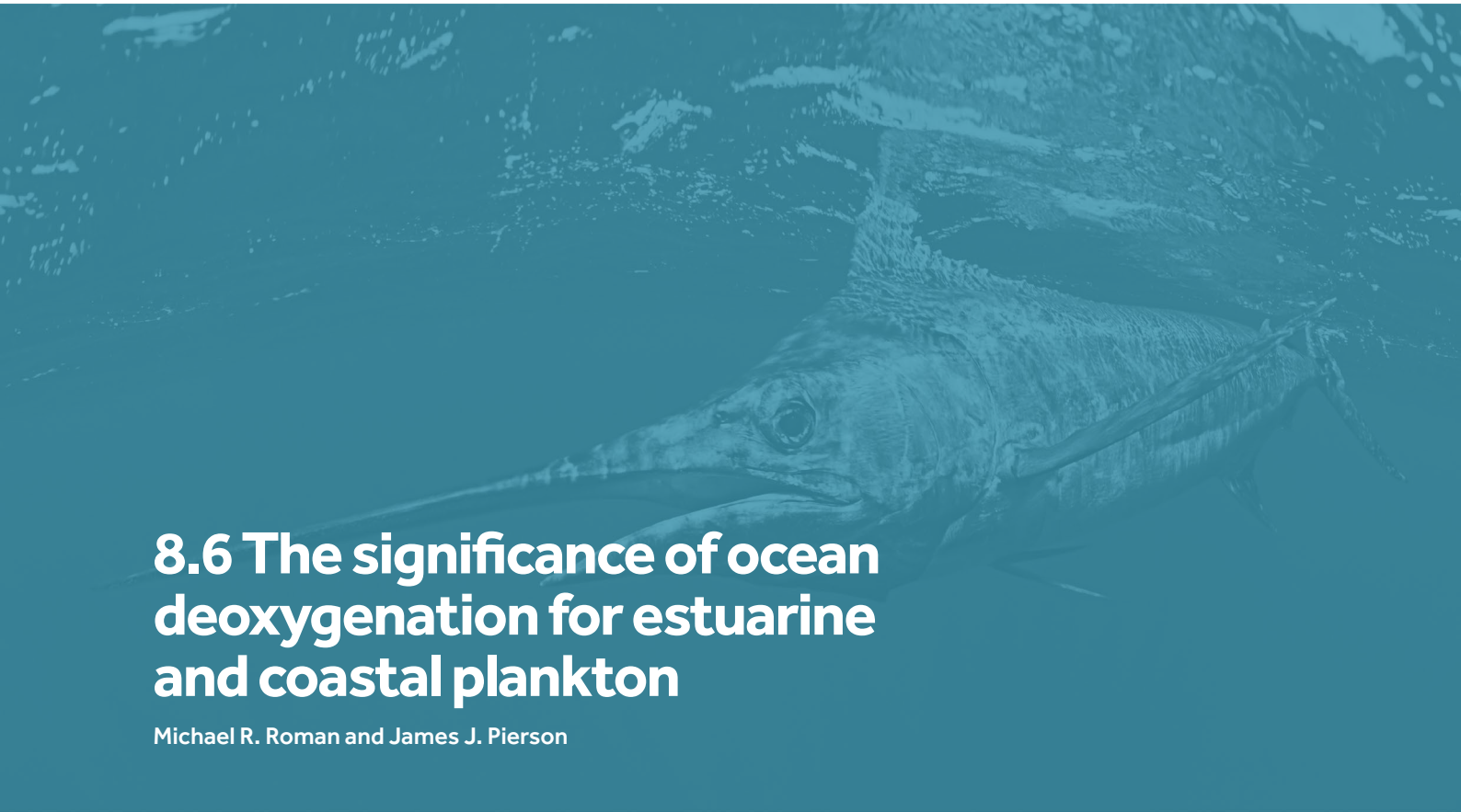# IUCN

Ocean deoxygenation: Everyone's problem
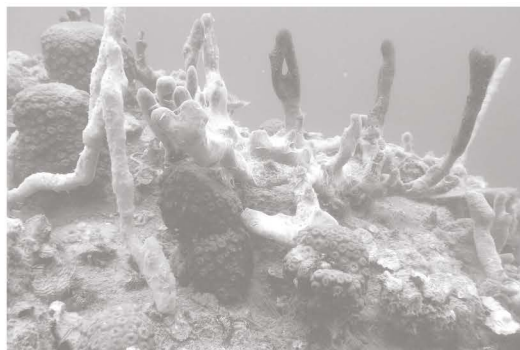
Causes, impacts, consequences and solutions

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8.6 The significance of ocean deoxygenation for estuarine and coastal plankton

Michael R. Roman and James J. Pierson

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8.6 The significance of ocean deoxygenation for estuarine and coastal plankton

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Summary

- Seasonal deoxygenation of estuarine and coastal ecosystems leads to a variety of impacts on zooplankton including: lower overall abundance; altered community structure with smaller, egg carrying taxa and gelatinous zooplankton increasing with decreasing dissolved oxygen; shallower vertical distributions and reduced vertical migration extent; sub-lethal impacts including reduced size at adulthood; and reduced growth rates.
- Pelagic predator-prey interactions can be altered if zooplankton prey utilize hypoxic waters as a refuge from fish predation. Conversely, avoidance of low oxygen bottom waters can result in zooplankton aggregations at the interface of hypoxic waters which can be sought out by zooplankton predators.
- In coastal ecosystems with shears and differential flow between surface and deep layers, avoidance of low oxygen bottom waters can influence spatial dynamics of zooplankton populations by altering emigration and immigration patterns, and residence times.
- Ecosystem models of estuarine and coastal seas should incorporate seasonal hypoxic bottom waters to better understand the impacts of current and future deoxygenation on pelagic food webs.

Low oxygen effects on estuarine and coastal zooplankton	Potential consequences
Low oxygen bottom waters may result in lower overall zooplankton abundances.	• Lower grazing pressure on phytoplankton. • May result in limiting food levels for zooplankton-feeding fish.
Low oxygen waters may result in zooplankton species changes with a shift to smaller sized individuals.	• Different zooplankton species may be less nutritious to their fish predators. • Smaller zooplankton prey may require that more zooplankton be consumed by fish to meet their nutritional needs.
Zooplankton may use mild hypoxic bottom water as a refuge from predation.	• Zooplankton-feeding fish may avoid the low oxygen bottom waters and thus have reduced consumption of zooplankton. • Zooplankton-feeding jellyfish can tolerate low oxygen waters more than fish and thus may replace fish as the dominant consumers of zooplankton.
Zooplankton may avoid severe hypoxic bottom waters and aggregate at the depth interface of rapidly decreasing oxygen.	• These zooplankton aggregations in surface waters may result in enhanced feeding zones for zooplankton predators.
The differences between environmental supply of oxygen and the organism's demand for oxygen drive the response of plankton to deoxygenation.	• The definition of hypoxia as a concentration does not account for the decreasing solubility of oxygen and increasing metabolic rate of organisms with increasing temperature. • At high temperatures organisms may be in stressful or lethal conditions even when the concentration of dissolved oxygen is above levels defined as hypoxic (< 2 mg L^{-1}). • The actual effect of hypoxia is very likely species and temperature specific, related to each species oxygen demand.

8.6.1 Definition of species group

Hypoxia exerts widespread and expanding stress on coastal ecosystems worldwide, triggered in large part by eutrophication. Hypoxia is often defined as dissolved oxygen concentrations < 2 mg O$_2$ L^{-1} (at 18 °C in sea water = 1.5 ml L^{-1} = 62.6 µM L^{-1} = 5.6 kPa oxygen partial pressure), although more biologically relevant definitions are required to define its impacts (Breitburg et al., 2009; Elliott et al., 2013; Vaquer-Sunyer & Duarte, 2008; Verberk et al., 2011). Physiologists usually express dissolved oxygen (DO) in terms of partial pressure because oxygen availability to aquatic organisms is dependent on the rate of diffusion across integuments or gills and is controlled by the partial pressure of O$_2$ (mm Hg or kPa). Oceanographers usually express DO in terms of concentration (mg L^{-1}, ml L^{-1}, or µM L^{-1}). Temperature and salinity directly influence the oxygen solubility in sea water and thus DO concentration and oxygen partial pressure, and temperature affect the metabolic demand of aquatic ectotherms. In order to effectively assess the impacts of hypoxic stress, it is therefore necessary to consider the effects of temperature on both oxygen availability and animal metabolism.

Hypoxic water formation is driven primarily by nutrient stimulation of largely ungrazed phytoplankton blooms. These blooms sink or are eaten and processed by zooplankton, and are subsequently decomposed by microbial activity, consuming much of the available oxygen in the lower water column (Diaz & Rosenberg, 2008; Howarth et al., 1996; Malone, 1991; Nixon, 1995). The type of deoxygenation that is addressed in this section is seasonal and confined to coastal bottom waters which are separated from the surface waters and contact with the air by a density interface (Figure 8.6.1).
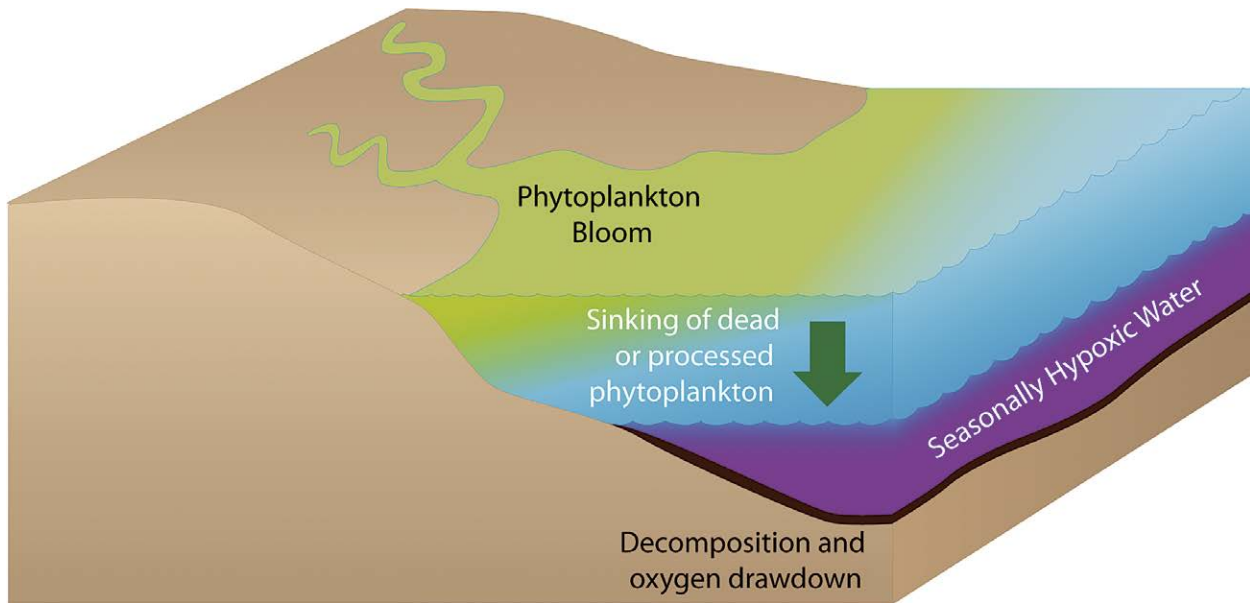
Figure 8.6.1 The formation process for coastal and estuarine deoxygenation. Graphic Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

The focus of this section is to review the effects of seasonal hypoxia on estuarine and coastal plankton. Plankton includes both the autotrophic phytoplankton and heterotrophic zooplankton. We focus on the animal zooplankton that require oxygen for their metabolic functions. These zooplankton include both the "temporary" meroplankton which are planktonic larval stages of benthic organisms (e.g. oysters, barnacles, polychaete worms, etc.) (Figure 8.6.2) and the "permanent" holoplankton, largely dominated by crustaceans (e.g. copepods, mysids, euphausids) (Figure 8.6.3) and jellyfish but including members of a wide variety of other phyla. Copepods are a diverse group of crustaceans that predominate zooplankton communities, in terms of both numerical abundance and biomass. They can be classified with respect to reproduction: those that carry their eggs until hatching and those that release their eggs (broadcast spawners). Copepod eggs are denser than sea water and thus sink to bottom waters where they can be affected by low oxygen conditions.

8.6.2 Trends and impacts

8.6.2.1 Effects of low oxygen waters on zooplankton metabolism

When considering the potential biological and ecological effects of hypoxia on coastal zooplankton, reduced rates of oxygen uptake are ultimately responsible for adverse effects such as reduced growth and increased mortality.

Oxygen solubility, partial pressure and diffusivity all can influence the rate of oxygen uptake (Verberk et al., 2011). Under low oxygen environmental conditions (relative to oxygen demand), aerobic respiration may not be fully supported by the consequent lower oxygen uptake rates, and respiration becomes oxygen limited (Childress & Seibel, 1998; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Pörtner & Knust, 2007; Seibel, 2011). As a

Figure 8.6.2 Barnacle larva © Papilio / Alamy stock photo.

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Figure 8.6.3 Mysid shrimp © Daniel L. Geiger / SNAP / Alamy stock photo.

result, zooplankton residing in hypoxic water must either implement specific adaptations to maintain the rate of oxygen uptake, make up the energy deficit through anaerobic respiration, or reduce their energy demand and oxygen requirements by decreasing metabolic rate (Childress & Seibel, 1998; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Seibel, 2011). In aquatic ectotherms, temperature controls these respiration and metabolic rates.

Specific adaptations that help maintain oxygen uptake under low DO (or increasing oxygen demand) include increased ventilation of the respiratory surfaces (e.g. gills), increased heart rate, reduced activity, and production of high affinity oxygen uptake molecules (Childress & Seibel, 1998; Herreid, 1980; Pörtner & Knust, 2007; Seibel, 2011). These types of responses are common among organisms in oceanic oxygen minimum zones, which likely have co-evolved with low oxygen concentrations for thousands of years. However, among coastal organisms, exposure to hypoxia is generally more ephemeral (seasonal) and in many cases is a relatively new stressor associated with cultural eutrophication. Since 1950, more than 500 sites in coastal waters have reported DO concentrations < 2 mg O_2 L^{-1}, with fewer than 10% of these systems known to have hypoxia prior to 1950 (Diaz & Rosenberg, 2008; Isensee et al., 2015). Consequently, estuarine and coastal zooplankton do not appear to have developed specific physiological adaptations to hypoxia in coastal systems (Childress & Seibel, 1998; Dam, 2013; McBryan et al., 2013). Instead, these organisms must either avoid hypoxia through behavioural mechanisms or reside in hypoxic water and tolerate some deleterious effects.

Two useful thresholds can be defined to evaluate effects of low environmental oxygen on zooplankton. These are the critical (P_{crit}) and lethal (P_{leth}) oxygen thresholds

(Childress & Seibel, 1998; Connett et al., 1990; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Pörtner & Knust, 2007; Seibel, 2011). Both of these thresholds reflect the balance between oxygen *supply* to the organism, a function of the rate of molecular diffusion, and oxygen *demand* by the organism, a function of respiration rate (and ultimately metabolic rate). As such, both thresholds are temperature dependent, and are expressed in terms of oxygen partial pressures. However, according to Fick's First Law of Diffusion across a membrane, oxygen uptake, and thus maximum potential aerobic respiration rate, will depend on oxygen supply as governed by the external (environmental) oxygen solubility, partial pressure, and diffusivity (Verberk et al., 2011). Thus, corresponding critical and lethal oxygen supply thresholds can be defined that account for oxygen solubility, partial pressure and diffusivity. These thresholds will depend on an organism's non-oxygen-limited (target) respiration rate, and the lowest sustainable (basal) respiration rate, respectively (Elliott et al., 2013). When maximum potential respiration rate drops below an organism's "target" respiration rate (P_{crit}), respiration rate becomes limited by oxygen supply, and sub-lethal effects of hypoxia can be expected. When the oxygen supply drops below an organism's "basal" respiration rate (P_{leth}), acute lethal effects of hypoxia can be expected. Thus, for coastal zooplankton lacking specialized adaptations to low environmental oxygen, oxygen uptake is more-or-less constant at the target level when PO_2 is above P_{crit}, then declines linearly as DO declines below the P_{crit} level (Figure 8.6.4). Because zooplankton lack gills, their oxygen uptake is a function of diffusion through their body surface. Under low oxygen conditions relative to copepod oxygen requirements, species with a higher surface/volume ratio would be favoured because of their greater oxygen diffusion potential.

Deoxygenation reduces the survival of copepods under controlled laboratory conditions (Marcus et al., 2004; Richmond et al., 2006; Roman et al., 1993; Stalder & Marcus, 1997; Vargo & Sastry, 1977). In laboratory experiments Marcus et al. (2004) and Richmond et al. (2006) showed that *Acartia* egg production and population growth rate were reduced in low-oxygen waters (0.7 and 1.5 mg O_2 L^{-1}) compared to normoxic (DO > 2 mg L^{-1}) controls. Low oxygen conditions have also been shown to reduce the ingestion rates of copepods in laboratory experiments (Elliott et al., 2013), as well as reduce their escape response (Decker et al., 2004). Copepod survival, growth rate, egg production
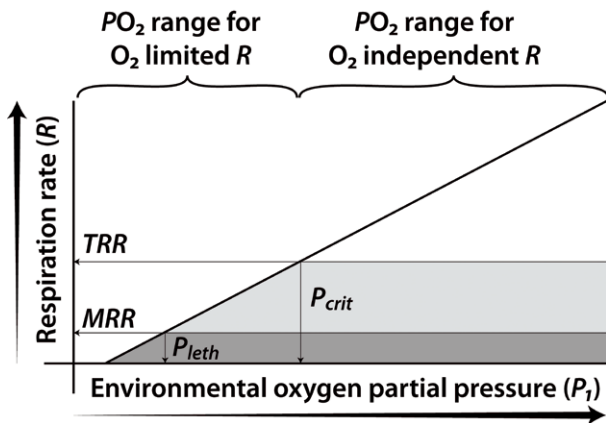
Figure 8.6.4 Relationship between an organism's respiration rate and the environmental oxygen partial pressure. Target Respiration Rate (TRR); Minimum survivable Respiration Rate (MRR), critical oxygen partial pressure (P_{crit}) and lethal oxygen partial pressure (P_{leth}) are shown. Adapted from Elliott et al. (2013).

and ingestion rate all decline with oxygen availability as predicted by the relationship given in Figure 8.6.4.

8.6.2.2 Effects of low oxygen on copepod egg hatching

Copepods in estuarine and coastal waters produce two types of eggs: diapause (resting) eggs which must complete a dormancy (refractory) period before hatching and subitaneous eggs which hatch within hours-days of being spawned, depending on temperature (Grice & Marcus, 1981). Low oxygen has been shown in laboratory experiments to severely reduce the hatching success of subitaneous copepod eggs (Invidia et al., 2004; Lutz et al., 1992; Marcus & Lutz, 1994; Marcus et al., 1994, 1997; Roman et al., 1993; Richmond et al., 2006). The eggs of dominant coastal copepods have sinking rates which range from 15 to 35 m d^{-1} (Jiang et al., 2006; Knutsen et al., 2001; Uye, 1980). Thus, if hatching times are longer than the time it takes eggs to sink to bottom waters, subitaneous (ready to hatch) copepod eggs will be subjected to low oxygen conditions (Jiang et al., 2006; Tang et al., 1998). For example, assuming an egg hatching rate of 24h and a sinking rate of 20 m d^{-1}, if the deoxygenated conditions begin 10 m below the surface and eggs are released at the surface, most would already be well within the low oxygen waters by the time they would have hatched. But if low oxygen conditions were more than 40 m below the surface, most eggs would hatch before sinking to the low oxygen waters. Low oxygen conditions can sometimes induce dormancy in these subitaneous eggs, which is reversed with increases in oxygen (Katajisto,

2004). Thus, the potential exists for subitaneous eggs to hatch if hypoxia dissipates or they are resuspended into normoxic waters. The length of time that subitaneous eggs can withstand hypoxia/anoxia and still remain viable to hatch varies with copepod species and abiotic conditions such as temperature and hydrogen sulphide levels (Broman et al., 2017; Hansen & Drillet, 2013; Katajisto, 2004).

Copepod diapause eggs have an obligatory "refractory phase" and sink to the sediment which is typically anoxic below a depth of several millimetres. Diapause eggs can withstand considerable periods of anoxia and toxic hydrogen sulphide (Marcus, 2001). In general, subitaneous eggs are less able to withstand prolonged exposure to low oxygen than diapause eggs because of their higher metabolic demand (Hansen & Drillet, 2013).

Coastal and estuarine waters which experience seasonal hypoxia in bottom waters may develop a significant "egg bank" of copepod eggs which if reaerated could hatch and make important contributions to copepod populations and their predators. A combined laboratory and modelling study by Broman et al. (2017) demonstrated that re-oxygenation of anoxic sediments activated copepod egg hatching which could make a substantial contribution to copepod populations in the Baltic, and perhaps in other similar systems (Figure 8.6.5). However, reduced hatching success of subitaneous eggs that do not have induced diapause may significantly affect copepod production during periods of hypoxia due to egg mortality (e.g. Roman et al., 1993). This was observed in the Chesapeake Bay, where copepod biomass was lower both within the region where hypoxia was present compared to outside of that region, and during the period of hypoxia compared to before and after hypoxia occurred (Roman et al., 2005).

8.6.2.3 Effects of low oxygen waters on zooplankton distributions

The general observation of reduced copepod abundances (integrated over the entire water column) in hypoxic water columns (Keister et al., 2000; Kimmel et al., 2012; Roman et al., 1993) suggests lower population growth, greater copepod mortality, predation and/or emigration in water columns with hypoxic bottom waters.
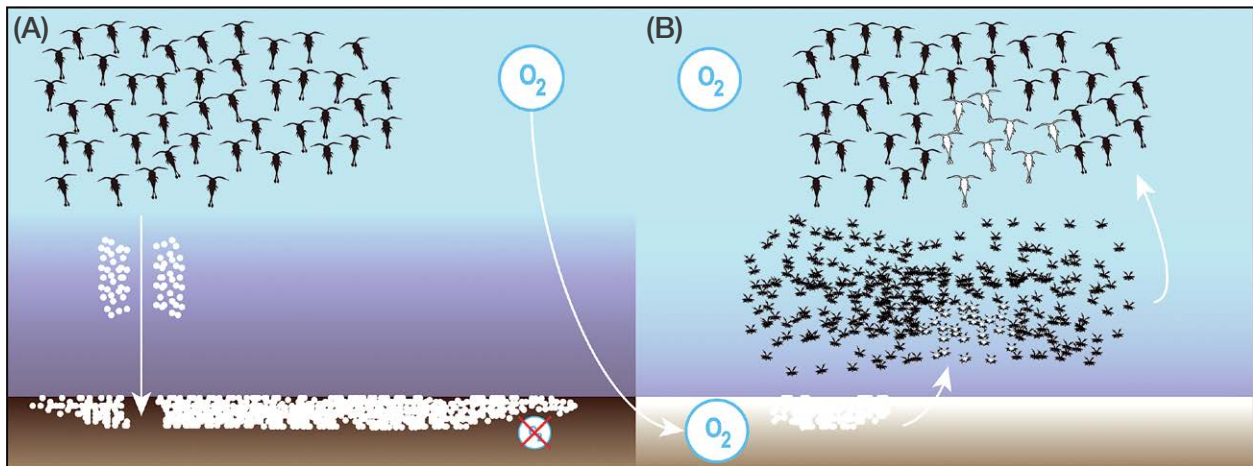
Figure 8.6.5 Showing how diapause eggs deposited by copepods in anoxic sediments can later contribute to a copepod population following re-oxygenation of sediment containing the diapause eggs. (A) sediments and bottom water are deoxygenated, and eggs are dormant. (B) the sediments are reoxygenated and eggs hatch, contributing up to 20% of the copepod population. Symbols Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Adapted from Broman et al. (2017).

Zooplankton are able to change their vertical position in the water column to avoid low oxygen bottom waters. However, the vertical compression of their distribution to the upper water column can make them more vulnerable to predation by visually feeding fish and thus alter food-web processes. In general, depth-stratified zooplankton sampling has shown that copepod abundances are higher in the surface mixed layer and within the pycnocline compared to hypoxic bottom water in coastal environments (Keister & Tuttle, 2013; Keister et al., 2000; Kimmel et al., 2009; North & Houde, 2004; Pierson et al., 2009b, 2017; Roman et al., 1993). This is not always the case (Qureshi & Rabalais, 2001; Taylor & Rand, 2003) and, even if most zooplankton are above the oxycline, significant amounts often occur in hypoxic bottom water for part of the day (Keister & Tuttle, 2013; North & Houde, 2004; Pierson et al., 2017; Roman et al., 1993; Taylor et al., 2007).

In most coastal and estuarine waters copepods exhibit diel vertical migrations, presumably to reduce predation by visual feeders by residing at depth during the day, and returning to the surface layer at night (Cahoon, 1981; Roman et al., 1988). Bottom-water hypoxia can clearly disrupt vertical migration behaviour. For example, when a wind event mixed the water column and reaerated hypoxic bottom water, copepods migrated to a deeper depth during the day (Roman et al., 1993). Generally, hypoxic bottom waters truncate zooplankton vertical migration behaviours, reducing the excursion distance (Keister & Tuttle, 2013; Pierson et al., 2009b, 2017; Roman et al., 1993, 2012). For example, zooplankton in the Gulf of Mexico avoided hypoxic bottom waters in their diel vertical migrations and the median depth

of their daytime distribution was 7 metres higher in the water column compared to daytime distributions of zooplankton in water columns with no hypoxic bottom waters (Roman et al., 2012). In Hood Canal and the Neuse River system, migration behaviour and vertical distribution of fish was more directly affected by bottom water hypoxia than zooplankton, creating a potential refuge for zooplankton (Parker-Stetter & Horne, 2009; Taylor & Rand, 2007). Thus, along with food levels (Hays et al., 2001; Huntley & Brooks, 1982; Pearre, 2000; Roman et al., 1988) and predators (Bollens & Frost, 1989; Frost & Bollens, 1992; Ohman, 1988), the presence of hypoxic bottom waters can influence diel shifts in the vertical distribution of neritic copepods (e.g. Keister et

Figure 8.6.6 Male (upper left) and female (lower right) adults of the copepod species *Acartia tonsa* from the Chesapeake Bay. © J. Pierson.
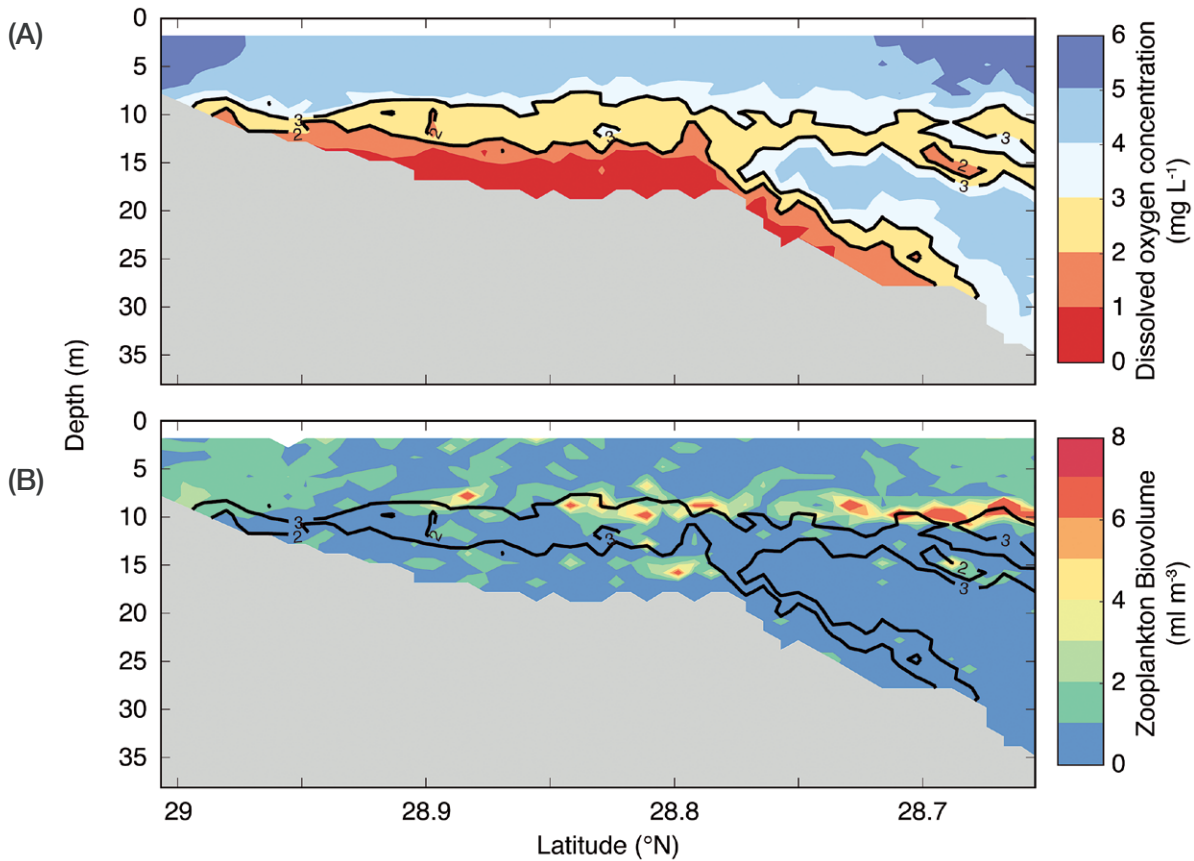
Figure 8.6.7 (A) Dissolved oxygen concentration and (B) zooplankton biovolume data shown as contour plots from a cross-shelf transect in the Gulf of Mexico in July 2004. The black lines on both plots are contours of the 2 and 3 mg L⁻¹ dissolved oxygen conditions, and on (B) they are shown to illustrate the close association between the oxygen gradients and the zooplankton biovolume.

al., 2000; North & Houde, 2004; Qureshi & Rabalais, 2001; Roman et al., 1993). Decker et al. (2003) reported that behavioural responses of copepods to hypoxia may differ depending on environmental history: *Acartia tonsa* (Figure 8.6.6) from Chesapeake Bay appeared to avoid hypoxic bottom waters in laboratory mesocosms while *A. tonsa* from Florida, not typically exposed to hypoxia, did not avoid low-oxygen concentrations in the same mesocosms. In addition, temporal analysis of vertical distributions of copepods has suggested that individuals display considerable variation in their vertical movements, often taking brief (hours) excursions between the surface mixed layer and sub-pycnocline depths (Hays et al., 2001; Pearre, 2000; Pierson et al., 2009a). Thus, it may be common for copepods in coastal waters with hypoxia to experience a range of oxygen concentrations over the day.

Oxygen gradients between hypoxic and normoxic waters can be abrupt, sometimes only centimetres thick (Breitburg et al., 1999, 2003; Donaghay et al., 1992). As a result of these sharp gradients, acoustic and optical sampling technologies can provide insights into the fine-scale distribution of zooplankton in relation to oxygen concentrations. Sharp gradients of oxygen embedded within the pycnocline can serve as loci for enhanced predator-prey interactions. Transects sampled with an optical plankton counter (OPC) in Chesapeake Bay and the northern Gulf of Mexico indicate significant amounts of zooplankton occurring in hypoxic waters, and often concentrated at the oxycline (Kimmel et al., 2009; Roman et al., 2012) (Figure 8.6.7). The food of copepods may also be concentrated within the oxycline. Microbial communities and micro-zooplankton are often aggregated at oxic/hypoxic interfaces in the water column (Coats & Revelante, 1999; Detmer et al., 1993; Fenchel et al., 1990, 1995). Thus, copepods could find food "hot-spots" within the oxycline which have higher food but lower oxygen concentrations.

8.7.2.4 Effects of low oxygen on zooplankton community composition

Low oxygen waters have been associated with changes in zooplankton species assemblages. These zooplankton species changes could be due to direct

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effects of low oxygen on the metabolic functions of the animal or indirect effects due to selective predation by zooplankton consumers. Long term increases in bottom water hypoxia may favour copepod species that carry their eggs as compared to broadcast spawners whose eggs would sink into anoxic/hypoxic bottom waters. For example, increased eutrophication and low oxygen bottom waters have resulted in an increase in the abundance of the small egg-carrying copepod *Oithona davisae* (Figure 8.6.8) in Tokyo Bay and decline in the occurrence of *Acartia omorii* and *Paracalanus* sp.; both of which release their eggs into the water column (Uye, 1994). A similar decline in the broadcast egg spawner, *Acartia tonsa* has been associated with the increase in bottom water hypoxia in Chesapeake Bay (Kimmel et al., 2012). Egg-carrying copepods showed more relative abundance in water columns with hypoxic bottom waters in the Gulf of Mexico as compared to nearby normoxic water columns (Elliott et al., 2012).

Smaller copepods have a higher surface to volume ratio which would favour their oxygen uptake over larger copepods in hypoxic waters and warmer waters where oxygen solubility is lower and oxygen demand (respiration) is higher. In laboratory experiments, Stalder and Marcus (1997) showed that the smaller copepod, *Acartia tonsa,* survived low oxygen conditions better than the larger *Labidocera aestiva* and *Centropages hamatus*. In similar types of laboratory experiments, Roman et al. (1993) found that the smaller copepod *Oithona colcarva* survived low oxygen conditions better than the larger *Acartia tonsa*. The same copepod species, *Acartia tonsa*, was smaller when reared under low oxygen conditions compared to fully oxygenated waters (Richmond et al., 2006) suggesting that decreased oxygen conditions favours smaller animals.
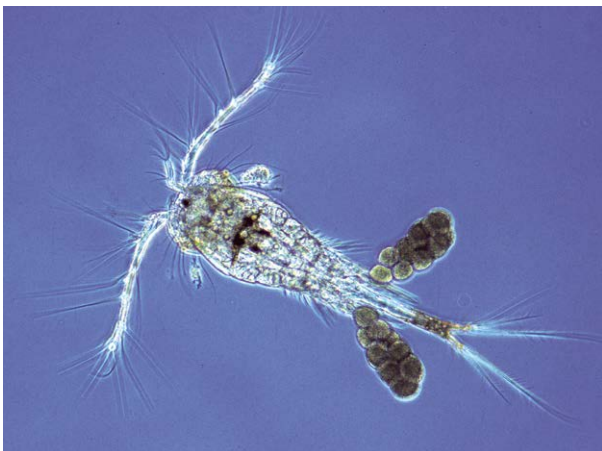

Figure 8.6.8 *Oithona davisae* © Albert Calbet.

Field observations on zooplankton species assemblages in/out of hypoxic areas have shown a variety of patterns. In both the Gulf of Mexico and Chesapeake Bay, the size distribution of zooplankton as measured with an Optical Plankton Counter (OPC) was shifted to smaller individuals in surface normoxic waters as compared to bottom hypoxic waters where there was larger zooplankton (Kimmel et al., 2009). The investigators interpreted these patterns as a consequence of larger copepods being removed from surface waters by visual predators (fish) which could not tolerate the hypoxic bottom waters. Analysis of depth-stratified zooplankton collections in the Gulf of Mexico confirmed OPC results, with larger copepod species relatively more prevalent in low oxygen bottom waters and smaller copepod species assemblages more prevalent in the oxygenated surface waters where selective predation by fish would likely reduce the abundance of larger copepod species (Elliott et al., 2012). In addition to species differences there may be sex differences in tolerance to hypoxia. Pierson et al. (2017) reported that male *Acartia tonsa* were found in lower oxygen waters than females in Chesapeake Bay. Males are smaller (Pierson et al., 2017; Figure 8.6.6), and thus have a higher surface/volume ratio than females which may also have a higher respiratory demand because of egg production (e.g. Castellani & Altunbas, 2014). Thus, in water columns with hypoxic bottom waters, female copepods may be restricted to the upper water column throughout the day and be more susceptible to predation by visual feeders. Not only are individual copepods smaller under deoxygenated conditions, but the assemablage of copepods that can exist in low oxygen conditions is smaller. This means that the overall amount of food available for predators feeding on zooplankton is reduced in hypoxic conditions, and these factors will propagate both through the food web and over time. Copepod egg production rate is partly controlled by female size, and so smaller copepods will produce fewer eggs, leading to population level effects. Also, the smaller, more deoxygenation tolerant species may or may not have the same nutritional value for predators, so the overall ecosystem trophic health and trophic dynamics can be severely altered by hypoxia.

8.6.2.5 Hypoxic impacts on planktonic food web interactions

Several lines of evidence suggest that the presence of low-oxygen bottom waters affects food-web interactions in coastal waters. Hypoxia may favour gelatinous over fish predators of copepods. For

Figure 8.6.9 Sea walnut jellyfish *Mnemiopsis leidyi* © aquapix / Shutterstock.com.

example, the ctenophore, *Mnemiopsis leidyi* (Figure 8.6.9), and scyphomedusan, *Chrysaora quinquecirrha*, have been shown to be more tolerant of low-oxygen water than fish (Breitburg et al., 1994; Purcell et al., 2001). Thus, gelatinous zooplankton are often found in greater abundance lower in the oxycline than fish larvae (Keister et al., 2000; North & Houde, 2004). Modelling research has demonstrated how complex interactions between bay anchovy and zooplankton prey, controlled by DO levels, may affect consumption and production of bay anchovy in Chesapeake Bay (Adamack, 2007; Kolesar, 2006) and potentially control consumption by predators on bay anchovy (Costantini et al., 2008). Peak concentrations of jellyfish in the main stem of Chesapeake Bay occur during summer, the peak period for bottom-water hypoxia. Decker et al. (2004) found that the copepod, *Acartia tonsa,* escape response was significantly reduced in hypoxic waters, and clearance of zooplankton by the ctenophore, *Mnemiopsis leidyi* was elevated at low-oxygen levels. Increases in the abundance of gelatinous zooplankton has occurred in the Gulf of Mexico along with the expansion of bottom water hypoxia (Graham, 2001) where seasonal low oxygen bottom waters can enhance the survival of jellyfish polyps (Miller & Graham, 2012). Grove and Breitburg (2005) suggest that jellyfish are favoured to assume a dominant trophic role in coastal waters experiencing deoxygenation.

Analysis of long-term records of copepods in Chesapeake Bay going back to the 1950s suggests a decline in the summer abundance of the dominant copepod, *Acartia tonsa*, is associated with the increase in bottom water hypoxia (Kimmel et al., 2012). Similarly, the abundance of the mysid, *Mysis mixta* has decreased by up to 50% with increasing hypoxia in the Baltic Sea off Sweden (Ogonowski et al., 2013). Increased eutrophication and low oxygen bottom waters have resulted in an increase in the abundance of the small egg-carrying copepod *Oithona davisae* in Tokyo Bay and decline in the occurrence of *Acartia omorii* and *Paracalanus* spp. both copepods which release their eggs into the water column (Uye, 1994). As more long-term time series are reported for coastal waters experiencing bottom water hypoxia, we will likely learn of more examples of changing coastal food webs experiencing deoxygenation.

8.6.2.6 Physiological and genetic adaptations

While a variety of physiological adaptations to low oxygen conditions have been described for open ocean zooplankton with permanent low oxygen zones, coastal zooplankton experience hypoxia which varies on daily to seasonal time scales. Without gills or haemoglobin, coastal zooplankton have limited options for adapting to low oxygen conditions. Oxygen binding proteins that
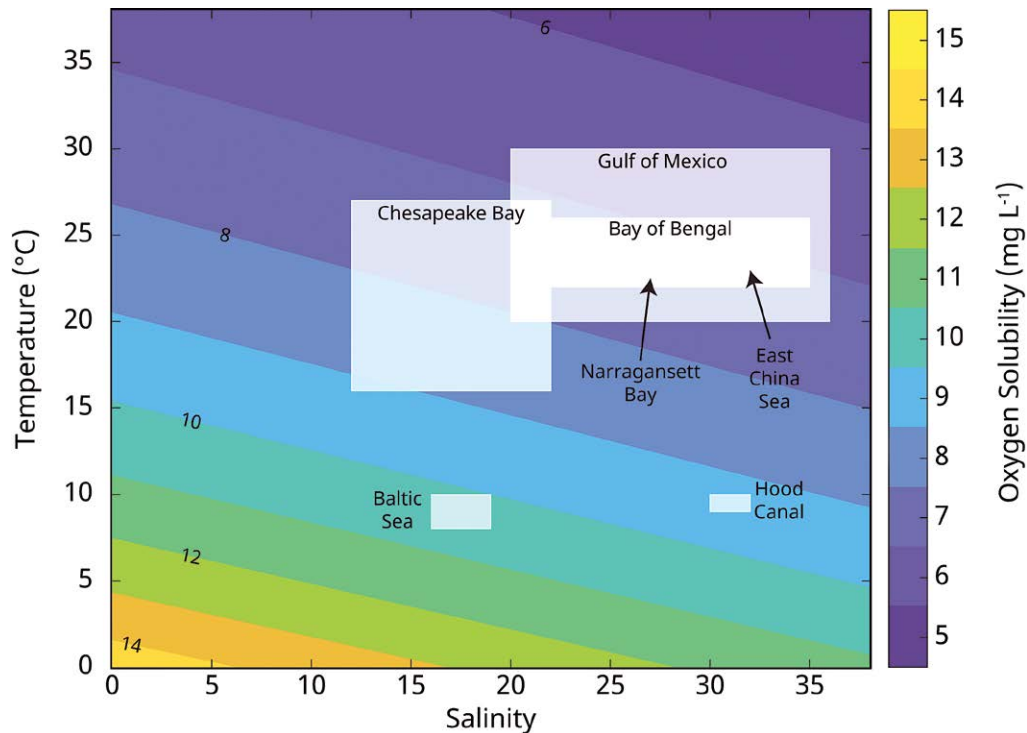
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Figure 8.6.10 Oxygen solubility (mg L^{-1}) is shown by the colour scale at different salinity and temperature (°C) conditions, with boxes indicating the range of salinity and temperature during periods of seasonal deoxygenation for different coastal and estuarine bodies of water around the world. Oxygen solubility calculated using the equations of Benson and Krause (1980, 1984), assuming surface water pressure.

have the potential to enhance survival at low oxygen conditions have not been identified in copepods (Thuesen et al., 1998). However, some biochemical adaptions to low oxygen may help zooplankton adapt to periods of hypoxia. Invertebrates that experience conditions of hypoxia with diel migrations to low oxygen bottom waters may enhance their antioxidant potential to deal with a physiological stress during the transition from hypoxic to normoxic conditions (Hermes-Lima & Zenteno-Savin, 2002). Mysids in the Gulf of Finland which migrated in/out of bottom hypoxic waters had higher antioxidant than conspecifics that remained in normoxic waters throughout the day, with no sign of oxidative damage (Webster et al., 2015).

8.6.2.7 Regional comparisons of hypoxia impacts on coastal zooplankton

Global comparisons of how bottom water hypoxia affects the habitat space of estuarine and coastal zooplankton reveal a variety of spatial and temporal patterns. While taxa-specific differences in hypoxia tolerance likely exist, the primary reason investigators have not found clear geographic and seasonal differences in the spatial distributions and physiological responses to low DO by zooplankton is the failure to consider and evaluate the role of temperature in

controlling oxygen availability, metabolic demand, and organism behaviour. For example, temperatures of hypoxic (< 2 mg O$_2$ L^{-1}) bottom water in the Gulf of Mexico can exceed 28 °C in contrast to the Baltic where hypoxic water temperatures are 8-10 °C (Figure 8.6.10). Such differences in bottom temperatures not only affect oxygen availability (partial pressure and solubility) for organisms, but also drive differences in respiratory demands of zooplankton which increase exponentially with temperatrue. This is illustrated by the Q$_{10}$ value for respiration, which for most zooplankton and is around 2. This means that for every 10 °C temperature increase, the respiration rate is doubled and so zooplankton require twice as much oxygen for every 10 °C increase in temperature. Thus, all "hypoxic" bottom waters, do not pose the same stress on zooplankton and their fish predators, and deoxygenation can generate different responses in spatial ecology and predator-prey interactions depending on other factors, especially temperature. For example, using the predictive response to decreasing oxygen (P$_{crit}$) developed for the copepod *Acartia tonsa* by Elliott et al. (2013), 2 mg O$_2$ L^{-1} bottom water in the Baltic (9 °C) would have an oxygen partial pressure of 4.24 kPa, which is slightly below the limiting P$_{crit}$ of *A. tonsa* predicted for this temperature (5.07 kPa). In contrast, 2 mg O$_2$ L^{-1} bottom water in the Gulf of Mexico (30 °C)

would have an oxygen partial pressure of 6.37 kPa, which is significantly below the limiting P_{crit} of *A. tonsa* predicted for this temperature (18.31 kPa) and approximately the same as the predicted lethal oxygen concentration (P_{leth} = 6.77 kPa). These predicted differences in oxygen availability and demand are a useful way to assess how low oxygen waters determine habitat availability for estuarine and coastal zooplankton. Thus, field surveys have shown that zooplankton generally avoid the warmer low oxygen waters of the Gulf of Mexico (e.g. Qureshi & Rabalais, 2001; Roman et al., 2012) but reside in the colder low oxygen waters of the Baltic for significant portions of the day, affording the zooplankton a potential refuge from predation (e.g. Appeltans et al., 2003; Webster et al., 2015). Because of the higher oxygen demand by estuarine and coastal zooplankton in warmer waters of the tropics and subtropics, the loss of habitat space by low oxygen bottom waters would be expected to more severe in these regions because the zooplankton are already living near their upper limit of thermal tolerance.

8.6.3 Ecosystem consequences

The presence of low oxygen bottom waters can have ecosystem consequences in estuarine and coastal waters by altering spatial and temporal predator-prey relationships, changing the size structure and species composition of zooplankton communities which will affect foraging, consumption and growth of fish species. Living under sub-optimum oxygen conditions can reduce temperature-dependent metabolic efficiencies, prey capture efficiency, growth and reproductive potential, and thus impact individual zooplankton fitness and population production. Hypoxic bottom water can reduce or eliminate low-temperature thermal refuges for organisms, increasing energy demands and respiration rates, and potentially reduce overall fitness. Thus, an important issue related to bottom water hypoxia in estuarine and coastal waters is whether zooplankton use the lower oxygen area as a critical habitat to avoid predation or must avoid it and remain in the upper water column where they are subject to greater predation (Figure 8.6.11). In theory, zooplankton could reside in hypoxic bottom waters if the oxygen supply is greater than its critical oxygen demand (P_{crit}) but not if the oxygen availability is well below P_{crit} or the lethal oxygen partial pressure (P_{leth}). Avoidance of low DO bottom waters can influence spatial dynamics of zooplankton and fish populations. For example, more hypoxia-tolerant zooplankton may use hypoxic

waters as a refuge from fish predation. Conversely, zooplankton avoidance of hypoxic bottom waters can result in prey aggregations at oxyclines which are used by fish predators. In coastal ecosystems with shears and differential flow between surface and deep layers, avoidance of low oxygen bottom waters can influence spatial dynamics of zooplankton populations by altering emigration and immigration patterns, and residence times. As more information becomes available on the oxygen demand of dominant estuarine and coastal zooplankton at different temperatures, we will be able to better assess if low oxygen bottom waters result in a loss of critical habitat.

Hypoxic conditions that affect spatial ecology and population dynamics can drive taxonomic and size shifts in the zooplankton community which will affect foraging, consumption and growth of fish species. Smaller zooplankton may be favoured in low oxygen conditions because their higher surface/volume ratio would be advantageous to oxygen uptake under hypoxic conditions. If hypoxic conditions resulted in a community shift to smaller zooplankton, there may be negative consequences for larval fish species feeding on smaller prey items. Similar food web consequences from changing of zooplankton species could occur if there was a succession to copepods that carry their eggs in water columns with hypoxic bottom waters (Uye, 1994). As mentioned previously, low oxygen waters may favour jellyfish over planktivorous fish because of the higher oxygen requirements of fish. Thus, shifts in the zooplankton food available to fish and greater competition by jellyfish can work together to alter pelagic food webs in estuarine and coastal waters experiencing seasonal bottom water hypoxia.

8.6.4 Societal consequences

The root cause of seasonal deoxygenation in estuarine systems is excess organic production that is decomposed in the bottom water, removing oxygen faster than it is replaced. That excess productivity is a result of cultural eutrophication, which can have its own societal consequences, ranging from harmful and nuisance algal blooms, poor water quality that limits use of water ways, and even the presence of human pathogens borne from run-off. Additionally, increasing water temperatures as a result of anthropogenic climate change can exacerabate the effects of deoxygenation by increasing the metabolic demand of organisms,
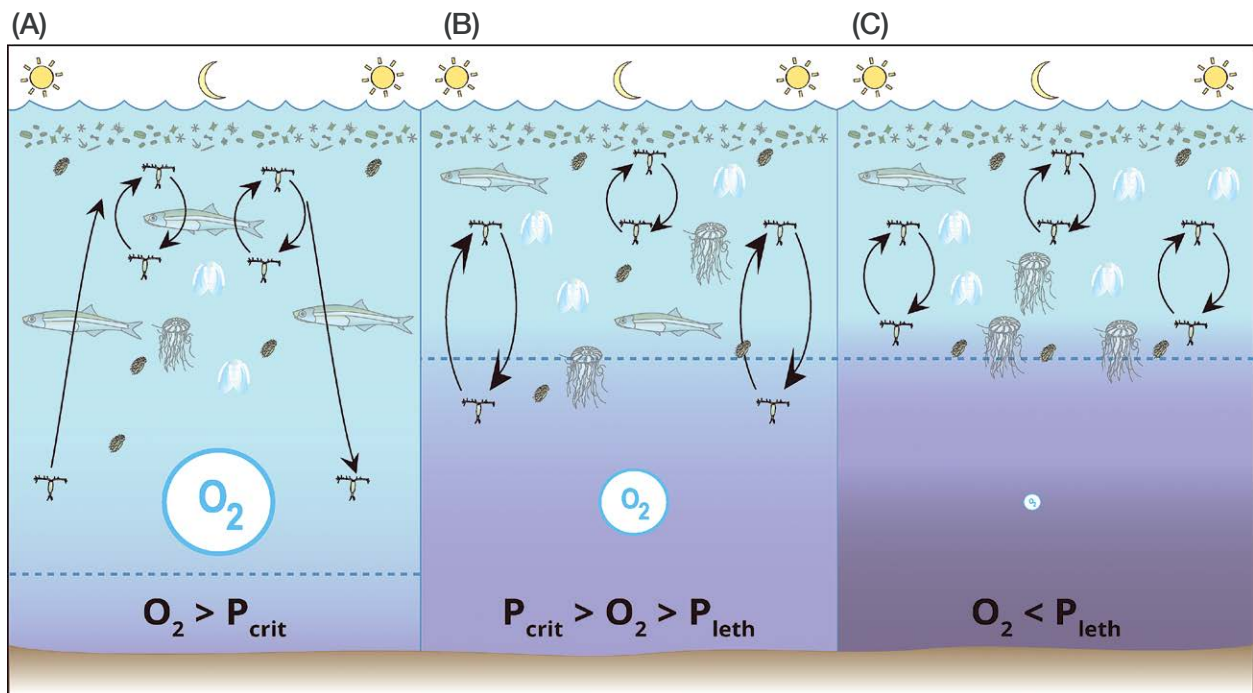
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Figure 8.6.11 Conceptual diagram of food web changes that occur over diel cycles between (A) normoxic conditions, (B) sub-lethal deoxygenation conditions, and (C) lethal conditions. The size of the symbol for O_2 and the colour indicates the relative amount of dissolved oxygen under each condition (with light blue indicating high oxygen concentration and purple indicating lower oxygen concentration). With decreasing oxygen concentration comes reduced habitat, truncated magnitude of copepod vertical migration (shown by length of arrows), increased gelatinous zooplankton abundance, and decreased forage fish abundance. Symbols Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

making the severity of the impacts greater than they would be at lower temperatures.

Plankton are able to change their vertical position in the water column and thus would not face imminent mortality under hypoxic conditions, unlike sessile benthic organisms such as oysters, worms and crabs which are unable to move or are severely limited in their mobility when faced with deoxygenated bottom water. However, negative consequences for plankton biodiversity, productivity, and sub-lethal biological effects are projected to result from expanding hypoxic bottom waters. Additionally, individuals growing in oxygen deficient waters would have reduced respiration rates, slower growth rates, and diminished escape responses, amongst other non-lethal effects. These effects are likely to cascade through the food web, ultimately impacting higher trohpic levels including economically important fish species that rely on plankton as prey. The changing zooplankton species composition and the use of hypoxic bottom waters as a refuge from predation could directly impact the larval forms of commercially important fish species, as well as small pelagic fish that are a critical food resource for picivorous fish. Indirect effects from the diminished escape responses could mean that predation mortality of plankton is increased

in the presence of predators that are tolerant of hypoxia. But in the case of hypoxia, there are likely to be some winners and some losers. Planktivorous fish are likely to be replaced with more hypoxic-tolerate gelatinous zooplankton, which can in turn increase their own predation on the plankton that are impacted by the low oxygen. This could result in more shortened, "dead-end" food chains, where the highest trophic levels are the gelatinous zooplankton and not the higher trophic levels that include commercially important fish species that rely on the replaced planktivorous fish as prey. Additionally, expanding hypoxic regions can alter the location of viable fishing grounds, and the added costs of longer transit times from dock to fishing areas can be a major impact on the fishing community.

8.6.5 Implications of continuing ocean deoxygenation

Warming estuarine and coastal waters will exacerbate the deleterious effects of low oxygen zones by increasing the respiration and oxygen demand of zooplankton, while decreasing the solubility of oxygen at the same time. Climate warming has the potential to increase the seasonal period and spatial extent of bottom-water hypoxia thus having longer term impacts on pelagic food

webs. While zooplankton may tolerate periods in low oxygen waters that limit their metabolic functions (DO < P_{crit} but > P_{leth}), greater eutrophication and warming seas may increase the severity of low oxygen waters to lethal levels (DO < P_{leth}) for estuarine and coastal zooplankton. Zooplankton would lose habitat, distributions would be concentrated in more oxygenated surface waters and with greater predation mortality and zooplankton populations would decrease. Deoxygenation in coastal waters may be more severe in lower latitudes where higher temperatures and respiration already create oxygen limiting conditions for zooplankton.

8.6.6 Conclusions / Recommendations

- Seasonal deoxygenation of estuarine and coastal ecosystems leads to a variety of impacts on zooplankton including: Lower overall abundance; altered community structure with smaller, egg carrying taxa and gelatinous zooplankton increasing with decreasing dissolved oxygen; shallower vertical distribution and reduced vertical migration extent; sub-lethal impacts including reduced size at adulthood and reduced growth rate.

- Continuing ocean deoxygenation will be accompanied by warmer temperatures and decreasing pH, thus estuarine and coastal zooplankton will experience multi-stressors that will impact their fitness, life histories and population dynamics.

- Management efforts to reduce eutrophication in estuaries and coastal seas should be increased to reduce organic loads which cause oxygen depletion in bottom waters.

- Global plans to reduce greenhouse gas emissions which are causing global warming and increased deoxygenation should be increased and implemented.

- Ecosystem Based Management (EBM) of estuarine and coastal seas should incorporate the seasonal hypoxic bottom waters to better understand the impacts of current and future deoxygenation on pelagic food webs and fisheries.

- To assess effects of the globally expanding coastal low oxygen zones, we need to determine if generic models can be developed to evaluate and

predict how low DO imposes temporal and spatial limitations on metabolic functioning of zooplankton. Because oxygen availability to these organisms is a function of the rate of diffusion across their integument, allometric relationships such as surface/volume, body mass, etc., can be developed for similar groups of zooplankton to predict oxygen limitation and its consequences, e.g. reduced growth or alteration of vertical distribution in hypoxic coastal waters. Allometric models for predicting temperature-dependent oxygen supply and demand in zooplankton and planktivorous fish will lead to improved size-structured models that serve to predict impacts of increasing coastal hypoxia on pelagic food webs and allow common, quantitative comparisons across coastal ecosystems.

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