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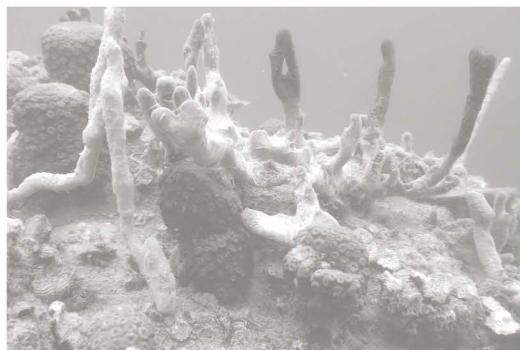
Causes, impacts, consequences and solutions

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8.3 The significance of ocean deoxygenation for kelp and other macroalgae

Larry B. Crowder, Crystal A. Ng, Timothy H. Frawley, Natalie H.N. Low and Fiorenza Micheli

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Summary

- Because kelps and other macroalgae are primary producers and absorb carbon dioxide and produce oxygen, one might expect the effects of hypoxia to be modest. However, kelps and macroalgae also respire, which requires oxygen. Therefore, hypoxia may have detrimental effects on processes like net primary production (NPP), which supplies organic matter to support kelp food webs and ecosystems. However, the effects of hypoxia are expected to vary widely depending on the species of macroalgae and their habitat, since this group of organisms is diverse in their morphology and distribution. Here we describe predicted impacts of deoxygenation on kelps and other macroalgae and discuss consequences for kelp ecosystems.

- Kelps and other macroalgae occur in nearshore systems across the world, which are dynamic and experience large fluctuations in oxygen, pH, and temperature. In dynamic coastal upwelling zones, low-oxygen events are often more episodic. Unlike respiration-driven hypoxia in bays and estuaries, these upwelling-driven exposures to hypoxia tend to be acute, with rapid onsets and recoveries, and typically lasting less than 24 hours each. It remains to be seen whether it is less likely for organisms in these systems to experience direct mortality due to adaptions to high degrees of natural variability in dissolved oxygen (DO) or whether they are close to their physiological limits.

- Very little is known about the direct impacts of deoxygenation on macroalgae. On one hand, hypoxia may detrimentally affect metabolic processes, leading to lower net primary production. These processes are also expected to be affected during various stages in the macroalgal life cycle. However, many marine algae photo-respire (using oxygen instead of carbon dioxide), reducing their photosynthetic efficiency, so decreasing oxygen concentrations may actually increase photosynthetic rates in some marine macroalgae. These predictions become complicated when considering the effects of oxygen in combination with co-occurring stressors like ocean acidification and warming. Depending on factors like calcification, proximity to the benthos, growth rate, and carbon concentration mechanisms, these three stressors are predicted to differentially affect groups of macroalgae.

- In addition to direct impacts on macroalgae, low oxygen (and upwelling-associated fluctuations in pH and temperature) could have profound effects on the grazers, decomposers, and predators that drive the structure and function of kelp ecosystems. There is a dearth of published studies on the responses of kelp forest organisms to low oxygen, but those that do exist suggest changes in foraging, feeding, and movement. Sedentary benthic invertebrates such as abalone may be detrimentally affected because depressions in the rocky bottom may retain pools of cold, acidic, low-oxygen water for hours after internal waves pass, much like a tide pool retains water from a retreating tide. Additionally, deoxygenation effects on organisms will likely alter trophic interactions and energy flow. Differences in vulnerability between grazers and predators may strengthen or weaken trophic cascades and top-down control on kelp populations.

Hypoxia effect	Potential consequences
Hypoxia may affect oxygen available for metabolic demands.	• Positive effects on photosynthesis (but this is species dependent) and negative impacts on respiration might alter NPP, which would have cascading effects on food webs.
Hypoxia may interact with other climate related stressors like ocean acidification, especially in upwelling regions where low pH and oxygen co-occur.	• Growth might be most negatively impacted, especially in calcified macroalgae. • Sub-canopy species under lower irradiances or rocky reef depressions might be disproportionately affected due to lower photosynthetic rates and exposure to more prolonged and more severe hypoxic conditions.
Hypoxia may differentially impact algae with different photosynthetic physiologies.	• Algae with high O_2 sensitivity might fare better (in terms of photosynthetic rate) under lower oxygen concentrations, since Rubisco can uptake CO_2 more efficiently. • Altered competitive interactions between different species, leading to changes in macroalgal assemblages (i.e. simplification).
Hypoxia may impact macroalgae throughout their life cycle.	• Increased bottlenecks at early life stages will impact macroalgal populations. • Buffering capacity of algae to low pH and oxygen, especially at boundary layers, could benefit algae at local scales.
Direct effects of hypoxia on macroalgae may impact food webs due to altered species interactions.	• Reduced transfer of primary productivity if macroalgal communities are altered (i.e. simplification or degradation). • Simplified food webs more susceptible to invasion by non-natives or closer to reaching "tipping points".

8.3.1 Introduction

Marine macroalgae and kelps provide a tremendous amount of primary production globally, capable of producing 1 Pg carbon year^{-1} (i.e. 1 Gigatonne) (Raven & Hurd, 2012; Smith, 1981). Macroalgae generally comprise a holdfast, stipe, and blade, but they are highly diverse in their morphology with many lacking one or more of these structures (Abbott & Hollenberg, 1976). This group which can have a range of body types from single-celled, multinucleate algae to large, structurally complex algae comprise various tissue layers (Graham et al., 2009). They provide important habitat, food, and refuge for other organisms in addition to providing extracts used in the food, pharmaceutical, and cosmetic industries, making them ecologically and economically important (McLachlan, 1985; Raven & Hurd, 2012).

Kelp forests are distributed in temperate seas worldwide (Steneck & Johnson, 2014) (Figure 8.3.1). Often

considered ecosystem engineers (Holdolero & Edwards, 2017; Jones et al., 1994), kelp and other macroalgae provide habitat and mediate energy flow across the diverse and highly productive marine ecosystems in which they are found (Steneck et al., 2002). The natural history of kelp forests and the processes that shape their associated animal and algal communities are relatively well understood (Schiel & Foster, 2015). But major gaps in knowledge remain concerning how these systems respond to the stressors and variability associated with climate change (Krumhansl et al., 2016). High temperature—and associated low nutrient conditions—and extreme storms can lead to full deforestation, though recovery is typically fast (1-5 years; Dayton et al., 1992; Edwards, 2004). Much less is known about the impacts of deoxygenation and acidification. Because kelps and other macroalgae are primary producers and absorb CO_2 and produce O_2, one might expect the effects of hypoxia to be modest. But diel swings in production lead to significant fluctuations in pH and O_2 levels.
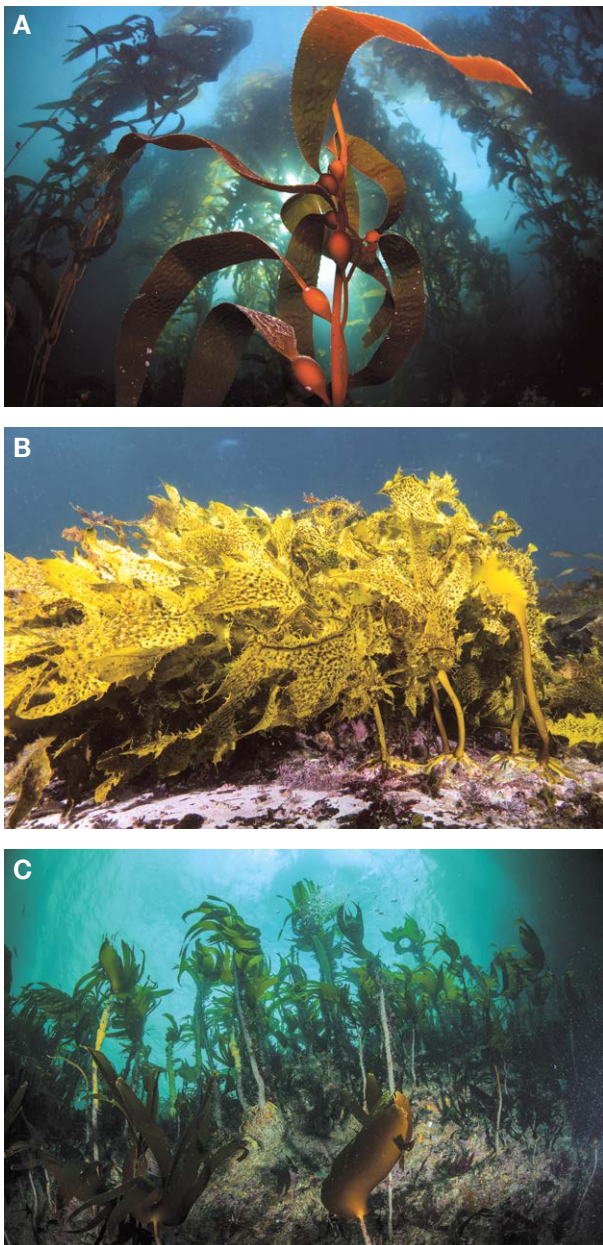
Figure 8.3.1 A) Giant kelp (*Macrocystis pyrifera*) © Shutterstock; B) *Ecklonia radiata* © John Turnbull; C) Cuvie (*Laminaria hyperborea*) © SNH/ George Stoyle.

These ecosystems are also impacted by both offshore and inshore processes that can drive deoxygenation (Walter et al., 2014; Woodson et al., 2018) In addition to direct impacts on kelps and other macroalgae, low oxygen (and upwelling associated fluctuations in pH and temperature) could have profound effects on the grazers, decomposers, and predators that drive the structure and function of kelp ecosystems. Given the significant overlap between the distribution of kelp forests and the deoxygenation of coastal, near-coastal, and open ocean waters worldwide (Figure 8.3.2), the need for further research is critical. Though the impacts

of deoxygenation on kelps, macroalgae and associated animals are likely to be biogeographically explicit, here we rely upon existing empirical evidence and primarily focus on relevant communities and populations across the Northeast Pacific.

In the California Current, waters are increasingly experiencing oxygen depletion (Chan et al., 2008), concomitant with an expanding Eastern Pacific oxygen minimum zone (OMZ) (Stramma et al., 2010). Some of these changes are in response to natural climate variability, such as the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) (Nam et al., 2011). But there also appear to be non-cyclical changes associated with climate variability affecting dissolved oxygen (DO) concentration of ocean waters across the Eastern Pacific (Brewer & Peltzer, 2009). Shoaling of deep, low-DO waters is particularly pertinent in the California Current because the Eastern Pacific Ocean contains the world's largest midwater OMZ (250-400 m deep) (Keeling et al., 2009), and the coastal region has a narrow continental shelf (Pennington et al., 2006) making the coastline susceptible to OMZ intrusion. Bograd et al. (2008) documented mean declines in DO concentration of 20% below the mixed layer from 1984–2006, and an 80 m shoaling of the hypoxic zone, with more intense shoaling at inshore locations of the Southern California Bight. Observed DO declines are not limited to OMZ depths, as oxygen-depleted offshore waters episodically intrude on the coast through seasonal upwelling, tides, and coastally trapped waves (Bakun, 1990; Booth et al., 2012).

Based on 50+ year data set from the Southern California Bight, Booth et al. (2014) documented changes in DO concentration similar to those reported offshore. But DO in sub–mixed layer nearshore waters (10 km from shore) declined up to four times faster than reported for offshore waters over the last 15 years. These rapid declines have no precedent over the past 50 years and are not attributable to large-scale climate variability in ocean DO. Coastal biophysical processes, including increased phytoplankton biomass in surface waters, are likely contributing to the recent elevated rate of DO decline in nearshore waters, as evidenced by higher rates of apparent oxygen utilization. The combined impact of shoaling of the oxygen minimum layer and possible coastal eutrophication can produce low DO dynamics that have detrimental impacts on kelp forest ecosystems, particularly on sedentary benthic invertebrates such as abalone (Micheli et al., 2012).

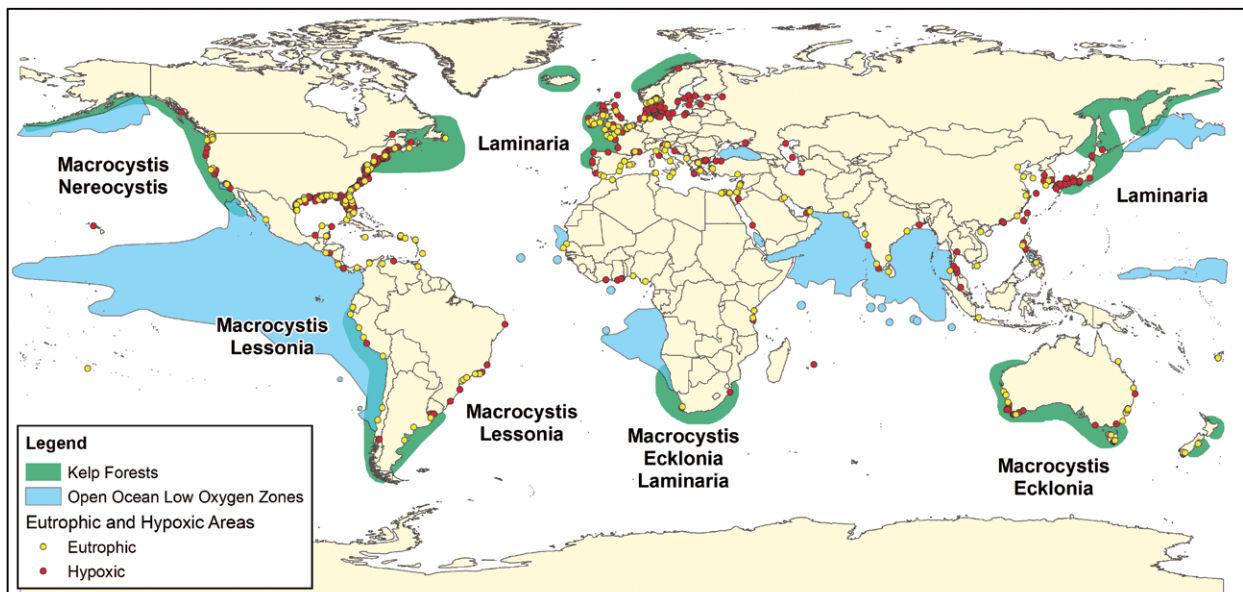## World Kelp Forests, Low Oxygen Zones, and Hypoxic and Eutrophic Coastal Areas

Figure 8.3.2 Global distribution of forest forming kelps (Steneck et al., 2002), open ocean low oxygen zones (2 mg L^{-1}of O or less) (Garcia et al., 2014), and eutrophic and hypoxic coastal areas (Diaz et al., 2011). Map produced by Hannah Blondin.

Laboratory studies indicate that biological impacts of hypoxia on marine invertebrates are compounded by co-occurring fluctuations in pH and temperature (Boch et al., 2017; Kim et al., 2013), but the cumulative impacts on kelps are still largely unaddressed.

8.3.2 Spatio-temporal variability in oxygen conditions within kelp forests

DO concentrations in kelp forests are highly variable in both space and time, and the potential effects of deoxygenation in this ecosystem must be considered within the context of natural patterns of variability. The substantial horizontal, vertical, and temporal oxygen variability in kelp forests is influenced by multiple physical and biological processes. Seasonal upwelling along the west coast of North America primarily occurs during the spring and summer months, and brings cold, acidic, low-DO, and nutrient-rich water onto the continental shelf. This deep water is then further transported into nearshore kelp forest ecosystems by internal waves (Booth et al., 2012; Walter et al., 2014). In southern and central California kelp forests, these internal waves drive semidiurnal and diurnal patterns of oxygen and pH variability (Booth et al., 2012; Frieder et al., 2012; Koweek et al., 2017). As a result, some of these kelp forests already encounter sublethal levels of hypoxia for animals according to the 4.6 mg L^{-1} threshold of Vaquer-Sunyer and Duarte (2008). Unlike respiration-driven hypoxia in bays and estuaries, these upwelling-driven

exposures to hypoxia tend to be acute, with rapid onsets and recoveries, and typically lasting less than 24 hours each. (Booth et al., 2012; Leary et al., 2017; Walter et al., 2014).

The intrusions of cold, acidic, low-DO deep water into the kelp forest lead to increased stratification of the water column, which creates strong gradients of oxygen and pH between the surface and the bottom (substrate) of the kelp forest (Frieder et al., 2012; Koweek et al., 2017). These vertical gradients in DO and pH can be amplified by vertical gradients in kelp photosynthesis. Kelp biomass is concentrated near the surface in the canopy region, so an increase in kelp photosynthesis can further elevate dissolved oxygen and pH in surface waters relative to deeper water (Frieder et al., 2012; Koweek et al., 2017).

Horizontal variability in dissolved oxygen at the kelp forest floor (substrate and benthos) is generated by the interactions of internal waves with upwelling conditions and bottom topography (Koweek et al., 2017; Leary et al., 2017; Walter et al., 2014; Woodson et al., 2018). For example, depressions in the rocky bottom may retain pools of cold, acidic, low-oxygen water for hours after an internal wave passes, much like a tide pool retains water from a retreating tide (Leary et al., 2017). These 'internal tide pools' of low-oxygen water can create a fine spatial mosaic of oxygen conditions within the kelp forest. At larger spatial scales, wave-exposed regions

of the kelp forest may experience different conditions than the wave-protected areas due to different levels of exposure to the internal waves which transport acidic, low-DO water into nearshore habitats (Koweek et al., 2017).

8.3.3 Impacts of deoxygenation on macroalgae and kelps

Due to their ability to photosynthesize, macroalgae are not thought to be vulnerable to deoxygenation directly. Despite many studies examining oxygen effects on macroalgae (e.g. Black et al., 1976; Downton et al., 1976; Dromgoole, 1978; Turner et al., 1956), virtually nothing has been published under the context of climate-driven hypoxia. While the literature focuses much more on the effects of temperature and ocean acidification (e.g. Shukla & Edwards, 2017), we argue that hypoxia should also be examined with a consideration of its effects on macroalgae throughout their life cycles. Because multiple climate change stressors are occurring concomitantly across the globe, it is also imperative to understand the impacts of hypoxia in relation to the impacts of other co-occurring stressors like ocean acidification and warming.

As well as photosynthesizing, kelps and macroalgae also respire, which requires oxygen. Thus, deoxygenation may impact net primary production (NPP), which supplies organic matter to support food webs and ecosystems. NPP considers both the production of oxygen through photosynthesis and the use of oxygen through respiration. Previous research has shown that photosynthetic capacity decreases with depth due to reduced light (Arnold & Manley, 1985; Gerard, 1986), so sub-canopy and smaller macroalgae may be impacted by an already lower photosynthetic capacity in addition to limitations on respiration by hypoxia. For large and canopy forming kelps that create habitat complexity and drive primary production within a system, understanding their fate under hypoxia is also important to consider, since canopy blades are closer to the air-sea interface and may not experience levels of hypoxia comparable to the benthos or in depressions in rocky reefs (Leary et al., 2017). With the large habitat-forming kelp *Macrocystis pyrifera*, canopy and apical blades have higher net photosynthetic rates even under high irradiance, raising the question whether these blades may be able to compensate for any negative effects that hypoxia may have on respiration for lower blades (Figure 8.3.3).

Figure 8.3.3 Giant kelp forest (*Macrocystis pyrifera)* with sheephead (*Semicossyphus pulcher*) in foreground. © Brent Durand.

SECTION 8.3

SPOROPHYTE (2N)
-Growth
-Cell differentiation
-Net primary production
-Chemical defense production
-Nutrient uptake

FERTILIZATION
-Detection of egg by sperm
-Fusion of sperm and egg

SPORANGIA
-Spore production
-Spore release

EGG (♀)

OOGONIA (♀)

SPERM (♂)

SPORES (N)
-Motility
-Settlement
-Germination
-Dormancy

GAMETOPHYTES (N)
-Growth
-Differentiation
-Sex-ratio
-Survival

ANTHERIDIA (♂)

Figure 8.3.4 General life cycle of macroalgae. Under the different life stages are important processes to consider when examining the impacts of deoxygenation.

Previous work looking at the effects of oxygen on kelp and other macroalgae gives us some insight into how these processes may be altered, particularly oxygen effects on photosynthesis. Many marine algae photo-respire, since Rubisco, the enzyme that catalyzes CO_2 for photosynthesis also catalyzes a reaction with oxygen, leading to the loss of fixed carbon (Bowes et al., 1971). Because of this, decreasing oxygen concentrations can actually increase photosynthetic rates in some marine macroalgae (Burris, 1980; Downton et al., 1976; Turner et al., 1956). Moving forward, it is important to consider the consequences of this for overall NPP, which would incorporate oxygen effects on both photosynthesis and respiration.

Largely missing from the literature on the effects of climate change on macroalgae is research on juvenile stages. Studies of the direct effects of hypoxia on the performance and success of macroalgae throughout their life cycles would provide insight into how these important organisms will develop under a changing climate. Despite the current research emphasis on the effects of ocean acidification on macroalgae, the understanding of its impacts on different life stages is very limited (Gaitán-Espitia et al., 2014; Harley et al., 2012; Roleda et al., 2012; Shukla & Edwards, 2017), whereas the effects of hypoxia are unexplored. Because macroalgae undergo significant morphological and physiological changes through their life cycle from spore to the adult stage, several processes could be impacted by low oxygen, including settlement, early post-settlement survival, gametogenesis, and growth (Figure 8.3.4). A focus on multiple stressors on the adult stage means over-looking other crucial periods within the macroalgal life cycle. For example, spores and gametes lack an outer cell wall, potentially making them more susceptible to climate stressors like low pH and oxygen (Gaitán-Espitia et al., 2014; Reed & Lewis, 1994), while small, low lying sporophyte stages that are expending energy for growth may be negatively impacted by hypoxia. However, also important to consider is that algae can modify micro-environments within their boundary layer, potentially buffering the effects of acidification and hypoxia (Cornwall et al., 2013), and smaller stages live within the diffusive boundary layer (Gundersen & Jorgensen, 1990), which experience different oxygen levels than the bulk water above. Therefore, it is important to consider several factors that influence macroalgae and kelps throughout their life cycles, since they undergo large transitions in size and metabolic demands, all of which could be influenced by deoxygenation.

Due to the co-occurrence of multiple stressors, deoxygenation will never act in isolation. In upwelling systems where physical processes force low DO, low pH waters to nearshore habitats like rocky reefs and kelp forests, both hypoxia and ocean acidification should be considered when designing experiments. With continued ocean warming, it is also important to consider the possibility of these three stressors acting in concert to affect macroalgae (Pörtner et al., 2005).

Figure 8.3.5 *Ecklonia radiata* kelp forest © Daniel Poloha / Shutterstock.com.

Under warming, rates of respiration may increase faster than rates of photosynthesis (Hancke & Glud, 2004; Masini & Manning, 1997; Tait & Schiel, 2013), which has implications for multiple stressor impacts on macroalgae and kelps. In macroalgal assemblages in New Zealand and Australia, rising temperatures led to higher rates of respiration compared to rates of NPP. This suggests that warming can alter the balance between respiration and photosynthesis, leading to overall declines in NPP. Sub-canopy algae that experience lower light may be particularly susceptible to warmer temperatures due to increased respiration rates in combination with reduced light for photosynthesis (Tait & Schiel, 2013). This increased rate of oxygen use may be inhibited if warming co-occurs with hypoxia. On the other hand, in upwelling systems where low oxygen and low pH often occur with lower temperatures, there may be a mitigating effect of low temperature by decreasing metabolic demands (Vaquer-Sunyer & Duarte, 2011). Interactions with low pH may also lead to variable responses, since acidification itself can negatively impact the growth of calcifying macroalgae (Kuffner et al., 2008), but because acidification can benefit photosynthesis (Koch

et al., 2013), this may counterbalance the negative impacts of hypoxia. As research moves forward, it is imperative to consider the effects of multiple stressors, since deoxygenation is occurring alongside ocean acidification and warming, and the interaction between these stressors may lead to unexpected consequences for macroalgal communities.

Macroalgae differ in their photosynthetic and respiration rates, so understanding the impacts of climate change on whole communities will require detailed experiments using multiple species to elucidate 'winners' and 'losers'. Few studies have examined how whole assemblages of macroalgae are affected under climate change but work in intertidal rock pools show that high temperatures and acidification impact biomass, productivity, and respiration (Olabarria et al., 2012). But the effects vary depending on species composition. For example, turf algae are thought to fare better under future scenarios, and work done in Australian *Ecklonia radiata* kelp forests (Figure 8.3.5) showed that warming and acidification act synergistically to promote the growth of turf algae over recruits of *E. radiata*, so climate change may directly benefit faster growing, more opportunistic algae (Connell & Russell, 2010; Russell et al., 2009). Some calcifying algae (Figure 8.3.6) have been shown to undergo necrosis and die under higher temperatures and lower pH (Martin & Gattuso, 2009), while others seem quite resilient to acidification (O'Leary et al., 2017). When thinking about hypoxia, different photosynthetic physiologies, including oxygen sensitivity (Beer & Israel, 1986; Kübler et al., 1999) and different strategies for carbon uptake (Cornwall et al., 2012; Hepburn et al., 2011; Koch et al., 2013), will play an important role in determining which species may fare better or worse under a changing climate.

Figure 8.3.6 *Lithophyllum sticitforme* complex © David Luquet.

8.3.4 Deoxgenation impacts on kelp fauna

In estuaries and inner shelf systems, prolonged hypoxic events can lead to mass mortality of both fish and invertebrates, generating areas devoid of life often referred to as 'dead zones' (Chan et al., 2008; Diaz, 2001; Grantham et al., 2004). In dynamic coastal upwelling zones low-oxygen events are often more episodic; it is less likely for organisms in these systems to experience direct mortality as they may be adapted to a higher degree of natural variability in DO. But deoxygenation and associated environmental stressors may impact kelp and other macroalgae indirectly, through lethal and sublethal impacts on grazers and predators (e.g. Low &

Micheli, 2018). Research from other systems suggests that the cumulative effect of sub-lethal impacts may be comparable to those of direct mortality (Breitberg et al., 2009). There is a dearth of published studies on the responses of kelp forest organisms to low oxygen, as most studies have been conducted on estuarine and infaunal organisms (e.g. Vaquer-Sunyer & Duarte, 2008), therefore we discuss general expectations.

Kelp forest ecosystems include structure-producing kelps and associated biota including marine mammals, fishes, crabs, sea urchins, and algae (Mann, 1973). Though these ecosystems persist between ecological processes driving their development and deforestation,
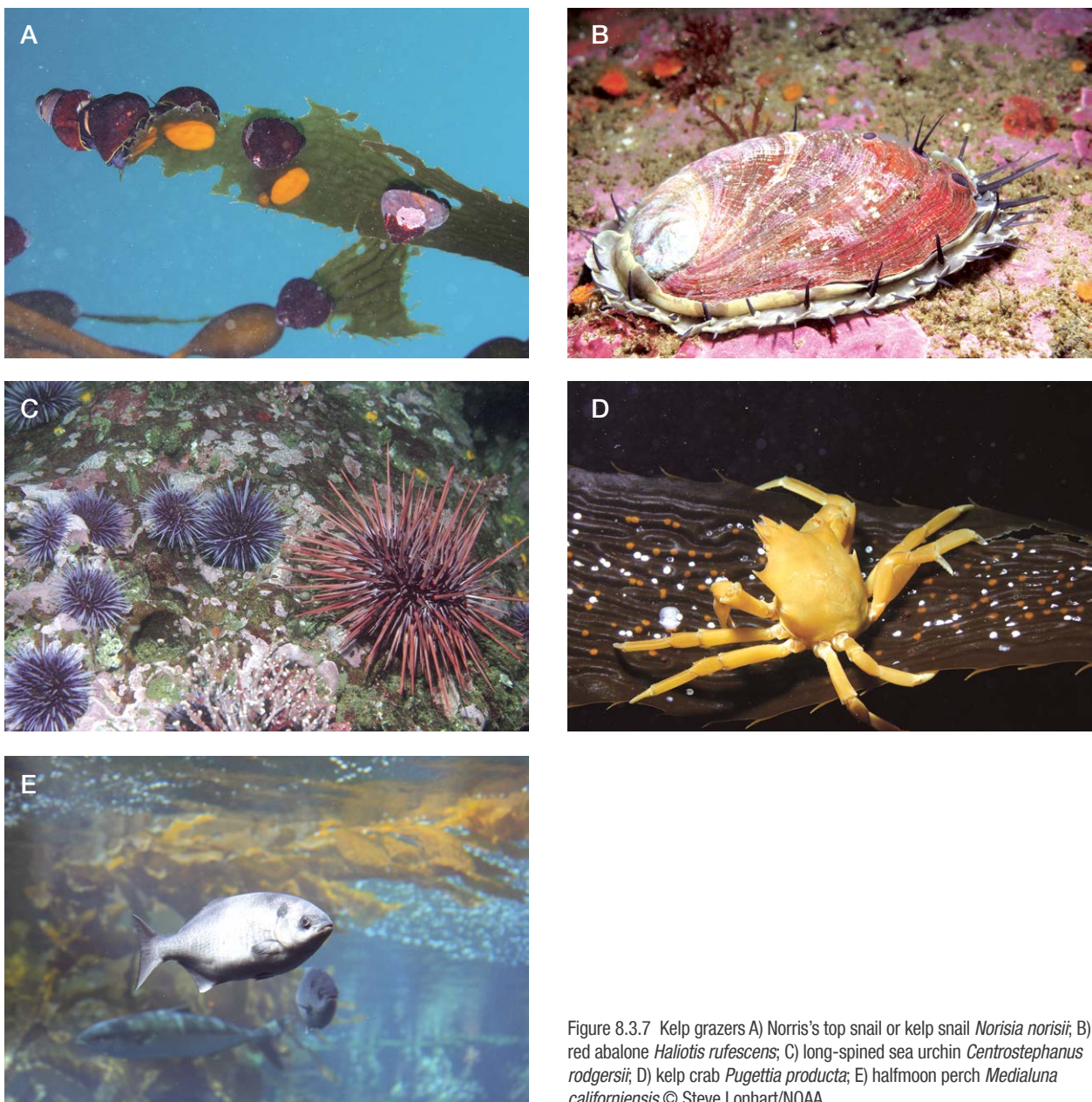
Figure 8.3.7 Kelp grazers A) Norris's top snail or kelp snail *Norisia norisii*; B) red abalone *Haliotis rufescens*; C) long-spined sea urchin *Centrostephanus rodgersii*; D) kelp crab *Pugettia producta*; E) halfmoon perch *Medialuna californiensis* © Steve Lonhart/NOAA.
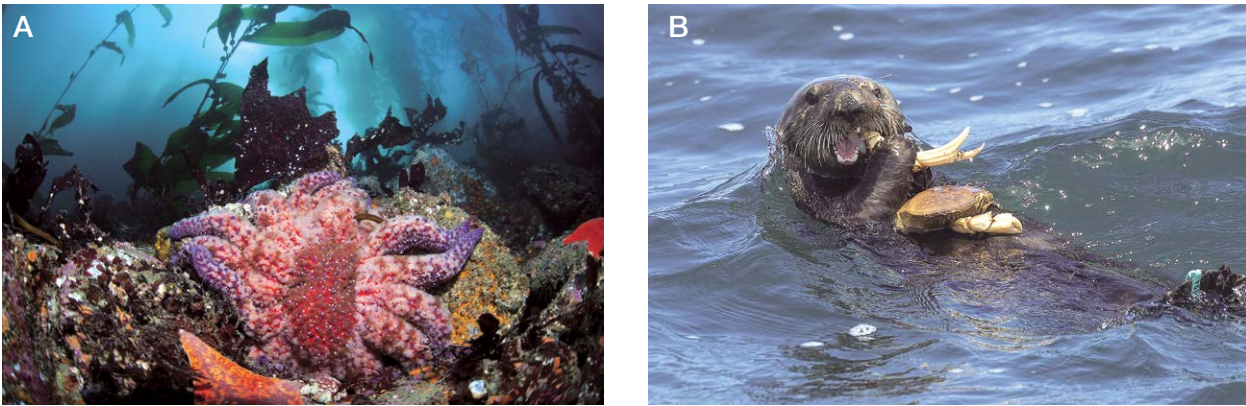
Figure 8.3.8 Kelp grazer predators A) sun star © Ethan Daniels; B) sea otter *Enhytra lutris* © Chase Dekker.

empirical evidence suggests that their structure and function is dictated primarily by top-down forces rather than bottom-up control (Halpern et al., 2006). Consumers structure kelp forest interactions via two primary 'drivers': herbivory by grazers and carnivory by predators of grazers. Kelp grazers span multiple taxa, including echinoderms (sea urchins), gastropods (snails, abalone), crustaceans (kelp crabs, amphipods, isopods), and herbivorous fish (Graham et al., 2008) (Figure 8.3.7). Predators of these grazers are also taxonomically diverse, including carnivorous crustaceans such as crabs and lobsters, echinoderms like predatory sea stars, invertivorous fish, and air-breathing mammals like sea otters (Figure 8.3.8). Sea urchins are particularly known for their ability to overgraze kelp forests and bring about ecosystem state shifts that produce 'urchin barrens' (Ling et al., 2015). The loss of predator control on sea urchin populations has led to well-documented trophic cascades in kelp forests (Estes et al., 1998). Other grazers such as gastropods may also have strong impacts on kelp populations, especially at the juvenile stages (Dayton et al., 1984; Henriquez et al., 2011; Sala & Graham, 2002) and the potential indirect effects of their predators on juvenile kelp are unknown.

Few published studies have examined how kelp forest organisms respond to low DO. Those that do exist, together with evidence from other ecosystems, suggest that changes in foraging, feeding, and movement are likely sublethal responses for many organisms (e.g. Eby & Crowder, 2002; Low & Micheli, 2018). Thresholds for these sublethal responses vary across taxa, with cnidarians among the most tolerant and crustaceans and fish being the most sensitive (Vaquer-Sunyer & Duarte, 2008). Air-breathing predators like sea otters will not experience any direct impacts from hypoxia. Mobile organisms may be able to avoid hypoxic areas, leading to the concentration of animals in habitat

refuges (Craig, 2012; Eby & Crowder, 2002), and impacts on density-dependent processes (Vanderploeg et al., 2009). Avoidance strategies may be dictated by the trade-offs between oxygen stress and other factors like predation risk and food availability (Craig, 2012; Vaquer-Sunyer & Duarte, 2008). For example, benthic fishes have been reported to move towards near-surface waters to breathe when bottom waters become hypoxic (Wu, 2002) while other fishes and crustaceans move to shallow waters (Bell, 2003). Such behavioural responses, in conjunction with decreased sensory abilities (Domenici et al., 2013), may increase the vulnerability of mobile taxa to natural predators and fishing effort (Domenici et al., 2007; Prince et al., 2010). Furthermore, kelp fauna across a wide variety of taxa may exhibit reduced feeding, growth, and reproductive processes under hypoxia (e.g. Kim et al., 2013; Low & Micheli, 2018; McNatt & Rice, 2004; Siikavuopio et al., 2007; Wu, 2009). Finally, micro-organisms involved in kelp and macroalgae decomposition, including bacteria and fungi, are also likely to be differentially affected by hypoxic conditions, but to our knowledge no studies have examined how kelp decomposition rates and nutrient regeneration may be influenced by hypoxia.

Although upwelling-driven hypoxia in kelp forests generally occurs together with exposure to low pH, even fewer studies have addressed how kelp fauna respond to these multiple stressors. Existing studies suggest that the co-occurrence of low DO and low pH is most likely to have negative synergistic impacts (Kim et al., 2013; Steckbauer et al., 2015), and much more work in this area is needed.

8.3.5 Ecosystem impacts

Due to human-mediated impacts upon their physical or biological components, many kelp forests today look

and behave differently from their historical counterparts (Steneck et al., 2002). Trophic cascades resulting from the local extirpation of the large predators are well-documented (Estes et al., 1989; Steneck, 1998). Complex interactions and non-linear thresholds (Tegner et al., 1996) complicate efforts to predict how kelp forests will respond to ocean deoxygenation, but global case studies confirm the existence of "tipping points" beyond which these systems will reorganize (Ling et al., 2015; Selkoe et al., 2015; Steneck et al., 2002)

The responses of kelp forest organisms to hypoxia will likely alter trophic interactions and energy flow in kelp forest food webs. Differences in vulnerability between grazers and predators may strengthen or weaken trophic cascades and top-down control on kelp populations (Menge & Olson, 1990; Menge & Sutherland, 1987). Effects are likely to be most severe in ecosystems where air-breathing marine mammal predators such as sea otters are absent and coastal food webs have been fished down. In regions where predation on sea urchins is driven by crustaceans and large fish, hypoxia may increase grazing and deforestation if predator species are excluded by the persistence of low oxygen waters and/or a decline in the availability of alternative prey species.

Community-wide impacts of periodic hypoxic events in other ecosystems include reduced community biomass and species richness (Dauer, 1993; Nilsson & Rosenberg, 1994). In kelp forests, this relationship is particularly troubling as diversity may buffer against phase shifts and facilitate recovery from physical disturbance. Kelp forest systems with functional redundancy among predators and herbivores are thought to be comparatively resilient while decreased diversity may amplify the effects of species interactions and accelerate the transition to alternative stable states (Steneck et al., 2002). If environmental and anthropogenic drivers reduce biodiversity in kelp forests, these systems may be more susceptible to invasion from non-native species (Stachowicz et al., 1999). Where limited diversity has simplified trophic interactions and community structure (Steinberg et al., 1995), deforestation has been linked to the range expansion of tropical, herbivorous fish (Vergés et al., 2016) and the proliferation of non-native algae and encrusting bryozoans (Levin et al., 2002). The role of disease in structuring the interaction between grazers and kelp may also be impacted by increases in the frequency and duration of low oxygen events. Hypoxic conditions create physiological stress that can

increase an organism's susceptibility to disease (Harvell et al., 1999) and the proliferation of species resilient to environmental stressors like hypoxia can set the stage for disease-related mass mortalities. Though disease outbreaks amongst grazer populations can facilitate the expansion of kelp forests (Lafferty, 2004; Pearse & Hines, 1979; Scheibling et al., 1999), when organisms associated with control and regulation of herbivore (i.e. sea star) populations are affected, destructive grazing and deforestation may increase (Schultz et al., 2016; Tegner & Dayton, 1987).

8.3.6 Conclusions

The substantial spatio-temporal variability in oxygen and pH within kelp forests poses a key challenge for our understanding of impacts and for management. Given the high natural variability they experience, kelp forest organisms may be pre-adapted to tolerate the low-oxygen, acidic conditions expected under climate change (Booth et al., 2012). But the low oxygen and pH conditions these organisms experience might also be close to their physiological limits. In this case, climate change may push these organisms over a tipping point as these periodic exposures become more prolonged or extreme. Most studies on organism responses to hypoxia have used extended, constant exposures, which may not be a good representation of the patchy, repeated and periodic low-DO exposures that kelp forest organisms experience. In addition, managers often use single, static thresholds for assessing oxygen conditions, which may not be appropriate for an ecosystem with naturally high oxygen variability. This supports the need for studies that specifically address the effects of spatial and temporal variability of hypoxic conditions and how patterns of exposure may interact with other environmental stressors to impact macroalgae and associated fauna.

Acknowledgements

8.3.7 References

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