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Effects of Ocean Warming and Acidification on Rhodolith/Maerl Beds

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Chapter 4: Effects of ocean warming and acidification on rhodolith/maerl beds

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Ocean warming and acidification are currently under scrutiny since in combination they are expected to reduce marine biodiversity and profoundly alter ecosystem function. Habitats where coralline algae play an important ecological role, such as rhodolith and maerl beds, are threatened by dissolution due to the high solubility of their high-magnesium calcite skeletons. Those in the Arctic, where carbonate saturation levels are already low and falling, are of particular concern. As well as direct corrosive effects on coralline algae, rising CO_2 emissions are expected to have knock-on effects on ecosystems because reduced seabed habitat complexity causes a reduction in biodiversity and simplifies food webs. We anticipate that degradation of coastal calcareous habitats due to ocean acidification will facilitate a proliferation of fleshy algae that may benefit from an increase in dissolved inorganic carbon, to the detriment of calcified algae. It is not all doom and gloom: coralline algae have survived previous mass extinctions and many species tolerate highly variable CO_2 levels. Which species survive the Anthropocene will depend upon their ability to acclimate and adapt. These topics warrant further research since coralline algae provide highly biodiverse habitats that benefit commercially important species of fish and molluscs. Data so far suggest that 1) this important algal group is especially vulnerable to ocean acidification and warming and 2) protecting these habitats has long-term benefits, not least because coralline algae provide habitat for species of commercial importance.

4.1 Climate change and ocean acidification

Anthropogenic emissions have increased the atmospheric carbon dioxide (CO_2) concentration from 280 ppm prior to the beginning of the industrial revolution (1750) to more than 390 ppm in 2013; this is *ca*. 100 ppm higher than at any time in the past 740,000 years. The present rate of increase in atmospheric CO_2 and temperature is unprecedented in recent Earth history (Hoegh-Guldberg et al. 2007).

Approximately 25 % of CO_2 emissions dissolve into the ocean, increasing pCO_2 in the surface water and altering seawater carbonate chemistry (Canadell et al. 2007). This CO_2 reacts with the water to form carbonic acid most of which dissociates into ions of hydrogen (H^+) and bicarbonate (CO_3^{2-}) (Fig. 1). The increased concentration of H^+ reduces pH ($pH = -\log_{10}[H^+]$) and carbonate ion (CO_3^{2-}) concentration and increases the concentration of HCO_3^-.

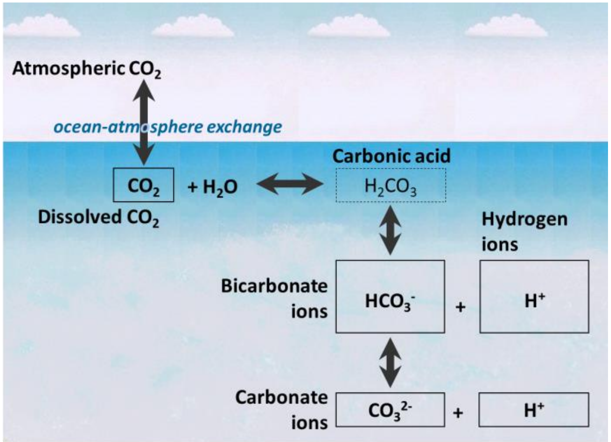

Fig. 1. Equilibrium between the three different species of dissolved inorganic carbon in seawater. Atmospheric CO_2 is absorbed at the surface of the oceans where it combines with the water molecules to form carbonic acid, which dissociates into bicarbonate, carbonate, and hydrogen ions. Different forms of dissolved inorganic carbon (DIC = $[CO_2] + [HCO_3^-] + [CO_3^{2-}]$) follow thermodynamic equilibria in seawater for the following reactions: $CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO_3^- \leftrightarrow H^+ + CO_3^{2-} + 2H^+$.

During the 20th century, increasing atmospheric CO_2 caused the surface ocean to warm by 0.7°C and to acidify by 0.1 pH units (Hoegh-Guldberg et al. 2007). The atmospheric CO_2 concentration is expected to reach between 490 - 1370 ppm by 2100 causing a global mean surface temperature increase of between 0.3 to 4.8°C and a surface ocean pH decrease of 0.06-0.32 units relative to the period 1986-2005 (IPCC 2013; Fig. 2). Ocean acidification and warming will not be regionally uniform; marine organisms in the Arctic region are thought to face more rapid and stronger warming and acidification than the global mean (Fig. 3).

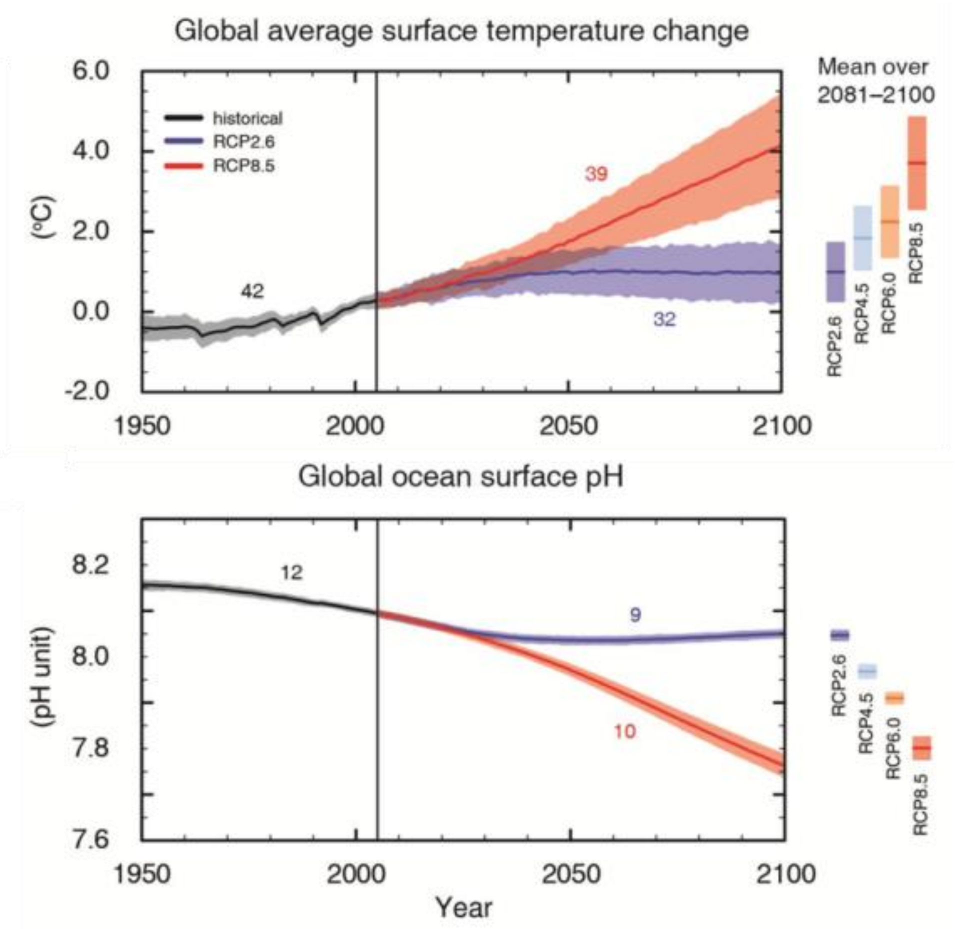

Fig. 2. Projected change in global annual mean surface temperature and global mean ocean surface pH, relative to 1986-2005 for Representative Concentration Pathway 2.6 (blue) and RCP8.5 (red) (Source: IPCC 2013).

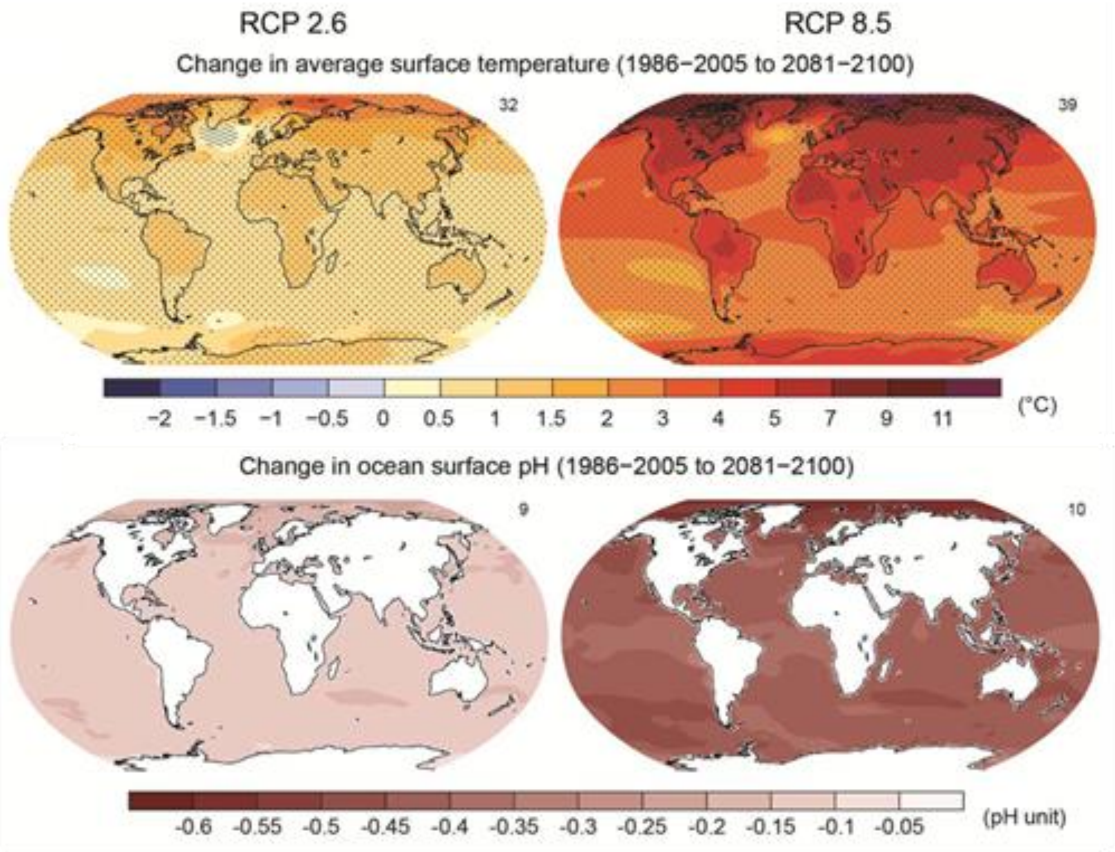

Fig. 3. Annual mean temperature and pH changes for the scenarios RCP2.6 and RCP8.5 in 2081-2100 relative to 1986-2005 (Source: IPCC 2013).

4.2 Effects of ocean warming and acidification on seaweeds

Global warming and ocean acidification will alter biochemical and physiological processes in seaweeds, causing changes in their ecological interactions (Koch et al. 2012, Harley et al. 2012). Here we base predictions about the fate of rhodolith/maerl beds upon a growing body of information about the effects of warming and acidification on seaweeds in general and on coralline algae in particular. While some seaweed taxa seem likely to benefit from ocean warming and acidification, coralline algae are expected to be adversely impacted, putting the habitats they form at risk. This is a concern since beds of rhodoliths and maerl form highly biodiverse but very slow-growing habitats (Pena et al. 2014).

4.2.1 Effects of ocean warming on seaweeds

Temperature directly affects enzymatic processes and so alters rates of photosynthesis and growth; it also determines whether seaweeds can survive and reproduce and sets limits to their geographic distribution (Lüning 1990). Seaweeds, as with other organisms, have thermal performance curves that show beneficial effects of increased temperature at suboptimal temperature but detrimental effects above a threshold (Lüning 1990). In order for some individual species of seaweed to survive rising sea surface temperature they will need to acclimate (on short timescales), adapt (on medium and long timescales) or migrate (by dispersion) (Wiencke & Bischof 2012). Seaweeds that are intertidal or have a broad biogeographic range are more tolerant of temperature extremes than subtidal species and those with narrower temperature ranges. The changes in temperature we see today are driving a poleward shift in seaweed biogeographical regions (Wernberg et al. 2011). The tropical region is widening polewards, to the detriment of organisms that occupy warm-temperate regions and the cold-temperate regions are shrinking. Arctic seaweeds are at particular risk due to warming winter temperatures (Wiencke & Bischof 2012). In coralline algae, a small rise in temperature, within the range of temperature experienced in natural habitats, can increase growth, photosynthesis and calcification in both temperate and tropical species (Martin et al. 2006, Steller et al. 2007) but this has limits and rising temperature above these levels is detrimental (Table 1). For example, Agegian (1985) showed that growth of tropical *Porolithon gardineri* slowed dramatically at temperatures above 29-30°C. An increase of +3°C above that normally experienced by coralline algae causes bleaching and adversely affects health, survival, and the rates of photosynthesis and calcification in both tropical and warm-temperate coralline algae (Anthony et al. 2008, Martin & Gattuso 2009, Diaz-Pulido et al. 2011, Martin et al. 2013; Table 1).

4.2.2 Impact of ocean acidification on seaweeds

Decreasing pH in the surface ocean will cause major shifts in seawater chemistry over the course of this century that are likely to affect photosynthesis and calcification since these processes use dissolved inorganic carbon (DIC: HCO_3^-, CO_3^{2-} and CO_2) as substrate

(1) Photosynthesis (left to right) and respiration (right to left) processes:

$$CO_2 + H_2O \leftrightarrow CH_2O + O_2$$

$$HCO_3^- + H_2O \leftrightarrow CH_2O + O_2 + OH^-$$

(2) Gross calcification (left to right) and dissolution (right to left) processes:

$$CO_3^{2-} + Ca^{2+} \leftrightarrow CaCO_3$$

$$2\ HCO_3^- + Ca^{2+} \leftrightarrow CaCO_3 + H_2O + CO_2$$

Algae can use dissolved CO_2 entering the cell by diffusion as the carbon source for photosynthesis but most of them have carbon concentrating mechanisms which actively take up HCO_3^- which is then converted to CO_2 in the cells (Raven et al. 2002, Hepburn et al. 2011, Cornwall et al. 2012). This mechanism counteracts the limited availability of CO_2 in seawater (Raven & Beardall 2003). An increase in seawater pCO_2 is expected to enhance photosynthesis in primary producers that rely exclusively on CO_2 diffusion (Kübler et al. 1991) and may be favourable to algae that can down-regulate their carbon concentrating mechanisms to save energy (Hepburn et al. 2011, Cornwall et al. 2012, Raven et al. 2012).

Coralline algae are thought to be one of the groups of species most vulnerable to ocean acidification due to the solubility of their high magnesium-calcite skeletons. Ocean acidification is causing a decrease in the saturation state of calcium carbonate ($\Omega = [Ca^{2+}] \times [CO_3^{2-}] / K_{sp}$) which is likely to affect the ability of marine calcifiers to form their carbonate skeleton or shells by a decline in calcification rates (Kroeker et al. 2010). Although the physiological response in terms of calcification is variable among taxa and species (Ries et al. 2009), seawater acidification is related to reduced growth rates in calcified macroalgae (Kroeker et al. 2013).The recruitment and growth of coralline algae are usually negatively affected under elevated pCO_2 (Table 1). Reductions in calcification rate at elevated pCO_2 have been demonstrated for most coralline algae (Harley et al. 2012) but this response is variable among species (Fig. 4, Table 1).

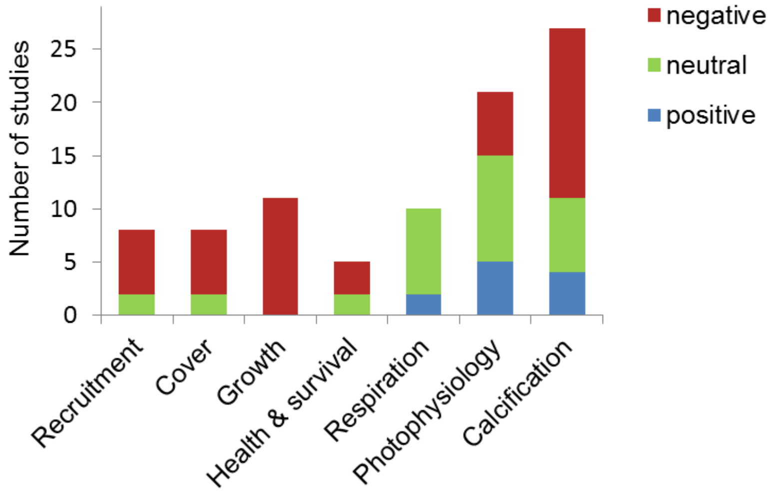

Fig. 4. Summary of the expected direct effects of ocean acidification on coralline algae this century (based on studies in Table 1). Negative, neutral and positive effects correspond to decreases, no change, and increases in the processes, respectively. Photophysiology includes both photosynthesis and photosystem II efficiency and relative electron transport rate.

4.2.3 Interactive effects of ocean warming and acidification on seaweeds

While the effects of climate change and ocean acidification on seaweeds have mostly been studied in isolation from each other, there is a lack of studies how these factors interact. The combination of these two factors could however have a larger impact than alone. Recent studies have effectively shown that the negative effect of ocean acidification on coralline algal calcification is exacerbated by further ocean warming (Anthony et al. 2008). Some authors reported a significant pCO_2 effect on coralline calcification, health and survival only in combination with increased temperature, suggesting that elevated pCO_2 aggravates the sensitivity of coralline algae to temperature (Martin & Gattuso 2009).

4.2.4 Physiological response of coralline algae to climate change and ocean acidification

Photosynthesis, respiration, and calcification in coralline algae are usually determined from measurements of oxygen, DIC and alkalinity in incubation chambers (Fig. 5). Most of these studies show that coralline algal calcification is negatively affected under elevated pCO_2 (Table 1) and that this effect is exacerbated by warming (Anthony et al. 2008). However, some work only shows a significant pCO_2 effect on calcification when this is combined with an increase in temperature (Martin & Gattuso 2009) and some experiments have shown a positive effect of moderate increases in pCO_2 (Smith & Roth, 1979, Ries et al. 2009, Martin et al. 2013, Kamenos et al. 2013). Such responses may be related to the ability of the algae to maintain an elevated pH at the site of calcification despite reduced external pH to facilitate $CaCO_3$ precipitation (Borowitzka 1987, Ries et al. 2009, Hurd et al. 2011, Cornwall et al. 2013b).

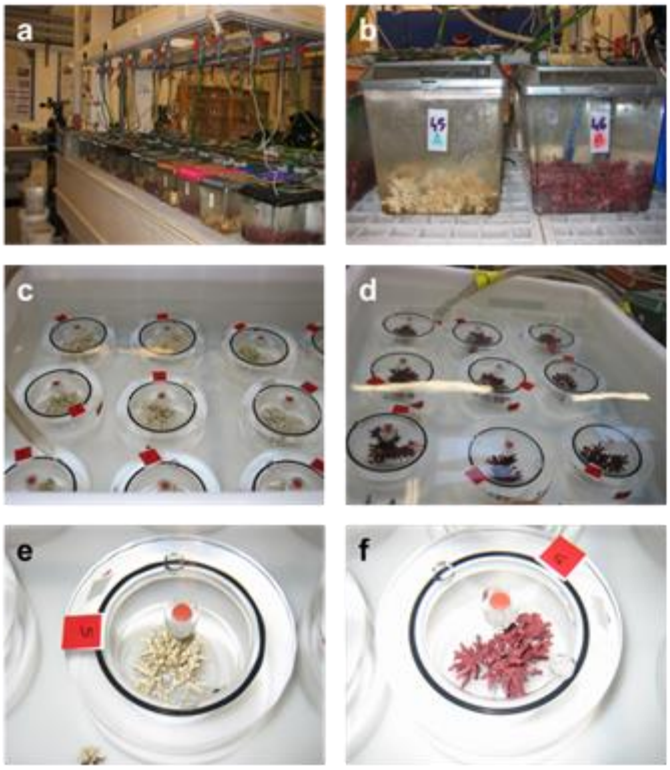

Fig. 5. Experimental set-up (a) with replicated aquaria (b) supplied with seawater at ambient or elevated *p*CO_2 containing alive or dead *Lithothamnion glaciale* maerl that were incubated in Perspex chambers for metabolic fluxes analyses (c,e, dead maerl and d,f, live). Photograph by Sophie Martin (Experiments performed at Plymouth Marine Laboratory).

The response of coralline photosynthesis to increased *p*CO_2 is also variable among species with negative, neutral, positive and parabolic responses (Table 1) that can depend on the light levels used (Martin et al. 2013). Studies investigating the effect of increased *p*CO_2 on respiration showed no response for most species (Fig. 4). Very few studies of coralline algae have investigated photosynthesis, respiration, and calcification all together yet we know that these processes are complex and tightly linked. Photosynthesis affects calcification through the formation of the fibrous organic matrix of the cell walls where the nucleation of calcite crystals is thought to occur (Borowitska, 1981). In addition, both photosynthesis and respiration affect calcification through changes in pH that occur in the cell walls at the site of calcification (Smith & Roth 1979, Gao et al. 1993) but also in the diffusion boundary layer between the algal surface and external seawater (Hurd et al. 2011). Photosynthesis (or respiration) increases (or decreases) pH and thereby increases (or decreases) $CaCO_3$ saturation state, promoting (or hindering) the precipitation of $CaCO_3$. Coralline algae are able to maintain calcification in the dark even at the relatively low pH values generated by respiration. Digby (1977) and Hofmann et al. (2012b) postulate that carbonic anhydrase may also play a role in the calcification of coralline algae by catalysing the conversion of CO_2 into HCO_3^- and then CO_3^{2-}. The stimulation of carbonic anhydrase activity could help prevent a decrease in calcification at elevated *p*CO_2 as reported for the Mediterranean crustose coralline alga *Lithophyllum cabiochae* (Martin et al. 2013). However, carbonic anhydrase is also used by photosynthesis to convert HCO_3^- to CO_2. The maintenance or enhancement of calcification rates under elevated *p*CO_2 in *L. cabiochae* may thus be detrimental to photosynthesis, as indicated by reduced photosynthesis under elevated *p*CO_2 (Martin et al. 2013).

The physiological response of maerl to warming and ocean acidification has been investigated in *Lithothamnion corallioides* which is a temperate species (Noisette et al. 2013b) and *Lithothamnion glaciale* which is a cold-water species (Büdenbender et al. 2011, Kamenos et al. 2013). In *L. corallioides* diel (24h) calcification decreased by 50% at 750 µatm and 80% at 1000 µatm, and in *L. glaciale* the thalli dissolve under elevated pCO_2 (Büdenbender et al. 2011). Kamenos et al. (2013) found that at night *L. glaciale* calcified in the control treatment but dissolved in the low pH treatment. In both species calcification is less affected by pCO_2 in the light that in the dark, although in *L. glaciale* upregulated calcification occurs at low pH cf. control treatments during the day (Noisette et al. 2013b, Kamenos et al. 2013). High latitude maerl beds are at risk as surface waters are becoming more corrosive which is expected to cause dissolution of these habitats (Büdenbender et al. 2011). Tropical rhodolith beds may also be affected since in multispecies rhodoliths, made up of *Lithophyllum*, *Hydrolithon* and *Porolithon* spp., there is a decrease calcification by 20-250% between control and acidified conditions (Jokiel et al. 2008, Semesi et al. 2009).

4.2.5 Response of early life stages to ocean acidification and warming

Although fragmentation is the main source of new thalli in beds of rhodoliths and maerl, they are initiated through recruitment from spores (Foster 2001). Unfortunately, there is mounting evidence that ocean acidification and warming will have negative impacts upon the recruitment and growth of early life history stages of coralline algae (Agegian 1985, Jokiel et al. 2008, Kuffner et al. 2008, Russell et al. 2009, Porzio et al. 2013, Bradassi et al. 2013; Table 1). Kuffner et al. (2008) found that impacts on settlement led to 90% lower tropical crustose coralline cover at pH 7.9 than at pH 8.2. Some coralline algal species show a reduction in reproductive structures in areas with naturally high pCO_2 conditions (Porzio et al. 2011) and germination of spores in the laboratory reveal developmental abnormalities and increased mortality in acidified conditions. Bradassi et al. (2013) found that in acidified conditions the germlings of an intertidal species of coralline algae were able to fight dissolution by up-regulating their rates of calcification; this must increase energy costs and helps explain why coralline algae are replaced by fleshy algae in naturally high pCO_2 conditions (Hall-Spencer et al. 2008, Porzio et al. 2013).

4.2.6 Ecosystem level responses

Most research into the effects of ocean warming and acidification has involved relatively short-term (1 year or less) experiments on single species which makes it difficult to scale-up and predict long-term effects at the community and ecosystem levels (Russell et al. 2013). To tackle this, areas with naturally high CO_2 (and/or low pH and low calcium carbonate saturation states) are being used to investigate which organisms can tolerate the long-term consequences of ocean acidification and reveal how communities of primary producers respond (Hall-Spencer et al. 2008, Johnson et al. 2012, Inoue et al. 2013). As with laboratory and mesocosm experiments, the vent systems cannot accurately mimic future ocean conditions; acidified areas are open systems so corallines can recruit from unaffected habitats and grazing fish can swim in and out, these systems typically have large variations in carbonate chemistry, and in some cases there are confounding factors that may mask or amplify the effects of CO_2. Some efforts have been made to determine the combined effects of warming and acidification at such sites, although such work has so far been restricted to corals, molluscs and bryozoans (Rodolfo-Metalpa et al. 2011). Some volcanic vents are proving to be particularly useful 'natural laboratories' for the study of ocean acidification as they reveal tipping points in recruitment, growth, survival and species interactions along pCO_2 gradients (Porzio et al. 2011, 2013). Many species of microalgae, macroalgae and seagrasses are remarkably tolerant of long-term exposures to high and variable carbon dioxide levels at tropical and temperate CO_2 seeps (Johnson et al. 2012, 2013, Russell et al. 2013). That they tolerate these conditions does not mean that they will necessarily thrive; seagrasses for example lose the ability to defend themselves against herbivores and become over-run by competing species of invasive seaweeds (Arnold et al. 2012).

One clear pattern in studies at multiple natural CO_2 gradients is that the Corallinales are adversely affected (Porzio et al. 2011, Fabricius et al. 2011) which is a particular concern since this group of organisms underpin maerl, rhodolith habitat production (Hall-Spencer et al. 2010). At Mediterranean CO_2 seeps the Corallinales dissolve at low carbonate saturation states (Martin et al. 2008) and are outcompeted by heterokont algae as CO_2 levels increase (Fig. 6). Epilithic diatoms, Dictyotales (e.g. *Dictyota* spp., *Padina* spp.) and Fucales (e.g. *Cystoseira* spp., *Sargassum* sp.) thrive as CO_2 levels increase although *Padina* spp. loose calcification (Porzio et al. 2011, 2013, Johnson et al. 2012). At the ecosystem level the coralligenous habitats loose biodiversity as carbonate levels fall along transects of increasing levels of CO_2; benthic recruitment is disrupted in calcified organisms (Cigliano et al. 2010); some organisms such as soft corals and anemones are tolerant but many are physiologically unable to cope with the increased CO_2 levels (Suggett et al. 2012, Calosi et al. 2013, Inoue et al. 2013). Reefs formed by an association between coralline algae and vermetid molluscs are expected to become extinct this century unless CO_2 emissions are reduces and emergency conservation measures are taken (Milazzo et al. 2014).

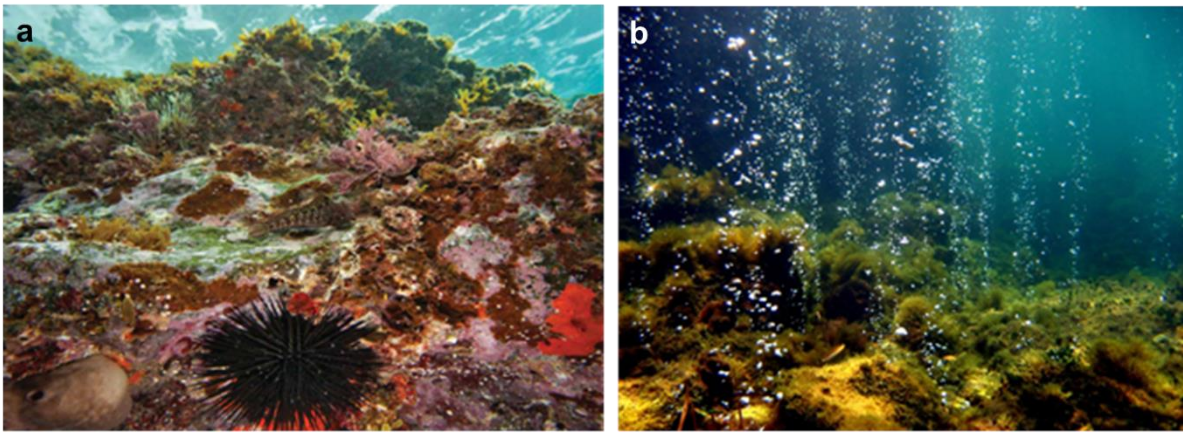

Fig. 6. Sea urchin and coralline algae dominated rocky shore at (a) ambient CO_2 (photograph by David Liittschwager, National Geographic) and (b) the loss of coralline algae and proliferation of diatoms and phaeophytes at a CO_2 seep off Ischia, Italy (photograph by Luca Tiberti, Associazione Nemo).

Additional insights into the community-level effects of warming and ocean acidification are beginning to come from longer-term multispecies laboratory experiments (Hale et al. 2011). These also demonstrate that future increases in CO_2 are likely to have strong negative effects on coralline algae and positive or neutral effects on noncalcified seaweeds both directly via improved growth and indirectly via reduced consumption by calcified herbivores such as sea urchins (Connell & Russell 2010, Diaz-Pulido et al. 2011, Cornwall et al. 2012, Olischläger et al. 2012, Roleda et al. 2012, Olabarria et al. 2013). It is clear that the impact of climate change and ocean acidification on rhodolith/maerl beds will depend on the combined influence of direct environmental impacts on individual species and indirect effects mediated by changes in interspecific interactions (Harley et al. 2012). For example, ocean acidification may disrupt invertebrate recruitment to maerl/rhodolith beds by altering chemical settlement cues associated with crustose coralline algae, as shown with coral recruits (Doropoulos & Diaz-Pulido 2013).

Ocean warming and acidification degrade the habitat complexity of coralline algal sediments with profound effects since these algae induce settlement and recruitment of numerous invertebrates. The rapid rate of physicochemical change is predicted to cause a shift from calcareous to fleshy algal-dominated coastal ecosystems (Hall Spencer et al. 2008, Hoegh-Guldberg et al. 2007, Anthony et al. 2011, Diaz-Pulido et al. 2011). Given that rhodolith/maerl habitats usually only form in waters that have high carbonate saturation states, the spread of low saturation state waters in upwelling areas, lowered salinity water masses and in polar waters, are likely to reduce their habitat complexity and thus cause biodiversity loss. Beds of unattached coralline algae provide nursery grounds and habitat for numerous commercial species of invertebrates and fishes (Kamenos et al. 2004a,b) so a decline in these habitats due to dissolution is also likely to have serious consequences for society and economy through the impact on fisheries.

4.2.7 Impact on global C and $CaCO_3$ budget

Rhodolith/maerl beds are a significant component of carbon and carbonate cycles in shallow coastal ecosystems, being major contributors to CO_2 fluxes through high community photosynthesis and respiration (Martin et al. 2005, 2007) and through high $CaCO_3$ production and dissolution (Martin et al. 2006, 2007). The habitats formed by coralline algae are expected to be degraded by ocean acidification and warming as they have slow growth rates and are easily corroded due to their soluble high Mg-calcite skeletons. Any major decline in coralline algae would have dramatic consequences since they cover vast areas of rock and can form very extensive beds on sediments (Amado-Filho et al. 2012). Changes in the balance between algal carbonate production and dissolution induced by elevated pCO_2 and temperature in maerl and rhodolith beds may have major implications for carbon dynamics in coastal systems by affecting the carbonate chemistry of the water column and the ability of the oceans to take up atmospheric CO_2 (Andersson et al. 2005).

In temperate maerl beds, *L. corallioides* calcification is expected to decrease by up to 80% at 1000 µatm pCO_2, relative to present day conditions of pCO_2 (Noisette et al. 2013b). This would cause a reduction in $CaCO_3$ precipitation from a current value of *ca*. 500 g $CaCO_3$ m^{-2} y^{-1} (Martin et al. 2007) to less than 100 g $CaCO_3$ m^{-2} y^{-1} in the near future under 1000 µatm pCO_2 (Noisette et al. 2013b). The net calcification in maerl/rhodolith beds could even become negative because the production of $CaCO_3$ will be exceeded by its dissolution (Martin & Gattuso 2009). Arctic maerl beds are at particular at risk due to seawater becoming corrosive to algal carbonate since live specimens of polar *L. glaciale* are corroded under elevated pCO_2 (Büdenbender et al. 2011). Dissolution also occurs in the dark in live maerl under elevated pCO_2 in temperate maerl species (Noisette et al. 2013b; Kamenos et al. 2013). As maerl beds are also composed of dead thalli, dissolution is likely to strongly increase; dissolution of dead *L. glaciale* thalli increases by more than 10 fold from ambient condition to elevated pCO_2 of *ca*. 1100 µatm (Kamenos et al. 2013). Precipitation and dissolution of $CaCO_3$ contribute to the global CO_2 balance through shifts in the seawater carbonate equilibrium. The precipitation of one mole of $CaCO_3$ ($Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 + H_2O + CO_2$) releases *ca*. 0.6 moles of CO_2 in seawater (Ware et al. 1992). In that way, the CO_2 released by calcification in maerl/rhodolith beds will also be reduced. These changes will thus have major implications for both carbon and carbonate budgets in coastal systems.

4.2.8 Acclimation and adaptation

The coralline fossil record for the past 300 Million years shows they have been able to survive past mass extinctions including periods of very high CO_2 (Wood 1999). However, the present rate of ocean change may be too rapid for genetic adaptation of habitat-forming coralline algae. Work at CO_2 vents that are 100s of years old indicates that corallines have a limited capacity to acclimate to ocean acidification, since most species are intolerant of chronic exposures to increases in pCO_2 levels predicted this century and those that can survive are outcompeted by fleshy algae (Martin et al. 2008, Porzio et al. 2011, Fabricius et al. 2012). Localised seeps with high CO_2 levels are not well suited to the study of coralline algal adaptation since they are open to colonization by algal spores from outside the acidified areas and so presently we have no knowledge about the ability of rhodolith/maerl species to adapt to present day rates of warming and acidification. We find it striking, however, that rhodolith/maerl beds are common along the Atlantic seaboard of the Americas, where carbonate saturation states are high, but they are scarce along the Pacific seaboard where carbonate saturation states are low.

Adaptation is the evolutionary response of a population over multiple generations to environmental changes but, according the current magnitude and rate of ocean warming and acidification, the potential for evolutionary adaptation is limited in organisms with long generation times such as coralline algae. However, coralline algae may have the potential to adjust to modified environment within their lifetime (acclimation). In particular, the ability of organisms to tolerate significant temperature and/or pCO_2 fluctuations may be a result of adaptation (a genetic trait shared by the population) and/or acclimation (owing to phenotypic plasticity of the individual). Organisms surviving in highly variable environments are likely to be more robust. For instance, Egilsdottir et al. (2013) reported that coralline algae inhabiting variable environments where pH/pCO_2 fluctuates naturally are likely to exhibit fewer negative responses to elevated pCO_2 than those inhabiting relatively stable environments, supporting the assumption of a greater resilience of organisms acclimated and/or adapted to highly variable pH/pCO_2 environments of future ocean acidification.

Coralline algae may be able to tolerate ocean acidification through changes in the composition of their skeletons (Agegian 1985, Ries et al. 2009, Egilsdottir et al. 2013). A decrease in mMg/Ca ratio would confer resilience to elevated pCO_2 as this would lower the solubility of their skeletons. However, it is questionable whether mineralogical plasticity associated with a decrease in Mg incorporation will help since warming simultaneously increases Mg incorporation (Agegian 1985). Dolomite ($MgCO_3$) rich crustose coralline algae have 6- to 10-fold lower rates of dissolution than predominantly Mg-calcite species (Nash et al. 2013). Dolomite-rich crustose coralline algae are widespread in shallow wave-exposed habitats in the tropics but have not been recorded in cooler waters suggesting that its formation may be constrained by temperature. Thus dolomite intracellular calcification may confer an advantage on tropical corallines but not those found at higher latitudes (Nash et al. 2011). It is clear that elevated pCO_2 weakens the skeletal structure in the high latitude maerl species *L. glaciale* (Ragazzola et al. (2012).

Society can also help mitigate adverse effects of warming and acidification. In the NE Atlantic steps have been taken to remove damaging dredging, fishing and aquaculture practices to protect maerl beds in a network of protected areas (Chapter ##). If this approach is adopted world-wide the reduced pressure on coralline algal systems would help increase their resilience to the adverse effects of acidification and warming.

4.3 Conclusions

Beds of unattached coralline algae are scarce in waters with naturally low saturation states of carbonate and are likely to decline in the near future as corrosive waters spread due to ocean acidification. This will lead to a degradation of these ecosystems, reducing habitat complexity and their associated biodiversity. Although responses to ocean warming and acidification are variable among species, beds of maerl and rhodoliths are at risk at high latitudes where seawater is becoming corrosive to their high Mg-calcite skeletons. Loss of both live and dead maerl is expected to spread to lower latitudes over the century. Work on the effects of ocean warming and acidification indicates that certain fleshy algae and non-calcified animals may benefit and outcompete corallines and those calcified animals that characterise these habitats (Fig. 7).

Given the importance of coralline algae, and the scale of the repercussions if they are adversely impacted by rising CO_2 levels, concerted efforts are required to test whether our concerns are justified. More detailed examinations of the physiology/ecology of corallines need to be undertaken as we have an incomplete understanding of how OA and temperature influence gross calcification, growth, dissolution and competitive interactions between seaweeds. Given that society relies upon coralline algae for ecosystems services, such as providing settlement cues or providing habitat for commercially important species, we recommend that biological monitoring programmes begin as soon as possible since changes may be occurring at a rate that will exceed the environmental niches of numerous coralline alga taxa, testing their capacities for acclimation and genetic adaptation.

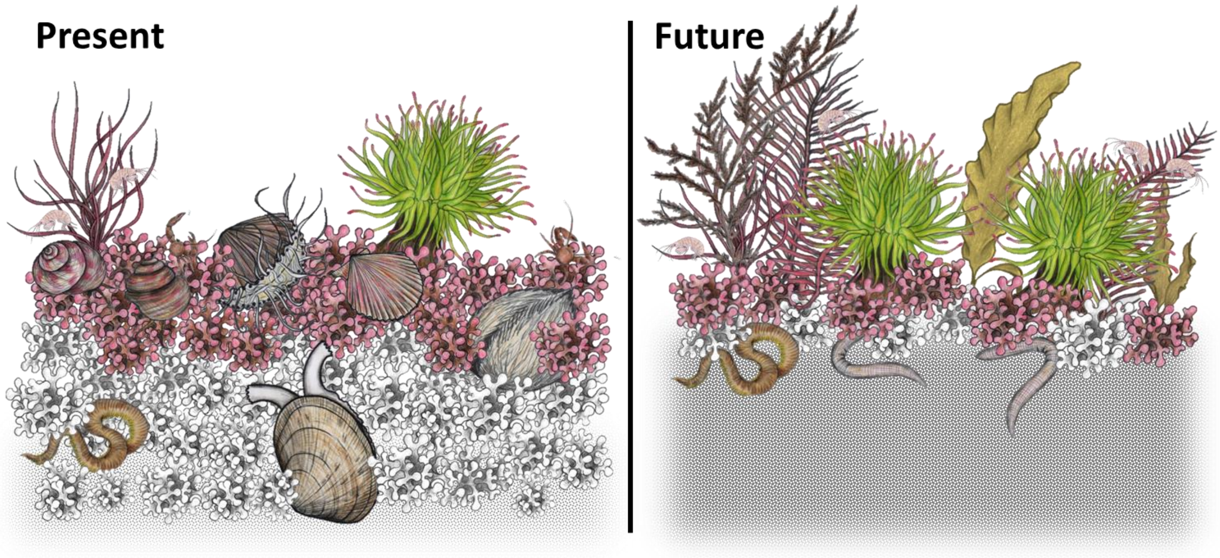

Fig. 7. Predicted changes to a typical maerl bed with rising temperature and CO_2 levels. Present day maerl beds with alive (above) and dead (below) unattached coralline are inhabited by a rich diversity of calcifying (e.g. gastropods, bivalves, decapods, echinoids) and non-calcifying species. As waters become corrosive to carbonate future maerl beds are expected to be degraded, with the loss of habitat complexity and biodiversity, although certain fleshy macroalgae and non-calcified fauna (e.g. anemones, polychaetes, amphipods) are expected to proliferate (drawing by Sophie Martin).

Credits

IPCC 2013: Summary for Policymakers. In Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Figure SPM.7 (a) and (c); Figure SPM.8 (a) and (d). [Cambridge University Press (in press)].

Aknowledgements

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Figure legends

Figure 1. Equilibrium between the three different species of dissolved inorganic carbon in seawater. Atmospheric CO_2 is absorbed at the surface of the oceans where it combines with the water molecules to form carbonic acid, which dissociates into bicarbonate, carbonate, and hydrogen ions. Different forms of dissolved inorganic carbon (DIC = $[CO_2] + [HCO_3^-] + [CO_3^{2-}]$) follow thermodynamic equilibria in seawater for the following reactions: $CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO_3^- \leftrightarrow H^+ + CO_3^{2-} + 2H^+$.

Figure 2. Projected change in global annual mean surface temperature and global mean ocean surface pH, relative to 1986-2005 for Representative Concentration Pathway 2.6 (blue) and RCP8.5 (red) (Source: IPCC 2013).

Figure 3. Annual mean temperature and pH changes for the scenarios RCP2.6 and RCP8.5 in 2081-2100 relative to 1986-2005 (Source: IPCC 2013).

Figure 4. Summary of the expected impacts of ocean acidification on coralline algae this century (based on studies in Table 1).

Figure 5. Experimental set-up (a) with replicated aquaria (b) supplied with seawater at ambient or elevated pCO_2 containing alive or dead *Lithothamnion glaciale* maerl that were incubated in Perspex chambers for metabolic fluxes analyses (c,e, dead maerl and d,f, live). Photo S. Martin (Experiments performed at Plymouth Marine Laboratory).

Figure 6. Sea urchin and coralline algae dominated rocky shore at (a) ambient CO_2 (photograph by David Liittschwager, National Geographic) and (b) the loss of coralline algae

and proliferation of diatoms and phaeophytes at a CO_2 seep off Ischia, Italy (photograph by Luca Tiberti, Associazione Nemo).

Figure 7. Predicted changes to a typical maerl bed with rising temperature and CO2 levels. Present day maerl beds with alive (above) and dead (below) unattached coralline are inhabited by a rich diversity of calcifying (e.g. gastropods, bivalves, heart urchins) and non-calcifying species. As waters become corrosive to carbonate future maerl beds are expected to be degraded, with the loss of habitat complexity and biodiversity, although certain fleshy macroalgae and non-calcified fauna (e.g. anemones, polychaetes) are expected to proliferate (drawing by Sophie Martin).

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