Threats to Ecosystem Engineering Macrophytes: Climate Change

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Warming and other climate changes: an overview

Anthropogenic activities are impacting Earth’s climate dynamics, causing rapid global climate change and increasing climate variability (IPCC 2007, 2012). Coastal marine ecosystems, which are among the most ecologically and socio-economically important on the planet (Costanza et al. 1997, Barbier et al. 2011), are already experiencing the effects of this physical forcing, with impacts on biodiversity and ecosystem functioning at multiple spatial and temporal scales (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010, Wernberg et al. 2011b, Doney et al. 2012).

Although geological records show climatic changes throughout the history of the Earth, anthropogenic activities have been causing a rapid increase in atmospheric carbon dioxide (Hansen et al. 2006, IPCC 2007, Meehl et al. 2007). This increase in CO2, in combination with other greenhouse gases, has intensified the infrared.

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opacity of the atmosphere and is generally believed to be the major cause of warming on the Earth’s surface (Sabine and Tanhua 2010). In May 2013, CO₂ levels reached 400 ppm for the first time in human history, in fact, the last time in Earth’s history that CO₂ concentrations were this high was 4.5 million years ago (National Oceanic and Atmospheric Administration 2013). Since 1960, mean land temperatures have increased by as much as 0.24°C decade⁻¹ (Hansen et al. 2006, Burrows et al. 2011). Oceans are currently taking up > 80% of the heat added to the atmosphere, and sea temperature consequently increases as the atmosphere warms. Over the past century, the mean global rate of ocean temperature increase has been 0.06–0.07°C decade⁻¹ although there has been pronounced heterogeneity in time and space (Burrows et al. 2011, Lima and Wethey 2012, Wu et al. 2012). In addition, the changing atmospheric conditions are also forcing changes in global wind patterns that are driving ocean circulation. This has resulted in a general strengthening of western boundary currents (Gulf Stream, Kuroshio Current, East Australia Current, Brazil Current and Agulhas Current) which carry warm tropical water towards temperate latitudes, further contributing to the net warming. The fastest warming ocean regions (0.09–0.23°C decade⁻¹) have therefore been found within these poleward-flowing currents (Wu et al. 2012). The increase in global sea temperature is accompanied by changes to patterns and strength of winds and ocean currents, upwelling and the associated nutrient supply, ocean stratification, a rise in sea levels, and changes in rainfall dynamics.

Oceans play a critical role in buffering the effects of increasing atmospheric CO₂ concentrations. In the last two centuries, around 50% of anthropogenic CO₂ emissions (118 ± 19 Pg C, each Pg C is 10¹⁵ g of Carbon) have been absorbed by the oceans. The increase in dissolved CO₂ in the oceans has increased bicarbonate (HCO₃⁻) concentrations, decreased the concentration of carbonate ions (CO₃²⁻) and caused a decline in pH of 0.02 units per decade over the past three decades (Hepburn et al. 2011; Doney et al. 2012).

On top of the gradual shift in mean environmental conditions, there have changes to the occurrence of extreme events (IPCC 2012, Trenberth 2012). In their recent analysis of satellite derived global sea surface temperatures for the last 30 years, Lima and Wethey (2012) found that 46% and 38% of the worlds’ coastlines have experienced a significant decrease in the frequency of extremely cold days and an increase in extremely hot days, respectively. Also, in 36% of temperate coastal regions the onset of the warm season was found to be advancing earlier in the year. Increases in extreme rainfall occurrences have resulted from the rising amount of water vapour in a warmer atmosphere (Trenberth 2012), modifying coastal salinity and stratification as well as increasing terrigenous sediment and nutrient runoff. Climate change models predict a further rise in the frequency and intensity of extreme events such as storms, including cyclones and hurricanes, and increasing wave heights, flooding and heat waves (IPCC 2012).

All of these physical and chemical changes interplay to impact marine macrophytes both directly and indirectly (Fig. 1) through changes in physiology, abundance, distribution, phenology and species interactions (Poloczanska et al. 2007, Kordas et al. 2011, Wernberg et al. 2011a, Gao et al. 2012, Harley et al. 2012, Richardson et al. 2012).
Climate change is not the only peril for marine macrophytes. The world’s oceans are simultaneously affected by multiple human activities, such as eutrophication, fishing, habitat destruction, hypoxia, pollution, and species introductions (Halpern et al. 2008, Wernberg et al. 2011b). Climate change, therefore, cannot be understood in isolation from these multiple stressors because complex interactions often determine the responses of organisms and ecosystems (Crain et al. 2008a, Wernberg et al. 2011b). Effects of climate change stressors can be subtle, but synergistic effects often cause loss of resilience making ecosystems more vulnerable to changes that previously could be absorbed (Folke et al. 2004, Ling et al. 2009a, Connell and Russell 2010, Wernberg et al. 2010).

### Ecosystem engineering macrophytes

Marine macrophytes, loosely defined as large primary producers in habitats substantially affected by salt water from the sea, play a critical role in most coastal ecosystems. Although marine macrophytes are very diverse taxonomically and functionally, they can be divided into four major groups: seaweeds, seagrasses, mangroves and salt marshes (Fig. 2).

Seaweeds (macroalgae) are found in most coastal habitats from tropical coral reefs to temperate and polar kelp forests (Mann 1973, Steneck et al. 2002). Usually seaweed habitats are associated with hard bottoms, although some soft bottom habitats can be dominated by unattached (e.g., Ulva, Gracilaria) or attached (e.g., Caulerpa) seaweeds (Thomsen et al. 2012). Even though seaweeds are generally restricted to coastal areas, they contribute about 50 Pg C year⁻¹, or approximately 5%, of the total global marine productivity (Duarte and Cebrian 1996, Israel et al. 2010). Seaweed
habitats are particularly sensitive to direct disturbances from high temperatures (Tanaka et al. 2012, Smale and Wernberg 2013) or storms (Filbee-Dexter and Scheibling 2012) as well as altered species interactions such as increased rates of herbivory (Steneck et al. 2002, Ling et al. 2009a). Currently, seaweeds are generally not carbon limited, and increasing CO₂ levels are likely to have little direct effect on many seaweeds (Beardall et al. 1998). However, decreasing pH associated with increased CO₂ levels in seawater may have longer-term physiological, mechanical and structural effects on calcifying seaweeds (Kuffner et al. 2008).

Seagrasses are the dominant ecosystem engineers in many intertidal and shallow subtidal soft-bottom ecosystems from tropical to sub-polar environments (Larkum et al. 1989). Seagrass ecosystems are among the most ecologically and economically valuable in the world (Short and Neckles 1999b, Connolly 2012). Seagrass are also highly productive and are recognized as significant ecosystems in most coastal zones. Since seagrasses inhabit shallow coastal waters they are highly sensitive to fluctuations in light, temperature, CO₂, nutrients and sediment variability (Short and Neckles 1999b, Connolly 2012). Physical damage and mass declines in seagrass populations are evident worldwide as a result of anthropogenic climate change (Short and Neckles 1999a, Duarte 2002, Orth et al. 2006, Waycott et al. 2009).

Mangroves are salt-tolerant terrestrial forests located at the interface between land and sea, predominantly along tropical and subtropical coastlines (Nagelkerken et al. 2008). These habitats occupy a total area of 181000 km² worldwide and are ecologically highly significant to marine systems (Alongi 2002). Their distribution is controlled by thermal regimes, tidal patterns and major ocean currents. Nevertheless, sea-level
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rise is probably the greatest climate change challenge that mangrove ecosystems face. Geological records indicate that previous sea-level fluctuations have created both crises and opportunities for mangrove communities (Field 1998). Mangroves can adapt to sea-level rise if it is slow enough, if adequate expansion space exists, and if other environmental conditions are met. Unfortunately, in many areas retreat is not possible due to urbanisation, increasing farmland and human utilisation of the coastal zone behind mangrove and saltmarsh communities. Consequently, mangroves experience a ‘coastal squeeze’ as sea levels rise. Loss of mangrove forest area will increase the threat to shoreline development, as well as reduce coastal water quality, biodiversity, nursery habitat, and result in major loss of coastal ecosystem function and damage to complex food-webs (Gilman et al. 2008).

Salt marshes are complex coastal systems made up of a diverse range of salt-tolerant plants which colonize wave-protected shores in temperate regions. The halophytic vegetation within a salt marsh bind sediments, limit water motion and provide vital nursery habitat and protection for many commercially and ecologically important species (Simas et al. 2001, Bertness et al. 2004). Salt marsh formation is dependent on a complex set of conditions, where the relationship between run-off, inundation, sediment type and protection from exposure must be well balanced. Salt marshes are particularly vulnerable to sea-level rise, but increased storms, precipitation and changed sediment and nutrient regimes will also limit salt marsh performance. Loss of salt marshes will have negative implications for inhabiting communities, as well as recruitment from nursery habitats to other marine areas. A reduction in salt marshes will also lead to a loss of protection of coastlines and human development from erosion and storm damage (Simas et al. 2001).

Marine macrophyte habitats have some of the highest rates of primary production on Earth (Fig. 3). Marine macrophytes are essential ecological engineers, with important structuring and functioning roles, serving as food resources and providing physical habitat or nurseries for aquatic organisms, such as invertebrates, fish and birds.

Figure 3. Net annual primary production (g C m⁻² year⁻¹) of the major marine macrophyte systems, compared with some terrestrial communities. Redrawn from Mann (1973).
Marine Macrophytes as Foundation Species


Because of their ability to moderate environmental conditions (i.e., engineer the ecosystem) and reduce stress on associated organisms, ecosystem engineering macrophytes will become increasingly important to the maintenance of ecosystem function in a warmer, more stressful, future (Halpern et al. 2007).

Responses of marine macrophytes to climate change

Knowledge of how marine macrophytes have responded, and will continue to respond, to the changing climate is important in order to understand ecosystem level impacts and to provide guidelines to manage and conserve marine communities. Yet, despite their substantial ecological and socio-economic importance, only ~ 20% of the combined experimental effort in climate change experiments has been directed towards primary producers (Wernberg et al. 2012a). Consequently, there is a relatively poor mechanistic understanding behind observed climate impacts on marine macrophytes.

Temperature

Changes in temperature directly influence the physiology of marine macrophytes. However, all physiological processes are not equally responsive to temperature change. For example, respiration is typically more temperature sensitive than photosynthesis (e.g., Stehr and Wernberg 2009), and so the metabolic ‘costs of survival’ increase faster than primary production. Where marine organisms live close to their thermal tolerance limits even relatively small increases in temperature can have dramatic effects on physiological processes, such as increased metabolic rates, cell protein damage and reduction in membrane fluidity (Eggert 2012), disruption to enzymatic processes, reduced nutrient uptake, photosynthetic inhibition, and respiratory stress (Davison and Pearson 1996). Prolonged exposure to increased temperatures can result in cellular and subcellular damage and reallocation of resources for protection and repair, leading to slowed growth, reduced productivity, delayed development, and eventually mortality (Harley et al. 2012). Extreme temperatures, if severe or prolonged, will lead to irreparable damage and death of macrophytes (i.e., disruptive stress sensu Eggert 2012). For instance, high temperatures associated with desiccation stress reduce recruitment of intertidal fucoïds by directly influencing survival, but also indirectly by suppressing growth and reducing the likelihood of escape from grazing (Hawkins 1981). Similarly, physiological stress over several weeks during an extended marine heat wave was likely the cause of the local extirpation and 100 km range contraction of a subtidal habitat-forming fucoid seaweed in Australia (Smale and Wernberg 2013).
While the physiological effects of thermal stress in macrophytes are relatively well established in the literature, the ecological relevance is mostly unknown. Few studies have focused on the relationship between the effects of sublethal thermal stress on the species fitness or their competitive abilities (but see Wernberg et al. 2010, Martínez et al. 2012a).

Beyond direct metabolic effects, water temperature is one of the main triggers for the timing of ontogenetic transitions such as spore production, flowering and seed germination in marine macrophytes (e.g., Diaz-Almela et al. 2007, Mohring et al. 2013). For example, temperature plays an important role in flowering induction and development in seagrass (Zostera sp.) on the Great Barrier Reef. In these populations the initiation of flowering occurs after a rapid rise in sea temperature, from the annual low, in conjunction with an increase in day length. Similarly, other species in this area flower in late spring before temperatures reach their summer peak. Therefore, changes to temperature regimes may disrupt these cues, and inhibit flowering and seed germination (Waycott et al. 2007). It is well known that different ontogenetic stages of both plants and animals have different temperature sensitivities. For example, kelp gametophytes are often described as more thermo-tolerant than sporophytes (Dieck 1993, Müller et al. 2012). A complete understanding of how temperature change might affect populations must therefore assess the thermal limits of all life stages (Russell et al. 2012).

Perhaps the most pervasive change due to rising ocean temperatures is the shift in distribution of many macrophytes (Lima et al. 2007, Fernández 2011, Wernberg et al. 2011a, Martínez et al. 2012b, Tanaka et al. 2012, Smale and Wernberg 2013). However, some species occur along coastlines with physical barriers, including
geological (e.g., substratum), geomorphological (e.g., depth, topography), oceanic (e.g., upwelling, off/alongshore currents), as well as human associated activities (e.g., around metropolitan areas). In these cases range shifts following the new temperature clines may not be possible and continued warming can therefore result in extinctions as species-ranges keep contracting until they eventually ‘fall off the map’ (Wernberg et al. 2011a). A study from Portugal showed differences between cool- and warm-water seaweeds in response to ocean warming. While warm-water species exhibited considerable range expansions cold-water species showed no clear patterns (Lima et al. 2007) perhaps illustrating the different population processes associated with range expansions and contractions. Vertical distribution shifts have also been observed in intertidal and shallow subtidal communities, with species shifting into deeper water where temperature fluctuations are less dramatic (Harley et al. 2012). Nevertheless, other factors not related (or indirectly related) to changes in temperature may also explain, in part, some of the distributional shifts (Lima et al. 2007). These include biotic interactions (e.g., grazing and competition, Ling et al. 2009b), and anthropogenic effects over the coast (e.g., pollution, coastal erosion, Coleman et al. 2008, Connell et al. 2008).

**CO₂ and pH**

Like all photosynthetic organisms, marine macrophytes use inorganic carbon during photosynthesis to create organic carbon-rich compounds. This does not, however, imply that the increasing CO₂ levels will benefit all marine macrophytes; large differences in the carbon uptake mechanisms between species prevent such clear-cut predictions. Carbon dioxide diffusion rates in seawater are four orders of magnitude lower than in air. Thus, for macrophytes that rely solely on CO₂ diffusion, increases in CO₂ could enhance photosynthetic performance and growth. This is the case for seagrasses, which evolved from terrestrial plants during the Cretaceous (~ 90 mya) when CO₂ levels were considerably higher than at present, and so are often carbon limited (Beardall et al. 1998). Carbon dioxide addition experiments have found that seagrasses exposed to high CO₂ levels, combined with increased nutrient concentrations, can access the greater concentrations of CO₂ and boost their photosynthesis rates (Beardall et al. 1998). It has been demonstrated that mangroves will also perform better when exposed to elevated CO₂. In a long term study from the Caribbean, *Rhizophora mangle* showed enhanced total plant biomass, higher root:shoot ratios, as well as increases in seedling biomass, stem length, and total leaf area when subjected to CO₂ concentrations double the atmospheric average (Farnsworth et al. 1996).

For seaweeds, predictions are more complicated as different species have different adaptations and strategies to deal with increasing carbon availability. Macroalgae that rely exclusively on CO₂ uptake through diffusion are most likely to show enhanced photosynthesis under elevated CO₂ levels. Conversely, macroalgae that use carbon concentration mechanisms (CCM) are predicted to show little response to elevated CO₂, although down regulation of CCMs could be induced by elevated CO₂ and allow the energy to be used for other purposes (Hurd et al. 2009). There is increasing evidence for the existence of CCMs in many species of macroalgae and in many
cases experimental studies have shown little growth response to CO₂ increases (Israel and Hopf 2002). However, studies have shown that a number of ephemeral, fast growing turf-forming algae respond positively to increased CO₂ when coupled with increases in other test-factors, such as, temperature and elevated nutrients (Russell et al. 2009a, Connell and Russell 2010). Moreover, evidence suggests that elevated CO₂ has variable, but often positive, effects on kelps like Nereocystis luetkeana and Macrocystis pyrifera (Thom 1996, Roleda et al. 2012).

Carbon availability for photosynthesis is, however, not the only issue. Higher CO₂-levels lead to lower seawater pH (‘acidification’), and this can result in reduced photosynthesis, poor growth and even death of some algae (Israel and Hopf 2002, Martin and Gattuso 2009). Calcifying algae, such as encrusting or articulated coralline algae, are among the most ubiquitous macrophytes in marine environments. Calcareous algae play a critical role in the settlement of many ecologically important invertebrates (Pearce and Scheibling 1990) and act as the ‘glue’ that consolidates reef structures, protecting them from storm damage (Madin et al. 2012). Calcifying algae are particularly sensitive to reduced pH in the ocean because it changes the solubility of different CO₂-species, increases the metabolic costs of calcification and, eventually the likelihood of dissolution. As such, reduced growth rates in calcified algae have been linked to increasing ocean acidification (Harley et al. 2012, Wernberg et al. 2012b). These effects are likely to be exacerbated by increasing temperatures. For example in the Mediterranean Sea, communities on rocky shores close to volcanic CO₂ vents showed a significant reduction in abundance of coralline algae with decreasing pH (Hall-Spencer et al. 2008). On temperate reefs, calcifying algae can occupy up to 80% of hard substrate, dominating space beneath canopies (Steneck et al. 2002, Wernberg et al. 2012b). Increasing oceanic CO₂ could therefore reduce the competitiveness of calcifying algae over non-calcifying species, which may result in a reduction of reef diversity, as well as habitat and protection for a range of dependent communities (Beardall et al. 1998). Although ocean acidification has been considered a major threat to marine organisms, effects are highly variable across and within taxonomic groups. Furthermore, a recent meta-analysis suggests that marine biota may be more resistant to ocean acidification than previously suggested (Dupont et al. 2010, Hendriks et al. 2010).

Changes in circulation patterns

Warming of the upper layers of the ocean combined with alterations to wind patterns, drive changes to major ocean currents (Wu et al. 2012), greater stratification of the water column and a deepening of the thermocline (Harley et al. 2006). The results include greater intrusion of warm, nutrient-poor waters at higher latitudes and reduced upwelling of nutrient-rich waters (Johnson et al. 2011). Upwelled nutrients fuel growth and reproduction in benthic and planktonic algae, and future changes in upwelling regimes/dynamics could have important consequences for ecosystem productivity (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010). For example, the decline of giant kelp (Macrocystis pyrifera) populations in Tasmania (Australia) has been attributed to an increase in the strength of the East Australia Current, now bringing warm and nutrient poor water onto the coast (Johnson et al. 2011). Altered circulation
patterns also affect species distributions. Shifts from kelp (*Ecklonia*) to *Sargassum* dominated communities have been reported in Japan as a result of a strengthening of the Kuroshio current, leading to regional warming (Tanaka et al. 2012). In Portugal, Lima et al. (2007) reported poleward expansions of warm-water species of seaweeds presumably as a result of a weakening of coastal upwelling. There are also cases of intensified upwelling allowing cool-water species to expand into previously warmer areas. This was the case in South Africa, where a dominant canopy-forming kelp (*Ecklonia maxima*) expanded its distribution limit by ~ 70 km (Bolton et al. 2012).

Many marine macrophytes rely on water movement for dispersal, and changes to ocean currents and upwelling are, therefore, also likely to have implications for population connectivity and recruitment. For example, Coleman and colleagues (2011) found strong positive correlations between the strength of coastal currents and genetic connectivity among kelp (*Ecklonia*) populations around Australia. Dispersal and recruitment of seagrasses and mangroves are also highly dependent on currents (Kendrick et al. 2012). For example the viability of mangrove (*Avicennia marina*) propagules diminishes over time, and seeds can only successfully establish within 4–5 days of release. In New Zealand, southern populations of this species are controlled by limited transport of propagules from northern populations; thus, any climate induced changes to circulation patterns may lead to poor population replenishment, and ultimately loss of mangrove stands (Osunkoya and Creese 1997).

**Sea level rise**

The average global sea level is rising at a rate of 3.3 mm year⁻¹ due to thermal expansion of the oceans and freshwater input from melting glaciers, and most models estimate that by 2100 sea levels will be between 0.5 to 1.2 m higher than today (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010). The most obvious result of increased sea level is that current macrophyte habitats above or near the surface will be permanently submerged, and current subtidal habitats will deepen, causing changes in physical conditions (e.g., reduced light penetration and wave exposure). This is particularly important in regions where the rocky shore is mostly horizontal (e.g., eastern Mediterranean) and in lagoons and estuaries with extremely low slopes. Since more than 14% of world’s coastline can be categorised as low sloping rapid sea-level rise would cause an inundation of the intertidal zone by seawater, turning the platforms into subtidal reefs (Cazenave and Lovel 2010). Vaselli et al. (2008) showed that on NW Mediterranean rocky shores a rise in sea level in the range of 5 to 50 cm would increase the availability of steep substrata (> 40°) by almost 60%, drastically modifying the dominant assemblages. Because they are highly specialized, and often live close to their tolerance limits, mangroves are particularly sensitive to minor variation in hydrological or tidal regimes. In the laboratory, *Rhizophora mangle* seedlings subjected to simulated increased tidal inundation showed reduced growth and photosynthetic rates, which would eventually lead to reduced recruitment and increased mortality (Poloczanska et al. 2007). Marshes will be also affected by rising sea level. Numerical models suggest that an increase in the rate of sea level rise together with a reduction in sediment supply will lead to greater inundation, expansion of channel networks, and conversion of marshland
into subtidal mudflats (Kirwan and Temmerman 2009). Many species are, however, expected to shift their distributions landward, and should be able to keep pace with predicted rates of sea level rise. However, a major hurdle for landward retreat is lack of habitat availability due to human development.

**Ultra-violet radiation**

Ultraviolet radiation is, strictly speaking, not a symptom of climate change. However, increased penetration of UV radiation from ozone depletion, as a result of human activities, also has a detrimental effect of marine systems on a global scale (Poloczanska et al. 2007, Harley et al. 2012). Ultraviolet (UV) radiation is known to harm physiological processes in marine macrophytes through damage to DNA and inhibition of photosynthesis and nutrient uptake. This can lead to a reduction in productivity and biomass (Beardall et al. 1998). For example, net photosynthesis of the mangrove seedlings (*Rhizophora apiculata*) decreased by 59% with a 40% increase in UV (Connolly 2012). Low levels of UV-A (long wave lengths, 315–400 nanometers) have been shown to enhance photosynthesis and repair photo-damaged molecules, whereas UV-B (short wave lengths, 280–315 nanometers) mostly has harmful effects. Importantly, responses to UV appear to be species specific, and are often determined by the environment that an organism inhabits. For example, the seaweed *Gracilaria lemaneiformis* showed reduced photosynthetic efficiency (on sunny days) with increased levels of UV-B, whereas photosynthetic efficiency (during the sunrise period) increased with elevated UV-A (Xu and Gao 2010). More generally, intertidal algae are better adapted, than subtidal algae to cope with the increased UV stress, and many species have evolved strategies such as (photo) repair mechanisms. Similarly, some seagrasses have adaptations to cope with UV-stress; for example, when exposed to increased UV shallow water *Halophila ovalis* shows less stress than the deeper water *Posidonia australis* (Beardall et al. 1998). As discussed for heat stress, increased UV typically has stronger negative effect on the juvenile phase of the life cycle, and recruits tend to be more sensitive to light fluctuations. For example, while mature *Rizophora mangle* trees perform best in full sunlight, their seedlings do better in the understory environment because the ontogenetic development in mangroves produces changes in light adaptation (Farnsworth et al. 1996). Similar ontogenetic changes have been observed in some kelp species. Fejtek et al. (2011) found that adult *Macrocystis pyrifera* can survive in much shallower waters than populations occur, but the susceptibility of the juveniles to high light and UV levels limit its vertical range. This is also the case for many other species of kelp around the world (Wienecke et al. 2006). A reduction in recruitment has implications for the replenishment of damaged populations; thus, the effects of UV are often interactive, and magnify other climate change conditions.

**Extreme events—storms and heat waves**

Biological responses to environmental conditions are often determined by extremes in conditions rather than average levels (Gaines and Denny 1993). A recent report from the IPCC (IPCC 2012) concluded that the magnitude and frequency of extreme
weather events is increasing as a consequence of climate change (see also Poloczanska et al. 2012, Trenberth 2012).

Storms and extreme heat wave events can cause mass mortality of marine macrophytes over short time periods. For instance, large losses of seagrass meadows have been observed in Australia following major storms and cyclones, as a result of physical disturbance to the substrate and undermining of roots and rhizomes (Connolly 2012), and in Canada, a hurricane severely decimated subtidal kelp beds (Filbee-Dexter and Scheibling 2012).

Sometimes the ultimate cause of impact associated with storms, are not the storms themselves. Storms are often also associated with disturbance to sediments and peak rainfall, which can result in large-scale flooding, the re-suspension of particulate matter, increased turbidity, sedimentation and nutrients from run-off, and fluctuations in salinity. All of these secondary effects can have detrimental effects on macrophytes through sedimentation and nutrient-fuelled blooms of algae causing reduced light penetration, smothering and hypoxia (Airoldi 2003, Thomsen et al. 2012). For example, in 1992 an intense tropical cyclone caused a pulse in re-suspension of particulate matter and turbidity which killed more than 1,000 km² of seagrass in Hervey Bay (Australia) in 1992 (Orth et al. 2006). Flooding and freshwater runoff also decrease salinity, and this can have dramatic effects on intertidal mangroves and seagrasses (UNESCO 1993, Short and Neckles 1999a, Vaselli et al. 2008). Mangroves are particularly susceptible to fluctuations in salinity, and rely on both freshwater run-off and tidal inundation for survival. When salinity is too high or low, mangrove growth and survival can be compromised. Most marine seagrasses grow best within a narrow salinity range, and many species suffer reduced growth, productivity, and die-back during salinity fluctuations associated flooding and increased rainfall (Waycott et al. 2009, Riddin and Adams 2010).

Heat waves are becoming more frequent and more severe, and their local and regional scale impacts on marine macrophytes are dramatic (Poloczanska et al. 2012). For example, in the summer of 2003 a heat wave in the Mediterranean Sea began in early June 2003 and lasted until mid-August, with air temperature records about 3–6°C above the seasonal average in many parts of Europe and seawater temperature up to 28.8°C (Sparnocchia et al. 2006). As a consequence, large-scale seagrass mortality occurred (Garrabou et al. 2009), and shoot mortality rates were unusually high, exceeding recruitment rates in most areas (Marba and Duarte 2010). Similarly, large-scale seagrass dieback occurred in Spencer Gulf, South Australia in February 2003, where air temperatures exceeded 40°C, coupled with exceptionally low tides in the middle of the day, over several consecutive days. During this heat wave seagrass shoots suffered high damage to chloroplasts, causing high mortality rates, resulting in the loss of nearly 13,000 ha of seagrass (Connolly 2012). Another more recent heat wave occurred off the west coast of Australia in 2011, where temperatures exceeded anything recorded for > 140 years, remaining significantly elevated for ~ 10 weeks across ~ 2,000 km coastline causing widespread ecological impacts (Pearce et al. 2011, Wernberg et al. 2013). The soaring temperatures led to detrimental physiological stress to habitat-forming seaweeds, causing extensive loss of seaweed canopies and a 100 km range contraction of a prominent endemic species with likely ecosystem-wide flow-on effects (Smale and Wernberg 2012, Smale and Wernberg 2013, Wernberg et al. 2013).
Biological stressors—diseases, epiphytes and invasions

In addition to the physical drivers associated with climate change itself, biologically stressors such as diseases, epiphytes and invasive species will also impact marine macrophytes.

Micro-organisms are ubiquitous in seawater, and the way they interact with macrophytes is likely to change under future climate scenarios (Campbell et al. 2011). Climate change can influence the prevalence and severity of disease outbreaks in marine ecosystems. Increased disease can contribute to declines of populations or species, especially for generalist pathogens. Increasing environmental stress associated with climate changes will likely decreases host susceptibility to diseases (Campbell et al. 2011), increase disease virulence and abundance, and increase disease vectors and the expansion of pathogen ranges (Hoegh-Guldberg and Bruno 2010, Wernberg et al. 2012b). For example, fungi (Fusarium sp.) can cause dieback of salt marsh (Spartina alterniflora) when the plants are subjected to high temperatures and drought stress (Alber et al. 2008). In the past, seagrass communities have been severely affected by diseases. For example, the Atlantic-wide loss of eelgrass (Zostera marina and Thalassia testudinum) meadows resulted from a combination of environmental stress and the wasting disease associated with a fungus (Labyrinthula zosterae, Duarte 2002). In kelps, bacteria are the causative agents of red spot disease, whereas the known pathogens of the dark spot disease are endophytic brown filamentous algae. Field observations from different parts of the world document massive rates of infection prevalence by endophytic brown algae with mostly unknown pathogenic effects (Eggert et al. 2010). Heat stress in seaweeds also cause lowered chemical defenses (Campbell et al. 2011), which can lead to heavy epiphytism with detrimental consequences for kelp forests (Andersen et al. 2011, Smale and Wernberg 2012).

Global climate change can effect species distributions and resources availability thus, inducing biological invasions (Occhipinti-Ambrogi 2007). Climatic change affects non-indigenous species by altering environmental conditions, resource levels and native communities of the invaded habitat (Thomsen et al. 2011). Global warming coincides with an increase in human transport activities, which increases vectors for introductions (Hoegh-Guldberg and Bruno 2010). Changes in temperature may favour the settlement of invasive species where it was previously too cold. For example, warming conditions in the Mediterranean favoured the establishment of the green seaweed Caulerpa taxifolia, which produces toxic secondary metabolites potentially leading to Posidonia oceanica die-back (de Villèle and Verlaque 1995, but see Glasby 2012, Thomsen et al. 2012 for alternative interpretations). Increasing sea temperature is also putting pressure on endemic species, reducing potential competitive advantage over invaders. In Australia, summer heat waves events associated with global climate change have seen large scale die-backs in kelp beds. This mass mortality facilitated the establishment of the invasive macroalga, Undaria pinnatifida (Valentine and Johnson 2003, Valentine and Johnson 2004).

Increasing temperature is not the only climate change-related factor affecting the outcome of invasions. Changes in atmospheric circulation, storm frequency, and precipitation alter the dispersion and invasiveness of non-indigenous species. In a recent laboratory experiment, increasing temperature and pCO₂ altered the success
and performance of the brown seaweed *Sargassum muticum* at multiple points in the life cycle (Vaz-Pinto et al. 2012). Finally, non-indigenous species that have become well-established in recipient communities are expected to alter community response to climate. For example, in rock pools of the western Atlantic coast of the Iberian Peninsula, macroalgal assemblages invaded by *S. muticum* might be more resistant to increasing temperature and CO$_2$ in future climate scenarios (Olabarria et al. 2012).

**Cumulative effects of multiple stressors**

Many climate and non-climate physical, chemical and biological changes in the environment are occurring simultaneously (Halpern et al. 2008, Wernberg et al. 2011b). Consequently, marine macrophytes are subjected to multiple concurrent stressors at any one time, and these are likely to act in concert rather than in isolation (Crain et al. 2008a). To this end, almost all observed impacts on marine macrophytes possibly related to climate change have involved multiple stressors (Wernberg et al. 2011b, Harley et al. 2012). For example, losses or declines of habitat-forming macroalgae in Australia over the past decades were attributed to historical overfishing of herbivore predators (Ling et al. 2009a), pollution and reduced water quality associated with urbanization (Coleman et al. 2008, Connell et al. 2008). In the Gulf of Maine, kelp beds have suffered dramatic changes in the last twenty-five years mainly due to an increase of seawater temperatures in summer, overfishing and the introduction of non-indigenous species (Harris and Tyrrell 2001), where temperature mediated outbreaks of invasive bryozoans cause extensive defoliation of kelps and increases in the invasive *Codium* seaweeds (Scheibling and Gagnon 2009).

Higher CO$_2$ and nutrient levels boost the growth and productivity of turf-forming seaweeds, which can block the recruitment of kelps (Gorman et al. 2009), while acidification reduces the calcification and recruitment of coralline crusts (Russell et al. 2009b), and these effects are further exacerbated by increasing temperatures (Martin and Gattuso 2009, Diaz-Pulido et al. 2012). In addition, ocean acidification may disrupt the feeding biology of some herbivores, limiting their ability to control the climate-enhanced growth of opportunistic turfs (Russell et al. 2009b, Falkenberg et al. 2010). Temperature and CO$_2$ concentrations can also modulate the effects of UV radiation on the germination, growth and survivorship of kelps and fucoids (Hoffman et al. 2003, Swanson and Fox 2007).

For mangroves, increasing temperatures are causing stress, which is being exacerbated by increased inundation as a result of sea level rise and rainfall. Storms can cause damage to trees and defoliation, and the runoff can compound the pressure by introducing higher sediment loads which smother pneumatophores. While high rates of sedimentation are detrimental to mangroves, moderate sedimentation can enhance growth through increased availability of nutrients (Ellis et al. 2004, Lovelock et al. 2007). More toxic chemicals are also likely to wash from local watersheds to have negative effects of mangrove trees. Changes in salinity also co-occur with storm runoff, and this can have a negative or positive effect; populations existing in estuaries where salinity is low are likely to be put under further pressure as salinities decline. Populations occurring in oceanic waters, or arid areas where salinity is extreme may
benefit from freshwater inflow and may exhibit increased growth rates, biodiversity and expansions in mangrove area (Gilman et al. 2008). Similarly, higher nutrient concentrations in runoff water may also have a positive effect on mangrove growth. Any one of these changing conditions has the potential to cause mortality, or at least reduced growth of mangroves, but in combination the effects are more severe (Gilman et al. 2008). Such effects may be exacerbated or ameliorated when acting with other anthropogenic stressors such as, nutrient loading or CO₂ (McKee and Rooth 2008, Cherry et al. 2009).

Seagrasses are often simultaneously influenced by multiple stressors at different temporal and spatial scales (Björk et al. 2008). For example, the negative effect associated with sea level rise and increased storm intensity/frequency is depth-dependant, and interacts with a reduction in the amount of available light reaching the seagrass canopy (Short and Neckles 1999a). In combination with organic enrichment, extreme events such as floods, droughts and heat waves, may also impact seagrass meadows. In the Mondego estuary (Portugal), which has experienced significant eutrophication in the last 20 years, drought events caused salinity to increase above 35 ppt, increasing pressure on the seagrass, Z. noltii, and negatively affected meadow biomass (Cardoso et al. 2008).

In order to fully understand the effects of global climate change on marine macrophytes, it will be important to understand interactive effects and possible synergies (Crain et al. 2008b, Wernberg et al. 2012b). Until recently most marine climate change research involved single-stressor experiments focused on animals, highlighting an urgent need to conduct more studies with macrophytes, and in particular using multiple-stress approaches (Wernberg et al. 2012a).

**Scaling up from physiological response to community—ecosystem level responses**

Marine biota does not respond uniformly to climate change stressors. Experimental work has shown that even species with similar ‘climate traits’ (i.e., similar effect of climate change on one or several ecosystem functions) can respond very differently to the same environmental stressors. For example, responses of macroalgae to increases in temperature and CO₂ varies greatly, even among species belonging to the same functional group (Martin and Gattuso 2009). The lack of uniform easy-to-predict responses will have important implications for marine ecosystems where some species play disproportionately strong roles in community structure and function (Kroeker et al. 2010).

Most marine research on climate change published to date have used highly controlled single species experiments to look for specific responses and improve our understanding of physiological mechanisms (Wernberg et al. 2012a). Whilst these experiments are extremely important, they represent highly artificial experimental conditions, being isolated from common biological interactions (e.g., competition, predation, facilitation). Biological interactions may buffer or amplify individual responses thereby altering predicted assemblage or ecosystem-level responses (Kordas et al. 2011). For example, increasing CO₂ can cause seagrass photosynthetic rates to
increase by 50% which may deplete the surrounding CO$_2$ pool, maintain an elevated pH and thus, protect associated calcifying organisms (Kroeker et al. 2010). Similarly, kelp loss might be exacerbated by the positive effects of increasing CO$_2$ and temperature on non-calcifying algal turfs, i.e., kelp inhibitors (Connell and Russell 2010).

Therefore, ecological change in coastal systems will reflect the combined influence of direct environmental impacts on individual species and indirect effects resulting from changes in interspecific interactions. Presently, there is little certainty of the actual effects of future climate change and how species will respond. When coupled with the intrinsic complexity of ecosystems, it is difficult to predict the consequences for biodiversity and ecosystem function. Ecosystem responses will depend on the pace and magnitude of climate changes and the longevity of species and their role in the ecosystem (Harley et al. 2012). Thus, it is important to conduct experiments with multiple species, simple assemblages or even complex subsets of whole ecosystems (Wernberg et al. 2012a). Such microcosm/mesocosm experiments have been used with great success to mimic pelagic ecosystems, but have yet to be fully exploited by researchers studying climate effects on benthic communities (but see Olabarria et al. 2012).

Climate related changes in species interactions are often a consequence of shifts in species ranges, resulting in new species interactions as well as disruptions of existing interactions. Higher trophic levels are often more sensitive to climate change than plants. Secondary consumers not only suffer their own specific climate related stress, but are generally dependent on these primary producers, which may be exhibiting reduced biomass, localised extinctions and rapidly altering their distributions. These bottom-up changes to food webs can lead to localised extinctions and important alterations to ecosystem function (Kordas et al. 2011, Wernberg et al. 2012b).

Research suggests that interspecific interactions shift from generally negative (e.g., competitive, predatory) when the environment is benign to generally positive (e.g., facilitative) when the environment is stressful (Bertness and Callaway 1994). For instance, in salt-marshes from New England (United States) the nature and intensity of interactions between neighbour plants depend on latitudinal and inter-annual variation in climate. In the south (where heat stress is common), species interactions tend to be facilitative, whereas in the north (where abiotic conditions are more benign) interactions are more competitive. Furthermore, interactions are more facilitative in warmer versus cooler years (Bertness and Ewanchuk 2002). Similar large-scale patterns have been found within a species; In Australia Wernberg et al. (2010) found that intra-specific facilitation dominated at warm northern latitudes (heat stressed) but intra-specific competition dominated at cool southern (more benign) latitudes. It is therefore expected that many interactions will shift from competitive to facilitative under increasing temperature stress associated with climate changes (Halpern et al. 2007). Additionally, important changes in interactions might result when the geographic range of species shifts, and when the seasonal timing of life history events of interacting species fall into, or out of, synchrony.
Integration adaption in the responses

Despite evidence illustrating the potential of microevolution to generate rapid phenotypic changes at short time scales (Pereyra et al. 2009), in species with lifespans like those of macrophytes, probably the most relevant component of adaptive potential to climate change are phenotypic plasticity and genetic variability. Both mechanisms are able to act within a generation, while evolutionary genetic changes involve multiple generations. Thus, understanding trait plasticity and limits to adaptation is essential to predict rates of extinction owing to climate change, as well as estimating the effect of environmental change on community ecology and ecosystem services (Bridle and Vines 2007). Together with phenotypic plasticity, genetic variability is the second immediate mechanism that allows a population to persist when its local environment changes (Chevin et al. 2010). Evidence of the importance of genetic diversity on the ability of macrophytes to cope climate change are already available in the literature. Ehlers et al. (2008) found a strong negative effect of warming and a positive effect of genotypic diversity on shoot densities of eelgrasses. Similarly, Pearson et al. (2009) provided evidences of mal-adaption to heat shocks and dehydration stress from low diverse edge population of the brown algae Fucus serratus.

Conclusions and future issues

Macrophytes are critical components of marine ecosystems, and while the evidence for substantial climate change impacts on marine macrophytes is increasing (Wernberg et al. 2011b, Harley et al. 2012), experimental work on macrophytes is substantially under-represented in the research effort (Wernberg et al. 2012a). A better understanding of interactions between macrophytes and climate change is critical because of the important contribution of this group to functioning of many ecosystems and its potential role on amelioration of environmental stress (Halpern et al. 2007). Despite the increase in the number of studies in the last decade, there are still significant gaps in our knowledge. Harley et al. (2012) summarizes these knowledge-gaps for macroalgae, but we contend that they apply generally to marine macrophytes and re-iterate them here: (1) the importance of rates, timing, magnitude, and duration of environmental change, (2) non-additive effects of multiple stressors, (3) population-level implications of variable environmental impacts among life-history stages, (4) the scope for population or species-level adaptation to environmental change, and (5) ecological responses at the level of communities and ecosystems, including tipping points and sudden phase shifts.

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References


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