3.3 Impacts and effects of ocean warming on seaweeds

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Summary

- Seaweeds (marine macroalgae) encompass a diverse group of marine plants comprising >13,000 species. They provide habitat, food and many other important ecological functions, and the value of ecosystem services (e.g. fishing, tourism, biodiversity) from seaweed habitats is conservatively estimated to be US$30,000 ha^{-1} year^{-1}. Seaweeds have complex life cycles with several stages that are sensitive to direct physiological effects of warming on metabolism and reproduction, and indirect effects associated with warming-mediated changes in abiotic conditions (e.g. light) and species interactions such as herbivory.
- Ocean warming has caused significant changes in seaweed distribution, especially at Arctic and temperate latitudes. Cool-water species have been contracting and warm-water species extending their range edges poleward. Recent range-changes have been from 26 km to 1250 km. In addition, many seaweed populations have changed their depth distribution and relative abundance.
- Ocean warming has caused significant changes in seaweed communities, and the evidence is substantial and globally comprehensive. Gradual warming, marine heatwaves and over-grazing range-shifting herbivores have forced and augmented regime-shifts in at least seven regions across four continents. Here, highly complex productive seaweed forests have been replaced by structurally simple coralline crusts, filamentous turfs or small fleshy seaweeds.
- Key challenges include establishing appropriate baselines to assess further change against, as well as identifying the mechanisms that underpin warming-induced changes in seaweed ecosystems.
- The ecological and socio-economical flow-on effects of changing seaweed ecosystems require better understanding. In particular, the knowledge of the range of services provided by seaweed dominated ecosystems, and the value of these services to regional economies, is rudimentary.
- Solutions for mitigating impacts of warming are required. Options include managing additional local stressors, boosting resilience through assisted breeding and selection of resistant genotypes, restoration through translocation or substitution with functionally similar species. Knowledge of the relative merits and feasibility of these solutions are largely unknown.

Ocean warming effects	Consequences
Increasing mean ocean temperature	Shifting habitat suitability Increasing physiological stress leading to reduced resilience Failure to reproduce in marginal populations leading to population attrition and eventually local extinction and range contraction Population expansion and poleward range extension of warm-water species
Increasing frequency of marine heatwaves	Rapid population collapse and poleward range contraction of cool-water seaweed populations
Increasing poleward flow of western boundary currents	Increasing poleward propagule pressure leading to range expansion of warm-water seaweeds and other species including sub-tropical and tropical herbivores Increasing grazing pressure leading to seaweed population collapse and/or reinforcing ecosystem transitions. Increase risk of marine heatwaves at mid-latitudes
Increasing glacial melt and retreating sea ice in Arctic and Antarctic	Release of new space for seaweed colonization Changes to spatial and depth distribution Increased light penetration and production in some area Low salinity and turbidity limiting survival and light in other areas

3.3.1 Introduction

Marine macroalgae, commonly known as seaweeds, are a large, heterogeneous group of plants (*sensu* Bolton, 2016; Figure 3.3.1) that are found in most coastal areas of all climate zones (Lüning, 1990). Seaweeds have three basic environmental requirements: sea water, sufficient light to drive photosynthesis, and for most species a firm attachment point at some stage in their life cycle. Beyond that, species-specific distribution and growth are primarily controlled by temperature, irradiance and photoperiod, nutrients, waves, currents, salinity and herbivores (Van den Hoek, 1982a; Kirst, 1989; Lüning, 1990; Hurd, 2000; Wernberg *et al.*, 2013a; Vergés *et al.*, 2014a).

Globally there are currently 13,761 species of seaweeds that have been identified (Guiry and Guiry, (2016), accessed on 18th of February, 2016). They can be divided into three main groups, distinguished by their thallus pigmentation: red algae (phylum Rhodophyta; 7,113 species), green algae (phylum Chlorophyta; 2,760 species) and brown algae (phylum Ochrophyta; 3,888 species). These groups have evolved along separate pathways, and differ considerably in many features in addition to photosynthetic pigments. They are, however, all important marine primary producers serving a multitude of ecological functions and providing valuable ecosystem services (Lüning, 1990; Smale *et al.*, 2013; Bennett *et al.*, 2016).

Seaweeds are more complex organisms than generally realized (Figure 3.3.1). They range in size from a few millimetres to tens of metres, and in thallus structure from single filaments and coenocytes to highly elaborate growth forms with specialized tissues (Lüning, 1990; Hay, 1994). Many seaweeds have complex life cycles involving both micro- and macroscopic phases and alternation between haploid and diploid stages that can be either isomorphic or heteromorphic (Coelho *et al.*, 2000; Garcia-Jimenez and Robaina, 2015). Because of their complex life cycles, there are many stages where temperature and other abiotic factors can affect seaweeds, and the sensitivity can change throughout a species life cycle.

3.3.2 Global and regional significance of seaweed ecosystems

Seaweeds play an important role in marine ecosystems as ecologically important primary producers, ecosystem engineers and habitat formers. They are the dominant organisms on many intertidal and shallow subtidal rocky reefs along approximately 25% of the world's coastlines (Figure 3.3.2), where their species-specific distributions often shape local marine communities (Wernberg *et al.*, 2003; Buschbaum *et al.*, 2006; Ingólfsson, 2008; Tuya *et al.*, 2009; Egan *et al.*, 2014). Seaweed dominated habitats are particularly prevalent and important at temperate to polar latitudes (Figure 3.3.2). For example, kelp forests – dense stands of large brown seaweeds – are among the most productive ecosystems on Earth (Mann, 1973) and they are arguably some of the most ecologically and socio-economically important habitats in temperate waters (Steneck *et al.*, 2002; Smale *et al.*, 2013; Bennett *et al.*, 2016).

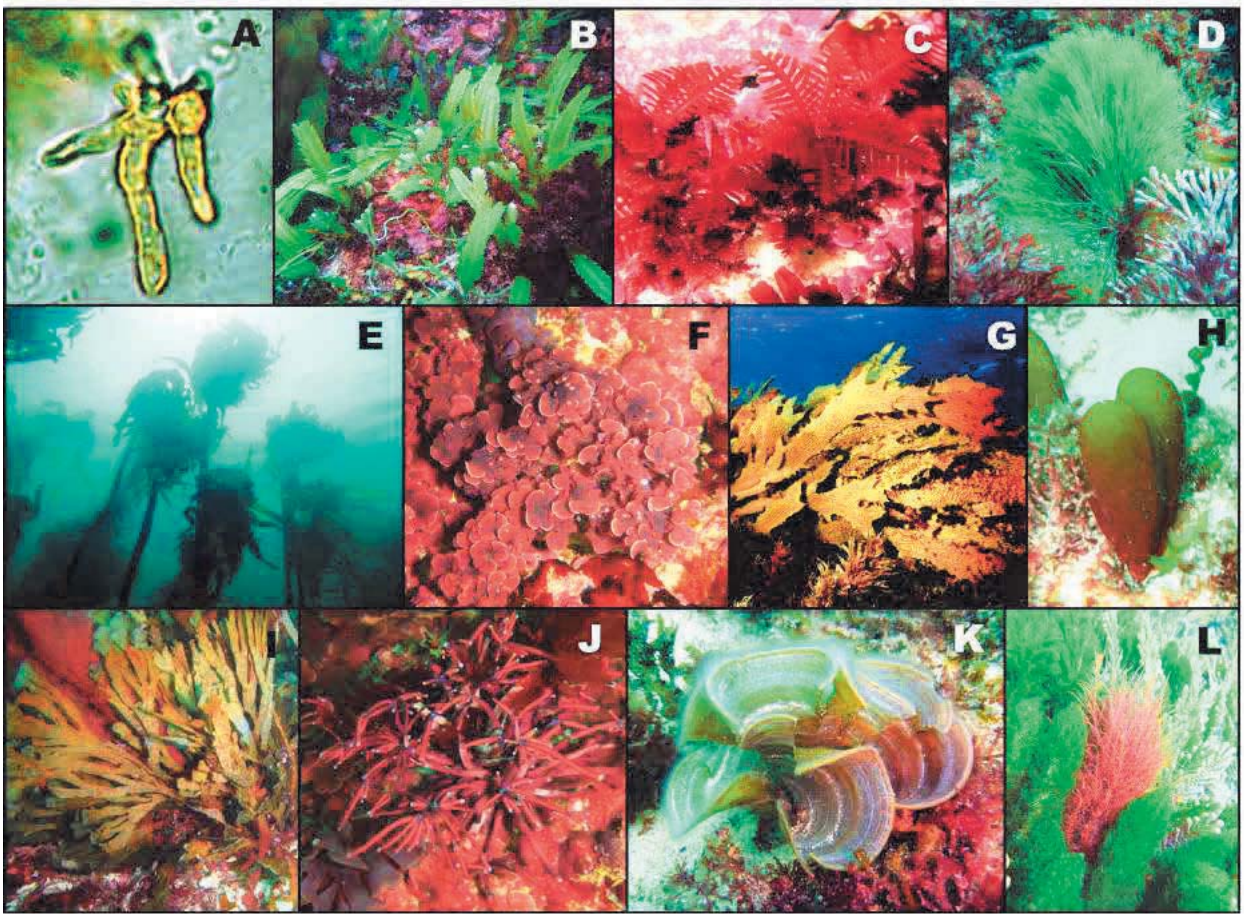

Figure 3.3.1 Seaweeds are a diverse group of marine plants. They are classified into red (C, F, H, J, L), brown (A, E, G, I, K) and green (B, D, L) algae based on their main pigments. Seaweeds display a broad range of morphologies including clusters of strings (D, J, L), fleshy blades (B, C, I, K), gelatinous bulbs (H) and highly differentiated structures with holdfasts, stipes and canopies (E, G), and some have calcified tissues (F, J, K). They can have complex life histories alternating between micro macroscopic phases (A *vs.* G) and range in size from a few centimetres to more than 10 metres (E). Male gametophyte of *Ecklonia radiata* (A, ~0.1 mm), *Caulerpa scalpelliformis* (B, ~10 cm), *Orthocladia rectangularis* (C, ~5 cm), Penicillus nodulosus (D, ~5 cm), *Ecklonia maxima*(E, ~10 m), *Metamastophora flabellata* (F, ~10 cm), *Ecklonia radiata* (G, adult sporophyte, ~1 m), *Gloiosacchion brownii* (H, ~10 cm), *Zonaria turneriana* (I, ~15 cm), *Metagoniolithon radiatum* (J, ~5 cm), *Padina* sp. (K, ~10 cm), *Caulerpa obscura* (green) and *Hypnea ramentacea* (red) (L, ~10 cm). The species shown here are all from Western Australia except *E. maxima* (E)*,* which is from South Africa. © Photo A. Mohring M.; Photos B, C, D, E, F, G, H, I, J, K, L. Wernberg T.

Kelps and many other seaweeds produce large amounts of biomass (Mann, 1973), affect their physical environment (Dayton, 1985; Hurd, 2000; Wernberg *et al.*, 2005) and increase the habitable surface area considerably (Boaden, 1996). Many marine species depend on these seaweed habitats for feeding, mating and nursing areas or protection from predators. Consequently, seaweeds provide the structural and trophic framework supporting diverse associated communities and complex food webs (Steneck *et al.*, 2002; Wernberg *et al.*, 2004, 2013b; Graham, 2004; Ling, 2008; Harley *et al.*, 2012; Smale *et al.*, 2013; Steneck and Johnson, 2013; Bertocci *et al.*, 2015; Graiff *et al.*, 2015; Paar *et al.*, 2015; Bennett *et al.*, 2016). The ecological importance of seaweeds extends well beyond their main habitat. As much as 80% of the primary production from kelp forests is exported to adjacent communities with lower primary production (e.g. deep sea, sandy beaches), where it subsidises and enhances secondary production (Krumhansl and Scheibling, 2012).

In addition to their ecological importance, seaweeds underpin valuable ecosystem services. Specifically, many commercial and recreational fisheries depend directly on seaweeds, including abalone, lobsters, and several species of fish (Bolognaand Steneck, 1993; O'Connor and Anderson, 2010; Fraser *et al.*, 2011; Rosenfeld *et al.*, 2014; Bennett *et al.*, 2016). Several seaweeds are edible and are harvested or grown for food or additives used in medicines and cosmetics, as well as industrial chemicals (Kain (Jones) and Dawes, 1987; Lüning, 1990; Smit, 2004; FAO, 2014). Others can be used for biofuel production, provide coastal

Box 3.3.1 Maerl

Maerl beds are accumulations of unattached live and dead coralline algae – heavily calcified red seaweeds – which form over thousands of years (Box Figure 3.3.1). They occur from the tropics to the poles and from the low intertidal down to 100m depth in the clear water of the Mediterranean (Blake and Maggs, 2003; Hall-Spencer *et al.,* 2010; Peña *et al.,* 2014). They provide a wide range of ecological niches and support high biodiversity (Barbera *et al.,* 2003; Grall and Hall-Spencer, 2003).

Maerl beds have high conservation status in European legislation due to their longetivity, high biodiversity and benefits for commercial species as nursery areas (Hall-Spencer *et al.,* 2010). In addition to being highly productive communities, maerl beds are considered an important source of calcareous sediment and they contribute to the pH balance of sea water (Canals and Ballesteros, 1997; Hall-Spencer *et al.,* 2010).


Figure 1 Maerl bed. ©SNH.

Maerl beds face many threats worldwide, including habitat destruction (from dredging, fishing gear, fish farms), the spread of invasive species, sewage pollution, and the combined pressures of ocean acidification and ocean warming (Grall and Hall-Spencer, 2003; Hall-Spencer *et al.,* 2010; Peña *et al.,* 2014). Due to very slow growth rates (<1cm per year, on average around 1mm/year), recovery from disturbances take a very long time or is impossible (Barbera *et al.,* 2003; Blake and Maggs, 2003; Hall-Spencer *et al.,* 2010; Brodie *et al.,* 2014).

Ocean warming is expected to have severe effects on maerl beds as their fragmented ranges and poor dispersal capacity makes them vulnerable to local extinction (Hall-Spencer *et al.,* 2010). Maerl species are expected to be affected directly, but information about thermal limits is missing. So far only indirect effects of warming via water quality and increases of invasive species have been associated with negative impacts of warming. Also, there is the possibility of regime shifts as fleshy seaweeds may be favoured over maerl under warming conditions, leading to major changes in maerl bed functioning and productivity (Hall-Spencer *et al.,* 2010; Noisette *et al.,* 2013).

protection or contribute to carbon capture and storage (Løvåsand Tørum, 2001; Duarte *et al.*, 2013a, Hill *et al.*, 2015).

The monetary value that these seaweed ecosystems contribute to society is difficult to estimate, mainly because of a lack of studies valuing ecosystem services specifically provided by seaweeds (in contrast to, for example, corals) (Bennett *et al.*, 2016). However, in Australia Bennett *et al.* (2016) estimated the direct contribution to gross domestic product (GDP; activities such as fishing and reef-related tourism) from the seaweed-dominated Great Southern Reef to be at least A$1,400 $ha^{-1}year^{-1}$, and account for more than 15% of regional economies. However, this estimate does not include substantial indirect values such as coastal protection, nutrient cycling, carbon storage and biodiversity. Estimates for more broadly defined marine macrophyte communities which do consider these indirect values place seagrass and seaweed beds as the third most productive systems globally, providing ecosystem services valued at ~US$30,000 $ha^{-1}year^{-1}$ (Costanza *et al.*, 2014). Even this is most likely a considerable under-estimation; coral reefs were recently found to be worth more than 40 times previous estimates, mainly because of new studies valuating additional ecosystem services (Costanza *et al.*, 2014). Properly valueing seaweed dominated ecosystems will likely reach similar conclusions (Bennett *et al.*, 2016).

3.3.3 Trends and impacts

Temperature plays a pivotal role in the biogeography of seaweeds. Distribution limits of individual species typically follow major marine isotherms (Van den Hoek, 1982b; Lüning, 1990), giving rise to strong relationships between seaweed communities and the temperature signatures of major ocean gradients (Broitman *et al.*, 2001; Schilsand Wilson, 2006; Tuya *et al.*, 2012; Wernberg *et al.*, 2013a). For seaweeds, these patterns are a product of two types of temperature thresholds: lethal boundaries, determined by the capacity to survive during the unfavourable season, and growth and reproduction boundaries, determined by the ability to grow and reproduce during the favourable season (Van den Hoek, 1982b; Lüning, 1990). In addition to these direct physiological effects determining the potential ecological niche, there is increasing evidence of indirect effects mediated by changing, sometimes novel, species interactions and abiotic conditions. Specifically, the consumption of temperate seaweed by range-shifting tropical herbivores also contribute to set, maintain, or change distribution limits of seaweeds, thus shaping the realized niche (Haraguchi *et al.*, 2009; Vergés *et al.*, 2014a, b; Bennett *et al.*, 2015a; Franco *et al.*, 2015; Takao *et al.*, 2015). Similarly, coastal darkening and ice free zones, indirect abiotic effects caused by retreating

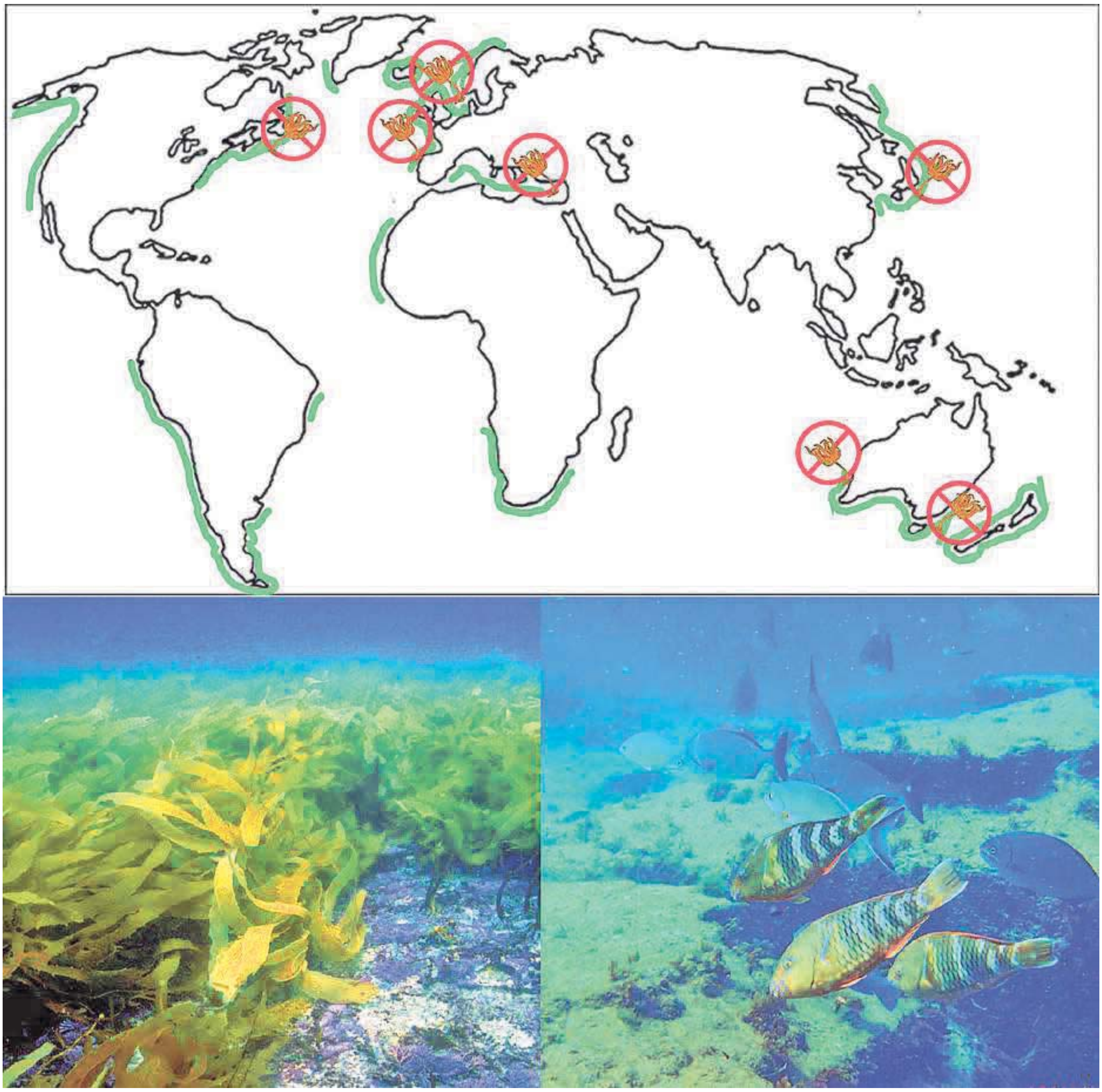

Figure 3.3.2 Seaweeds dominate intertidal and shallow subtidal rocky reefs along ~25% of the world's coastline. The map show the global distribution of seaweed forests (green, adapted from Steneck and Johnson, 2013). However, ocean warming has led to regime-shifts in several regions (red symbols), where complex, highly productive seaweed forests have been lost and replaced by structurally simple coralline crusts, filamentous turf or small foliose seaweeds. The photos show rocky reef habitats in Western Australia before (2005) and after (2013) a marine heatwave caused a 100 km range contraction of kelp (*Ecklonia radiata*). At the same time, subtropical and tropical herbivorous fishes such as parrotfish (*Scarus* sp.) increased substantially in abundance and they now suppress the recovery of kelp forests (Wernberg *et al.*, 2016a). © T. Wernberg.

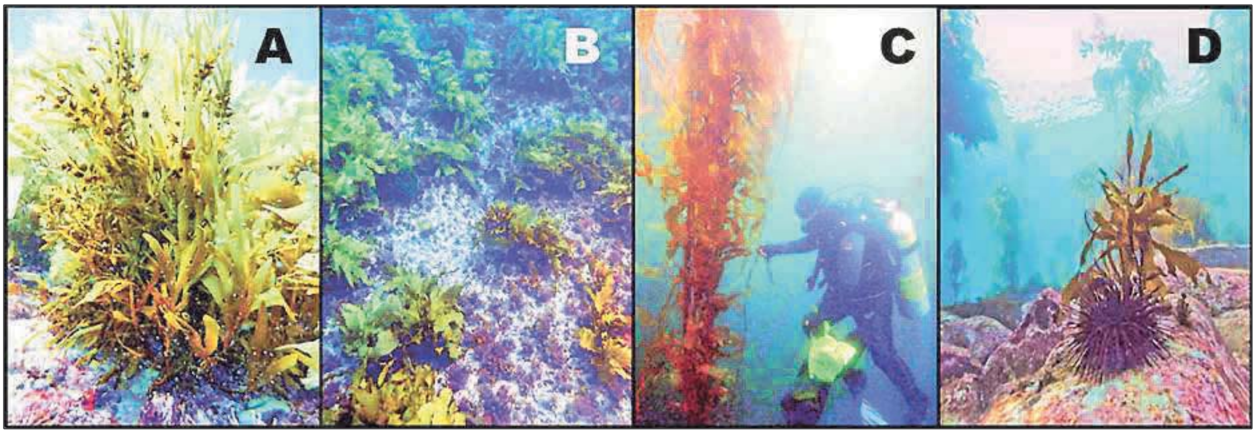

Figure 3.3.3 Seaweeds under threat from warming. In Western Australia, the ~0.5-1 m tall fucoid *Scytothalia dorycarpa* (A) succumbed to direct physiological stress associated with an extreme marine heatwave, causing a 100 kilometre range-contraction and leaving behind big gaps in the surrounding canopy cover leaving patches of *Ecklonia radiata* (B) (Smale and Wernberg, 2013) (In Tasmania, giant kelp (*Macrocystis pyrifera*) (C) has been in dramatic decline due to decreasing nutrient levels and increasing temperatures, and together with common kelp (*Ecklonia radiata*) has been severely impacted by range-extending sea urchins (*Centrostephanus rodgersii*) (D) (Johnson *et al.*, 2011). © Photos A, B, C. Wernberg T.; Photo D. Ling S.

ice-borders, are shaping local seaweed communities on Arctic and Antarctic rocky shores. The net effects can, however, be in opposing directions as ice free zones provide new habitat for seaweed colonization, increasing biomass and diversity, whereas glacial melt reduces salinity and increases turbidity, altering production rates and causing an upward shift of seaweed distributions (Bartsch *et al.*, 2012, 2016; Deregibus *et al.*, 2016). In other words, changes in temperature directly alters the distribution and abundance of seaweeds, associated species and abiotic conditions which in turn has unprecedented indirect consequences for interactions, food web structure and habitat configuration in seaweed dominated ecosystems (Wernberg *et al.*, 2011a; Harley *et al.*, 2012; Vergés *et al.*, 2014a; Straub *et al.*, 2016).

Kelps are cool-water organisms and kelp forests and other temperate to polar seaweed ecosystems are particularly under threat from direct and indirect effects of ocean warming (Figures 3.3.2 and 3.3.3) (Johnson *et al.*, 2011; Wernberg *et al.*, 2011a; Vergés *et al.*, 2014a). Globally many rocky reefs previously dominated by kelp forests have experienced regime-shifts due to warming in the past 2-3 decades, where kelps have been replaced by turfs or crustose coralline algae (Connell and Russell, 2010; Andersen *et al.*, 2011; Ling *et al.*, 2015). This has been observed in western Australia (Wernberg *et al.*, 2016a), Tasmania (Ling *et al.,* 2015), eastern Canada (Filbee-Dexter *et al.*, 2016), southern Norway (Andersen *et al.*, 2011; Moyand Christie, 2012) and northern Spain (Díez *et al.*, 2012; Voerman *et al.*, 2013).

In Nova Scotia, warming over several decades has exceeded the temperature threshold of the main canopy-forming seaweeds (*Saccharina latissima*, *Laminaria digitata*) causing an 85-99% decline in kelp forests and a shift to turf-dominated rocky reefs and invasive seaweeds (Filbee-Dexter *et al.*, 2016). Sediments are now stabilizing the new turf state, making it virtually irreversible (Filbee-Dexter *et al.*, 2016). A similar regime-shift has occurred in southern Norway, where sugar kelp (*Saccharina latissima*) (Figure 3.3.4) has been lost and replaced by filamentous seaweeds following decades of warming and eutrophication (Moyand Christie, 2012). In Norway most sugar kelp forests along the more sheltered areas disappeared in, 2002 after several warm summers, and a reduction in sugar kelp distribution has also been observed in Sweden, Denmark and Germany, with increased sea temperatures, nutrients and epiphytism, and particle levels suggested as the main reasons (Andersen *et al.*, 2011; Bekkby and Moy, 2011; Moy and Christie, 2012)

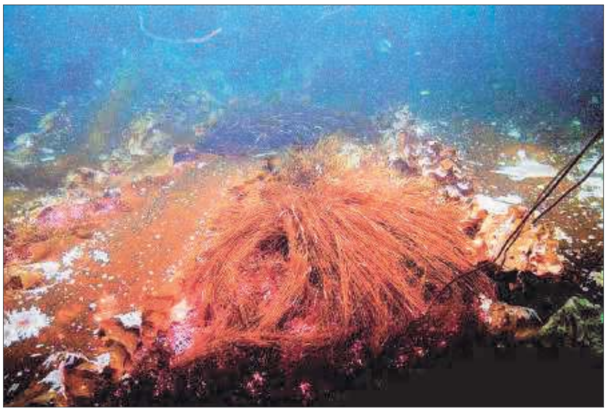

Figure 3.3.4 Sugar kelp (*Saccharina latissima*) and other filamentous brown algae. © SNH.

In contrast to changes seen over decades of gradual warming, in Western Australia kelp forests collapsed when extreme temperatures exceeded the physiological limit during a marine heatwave (Smale and Wernberg, 2013; Wernberg *et al.*, 2013b). Over a few months kelp (*Ecklonia radiata*) and strapweed (*Scytothalia dorycarpa*), an endemic fucoid, disappeared from extensive areas, causing a 100 km range contraction of both species and substantial re-configuration of the benthic ecosystem (Figures 3.3.2 and 3.3.3 A,B). These seaweeds have also been replaced by turfs, recovery being suppressed by herbivorous fishes (Bennett *et al.*, 2015a; Wernberg *et al.*, 2016a).

3.3.3.1 Physiological impacts

Seaweeds have a temperature range within which they can survive, and an optimum temperature where processes like growth and photosynthesis are reaching their maximum. These direct physiological effects of temperature are associated with the mechanics of cellular processes (protein stability, enzyme activity, membrane permeability, etc.) (Davison, 1991; Kordas *et al.*, 2011).

Temperature dependency of physiological performance has been documented for many seaweeds, including crayweed (*Phyllosphora comosa*), a temperate fucoid endemic to south-eastern Australia. Flukes *et al.* (2015) demonstrated how photosynthesis, growth and survival were negatively affected at current summer maximum temperatures. This implies that unless rapid adaptation occurs, continued warming of south-eastern Australia, which has been warming four times faster than the global average, will have strong negative impacts on the distribution and abundance of *P. comosa* (Flukes *et al.*, 2015). Similarly, reproduction (sporogenesis) in *Laminaria digitata*, (Figure 3.3.5) a summer reproductive kelp, was negatively affected during warm summers at Helgoland (Germany) indicating that reproduction is the limiting life cycle stage and that future summer warming could further restrict the distribution of this species (Bartsch *et al.*, 2013).

Figure 3.3.5 *Laminaria digitata* exposed at extreme low water spring. © John M Baxter.

In most cases, however, warming is likely to be sublethal with physiological effects manifesting through altered requirements for, or availability of, resources such as light and nutrients or reduced capacity to respond to other perturbations. Photosynthesis and respiration rates in seaweeds are temperature dependent (Davison, 1991; Wiencke *et al.*, 2006; Staehrand Wernberg, 2009; Wernberg *et al.*, 2016b) and warming increases the light requirements to maintain a positive metabolic balance. This implies a reduction in depth of the compensation point and an increased sensitivity to reduced water quality (Staehr and Wernberg, 2009). Subtle differences in physiological performance breadth (temperature range over which net photosynthesis is greater than 80% of maximum, Eggert *et al*., 2003; Wernberg *et al.*, 2016b) were found to correspond with differences in distribution as well as responses to a marine heatwave for three seaweeds along a temperature gradient in Western Australia (Wernberg *et al.*, 2016b). *Scytothalia dorycarpa* had a narrower performance breadth over cooler temperatures than *Sargassum fallax*; the species were distributed towards cooler and warmer latitudes, respectively and over three consecutive warm summers *S. fallax* populations expanded where *S. dorycarpa* populations perished or diminished (Smale and Wernberg, 2013; Wernberg *et al*., 2016a).

Warming-induced changes in nutrient and light availability have also been associated with changes in seaweed populations. For example, a dramatic 95% decline in Australian giant kelp (*Macrocystis pyrifera*) forests has been attributed to increasingly frequent incursions of warm nutrient poor water from the East Australia Current (Johnson *et al.*, 2011, Figure 3.3.3D), and in the Arctic warming has led to changes in abundance and depth distribution of several seaweeds, although the responses reflect a complex interaction between the opposing forces of reduced ice cover (more light) and glacial melt reducing salinity and increasing turbitidy (less light) (Krause-Jensen *et al.*, 2012; Bartsch *et al.*, 2016).

Most seaweeds can adjust their metabolic machinery to accommodate variation of temperature regimes

(Davison, 1991; Eggert, 2012). However, these changes can have consequences for the ability to respond to changes in other environmental factors. Sporophytes of the kelp *Ecklonia radiata* exhibit substantial differences in physiology under different climatic conditions with warm-adjusted kelp showing 50% lower photosynthetic rates and 90% lower respiration rates at optimal temperature in comparison to cool-adjusted kelps (Staehrand Wernberg, 2009). The kelp optimizes its metabolic balance under elevated temperatures through a reduction in the temperature sensitivity of photosynthesis and respiration (Wernberg *et al.*, 2010). However, these changes are linked to supressed capacity to respond physiologically to changes in light levels and disturbance regimes – and therefore lower kelp forest resilience - presumably because the cellular processes involved in temperature control also are critical to regulating responses to other conditions such as light levels (Wernberg *et al.*, 2010).

For some species warming might have a direct positive physiological effect but with negative indirect consequences. Endo *et al.* (2013) found that *Sargassum patens* had a higher growth rate under elevated temperatures, which led to lower phlorotannin (defensive compound) concentration in the upper parts of the thallus, making the apical meristems more palatable to herbivorous fishes feeding during warm summer temperatures. A similar effect was seen for the kelp *Agarum clathratum* in Nova Scotia (Simonson *et al.*, 2015). Overall, however, effects of temperature on the secondary chemistry of seaweeds are still poorly understood.

3.3.3.2 Impact on reproduction and early life-cycle stages

Life cycle events are often tightly cued to seasonal changes in environmental conditions and many seaweeds exhibit distinct temporal patterns in reproduction and recruitment, often with species- and life-stage specific temperature thresholds (Steinhoff *et al.*, 2011; Bartsch *et al.*, 2013; Mohring, 2013; Andrews *et al.*, 2014; Bennett *et al.*, 2015b).

Temperature-mediated mismatches in the timing of life cycle events could have substantial impacts on seaweeds. For example, the annual brown seaweed *Desmarestia viridis* accumulates sulphuric acid during growth from recruit to adult. Summer temperatures trigger a synchronized die-off by mass releases of sulphuric acid at the time of reproductive maturity (Gagnon *et al.*, 2013). However, *D. viridis* has a low temperature tolerance, and further warming could initiate die-off before reproductive maturity (Gagnon *et al.*, 2013).

Early life stages are usually more sensitive to warming than the later stages, and the thresholds for impact can be abrupt. For example, in Arctic Norway 98% of kelp zoospores (*Saccorhiza dermatodea*) germinated between 2-12°C, but above 12°C (the projected local temperature at the end of century) germination declined by 80% at 17°C (Steinhoff *et al.*, 2011). Similarly, in Tasmania early development of *Ecklonia radiata* gametophytes and sporophytes peaked between 15-22°C, but decreased above 22°C where no sporophytes developed (Mabin *et al.*, 2013). Temperature responses for early life stages sometimes reflect a trade-off between growth and survival. For germlings of *Fucus serratus* in Scotland (Figure 3.3.6), increasing temperature had a positive effect on growth while simultaneously also causing lower survival (Nielsen *et al.*, 2014). A similar response has also been reported for kelp (*E. radiata*) gametophytes in Australia, where gametophytes grown under warm conditions were larger but had lower survival than those grown under cool conditions (Mohring *et al.*, 2014).

Figure 3.3.6 *Fucus serratus*. © John M Baxter.

3.3.3.3 Impacts of herbivores

A widely documented consequence of ocean warming is the poleward range shift in the distribution of many marine taxa, including herbivorous fishes and sea urchins (Ling *et al.*, 2009a; Bates *et al.*, 2013; Feary *et al.*, 2014; Vergés *et al.*, 2014a; Figures 3.3.2 and 3.3.3D). The effects have been most pronounced where ocean current run poleward, pushing warm water and subtropical and tropical species towards temperate latitudes (e.g. western boundary currents, Vergés *et* *al.*, 2014a). Herbivorous fishes have traditionally been considered to play a minor role in structuring temperate benthic communities (Choat, 1982). However, evidence is emerging that range-expanding subtropical and tropical fishes are having strong impacts on ecologically important temperate seaweeds - overgrazing by tropical herbivores has been documented on temperate reefs in the Mediterranean Sea (Vergés *et al.*, 2014b), around Japan (Haraguchi *et al.*, 2009), and in Australia (Vergés *et al.*, 2014a; Bennett *et al.*, 2015a).

In the Mediterranean Sea, canopy seaweeds (*Sargassum vulagere* and *Cystoseira compressa*) have become 65% less abundant where two species of tropical rabbitfishes have become dominant (Vergés *et al.*, 2014b). In Japan, kelps (*Ecklonia cava*) declined due to the combined effects of ocean warming and fish and urchin herbivory (Haraguchi *et al.*, 2009) whereas in Western Australia subtropical and tropical herbivorous fishes have kept seaweeds from recovering after they were decimated by an extreme marine heatwave (Bennett *et al.*, 2015a; Wernberg *et al.*, 2016a; Figure 3.3.2). A common feature in these cases has been that herbivores have not simply increased in abundance but also in functional diversity; temperate fish were found to feed only on adult seaweeds, whereas new subtropical and tropical fishes such as rabbitfishes feed both on adult seaweed and on seaweed recruits (Vergés *et al.*, 2014b; Bennett *et al.*, 2015a).

Overgrazing can also occur by warm temperate species, as documented in Portugal where intense fish and urchin herbivory at a warm location restricted kelps to crevices with zero survival in open habitat. This contrasted with a cool location where herbivory was virtually absent (Franco *et al.*, 2015). In south-eastern Australia, the warm-temperate sea urchin *Centrostephanus rodgersii* expanded its range into Tasmania as a consequence of ocean warming. Here, populations expanded due to overfishing of urchin predators (large lobsters), triggering overgrazing resulting in widespread decimation of foliose seaweeds and establishment of extensive urchin barrens (Ling *et al.*, 2009b, 2015; Johnson *et al.*, 2011), which are characterized by low structural complexity and primary productivity, and low food web complexity) (Filbee-Dexter and Scheibling, 2014). Shifts from kelp forests to urchin barrens have also been observed in Canada, Norway, New Zealand and many other places (Filbee-Dexter and Scheibling, 2014 and references therein). In some systems barrens have existed for more than 40 years (Newfoundland, Canada), while other systems are undergoing repeated regime shifts between urchin barrens and kelp beds, either as a consequences of variation in top predators (sea otters, Aleutian Islands and California) or changing oceanographic conditions (California, Maine and northern Chile) (Filbee-Dexter and Scheibling, 2014 and references therein).

3.3.3.4 Interactions between warming and other stressors

Warming is arguably the most pervasive environmental stressor associated with global climate change. However, warming rarely operates independently of other regional and local conditions. Instead multiple stressors interact cumulatively and exposure to one stressor can affect the tolerance to another stressor (Campbell *et al.*, 2011; Wernberg *et al.*, 2011a; Nema *et al.*, 2012; O'Brien *et al.*, 2015; Simonson *et al.*, 2015, Xiao *et al.*, 2015).

Warming can reverse grazer-macroalgal interactions, and wave action and temperature have been found to have interactive effects on macroalgal assemblage structure (Mrowicki and O'Connor, 2015). Similarly, warming can affect the direction of interactions between seaweeds with competitive (negative) interactions under cool conditions and facilitative (positive) interactions under warm conditions (Wernberg *et al.*, 2010; Bennett and Wernberg, 2014; Bennett *et al.*, 2015c).

Studies in Nova Scotia have shown that warmer temperatures increase outbreaks of kelp encrusting bryozoans (*Membranipora membranacea*) (Saunders and Metaxas, 2008; Scheibling and Gagnon, 2009) as well as altering feeding and metabolic rate of herbivores (O'Connor, 2009). The cumulative effects of direct temperature damage to kelps, increased encrustation by bryozoans, which increases kelp fragmentation and reduces kelp reproduction, and higher herbivory rates resulted in weakened seaweeds that were more vulnerable to disturbances during storms (Chapman *et al.*, 2002; Simonson *et al.*, 2015).

Warming can also interact with other anthropogenic changes in the environment. High pCO_2 (ocean acidification) and elevated temperature can interact synergistically in their effects on early life stages of the giant kelp *Macrocystis pyrifera* with detrimental effects on germination and mortality of zoospores (Gaitán-Espitia *et al.*, 2014). Similarly, the cumulative effects of warming and UVB radiation have been found to severely inhibit growth and photosynthesis of three habitat-forming seaweeds (*Ecklonia radiata*, *Scytothalia dorycarpa*, *Sargassum* spp.) from Western Australia (Xiao *et al.*, 2015). Interestingly, responses showed that species-specific sensitivity and acclimation potential might alter the balance and competitiveness between these dominant canopy-formers in the future (Xiao *et al.*, 2015).

It is noteworthy, however, that warming is not always a stressor and that the combined effects of multiple stressors are not always negative. For example, in the Arctic, zoospores of the kelp *Alaria esculenta* were found to be less vulnerable to UV radiation in warm (7°C) compared to cold (2°C) conditions (Olischläger and Wiencke, 2013). Whether or not the cumulative effects of multiple stressors are agonistic or antagonistic likely depends on species, life stages, season or where in the tolerance range the stressors are. Importantly, a recent review of marine climate change experiments showed both an over-representation of single-factor studies and an under-representation of marine macrophytes including seaweeds (Wernberg *et al.*, 2012). Moreover, only very rarely do studies adopt a complete life cycle approach (Russell *et al.,* 2012) where the vulnerability of all life stages are assessed (see Bartsch *et al.*, 2013 for a rare example). This highlights strong knowledge gaps in the understanding of cumulative effects of multiple stressors on seaweeds, and what life stages will be limiting seaweed distribution and performance in the future.

3.3.3.5 Impacts of pathogens

It is expected that seaweed disease outbreaks will increase in occurrence and severity because ocean warming and other anthropogenic stressors make seaweeds more susceptible to opportunistic pathogens while also increasing their virulence (Gachon *et al.*, 2010; Campbell *et al.*, 2012; Egan *et al.*, 2014).

Warming has been linked to shifts in surface bacterial assemblages leading to bleaching and reduced levels of chemical defences in the red seaweed *Delisea pulchra*. (Campbell *et al.*, 2011). Similarly, microbial communities have been linked to bleaching in kelp (*Ecklonia radiata*) where bleached individuals suffered lower photosynthetic efficiency reducing overall kelp performance (Marzinelli *et al.*, 2015). In general, however, little is known about the role and prevalence of pathogens in natural seaweed populations (but see also Bengtsson *et al.*, (2012) and Campbell *et al.*, (2015).

3.3.3.6 Range shifts

To date, only one seaweed species has been declared globally extinct (Brodie *et al.*, 2009). However, the multitude of effects of warming on seaweed physiology and ecological interactions ultimately lead to changes in distribution as a consequence of local extinctions (Bates *et al.*, 2014). Several warming-related shifts in seaweeds distribution ranges have been documented globally (Sorte *et al.*, 2010; Wernberg *et al.*, 2011b, 2016a; Harley *et al.*, 2012; Poloczanska *et al.*, 2013; Straub *et al.*, 2016; Table 3.3.1). These range shifts have included both contractions at the equatorward range-edge, and expansions at the poleward range-edge (Straub *et al.*, 2016). It is noteworthy that range contractions and expansions are fundamentally different processes, and require substantially different evidence to document. Range contractions require the elimination of all individuals of a species whereas range expansions only require the successful establishment of one or a few individuals in a new habitat (Bates *et al.*, 2014). Contractions are often preceded by periods of declining abundance and failed recruitment while adult individuals persist in the unfavourable area (Hampe and Petit, 2005; Bates *et al.*, 2014), in other cases contractions can be abrupt, when temperatures greatly exceed thermal tolerances (Smale and Wernberg, 2013; Wernberg *et al.*, 2016a).

In northern Spain, range contractions have been reported for several canopy-forming seaweeds including *Fucus serratus* and *Himanthalia elongata* (Figure 3.3.7) which have shifted westwards in the Bay of Biscay in response to warming since the late, 19th Century (Duarte *et al.*, 2013b). *H. elongata* shifted 330 km over 120 years, whereas *F. serratus* shifted, 197 km over 114 years and also declined dramatically in abundance in its remaining range. For both species the rate of contraction

Figure 3.3.7 *Fucus serratus* and *Himanthalia elongata* luxuriant growth on shore in Orkney. © John M Baxter.

Table 3.3.1 Summary statistics for recently observed climate-driven range-shifting seaweeds. The taxa listed are those for which sufficient data exists to estimate range-shift distance and speed (from Straub *et al.,* 2016)

	Extension (22 taxa)	**Contraction (n=9 taxa)**
Median shift (range)	192 km (26 – 593)	116 km (35-1250)
Median time (range)	50 years (2 – 75)	31 years (1- 66)
Taxa (n=41)	*Ahnfeltia plicata* *Bifurcaria bifurcata* *Chondrus crispus* *Codium adhaerens* *Desmarestia aculeata* *Desmarestia ligulata* *Dumontia contorta* *Ecklonia maxima* *Fucus serratus* *Fucus vesiculosus* *Halidrys siliquosa* *Halopithys incurva* *Himanthalia elongata* *Hypnea musciformis* *Laminaria ochroleuca* *Padina pavonica* *Palmaria palmata* *Pelvetia canaliculata* *Sargassum flavifolium* *Sargassum illicifolium* *Turbinaria ornata* *Valonia utricularis*	*Assemblage (collection of species)* *Durvillea potatorum* *Ecklonia radiata* *Fucus serratus* *Fucus vesiculosus* *Himanthalia elongata* *Sargassum micracanthum* *Sargassum yamamotoi* *Scytothalia dorycarpa*

appears to have accelerated in recent years (Duarte *et al.*, 2013b). The ecological implications of these two range contractions are largely unknown (Duarte *et al.*, 2013b), although both species (and several other large, retreating canopy-forming seaweeds) are important habitat-formers for smaller epiphytes and mobile animals (Hawkins and Hartnoll, 1985; Wernberg *et al.*, 2004; Ingólfsson, 2008; Thomsen *et al.*, 2010).

The warm-water kelp *Laminaria ochroleuca* was first recorded in England in 1948, and subsequently expanded its range eastwards to the Isle of Wright at a rate of 5.4 km per year, as well as expanded northwards to Lundy Island at a rate of 2.5 km per year (Straub *et al.*, 2016). Recent re-surveys of the inhabited area suggest that *L. ochroleuca* also expanded from the initially colonized sheltered coastline to moderately wave-exposed open coasts, accompanied by a significant increase in abundance, most likely in response to recent warming (Smale *et al.*, 2014). In the area where *L. ochroleuca* most recently colonized, it competes with the native dominant *L. hyperborea*. As both species appear morphologically and functionally similar, it was initially assumed they would have similar ecosystem function with little impact on the colonized ecosystem (Terazono *et al.*, 2012). However, even small morphological differences may incur large cascading ecosystem effects. For example, Smale *et al.* (2014) showed that epiphyte load on the smoother stipe of *L. ochroleuca* was dramatically lower than on the rough stipes of *L. hyperborea* (Figure 3.3.8). Thus, a reduction of the epiphytic habitat can be expected if *L. ochroleuca* replaces *L. hyperborea*, potentially with dramatic effects on associated fauna (Christie *et al.*, 2009),

Figure 3.3.8 Heavy epiphytic growth on the stipes and fronds of *Laminaria hyperborea*. © SNH.

trophic interactions (Smale *et al.*, 2014) and biodiversity (Thomsen *et al.*, 2010).

These range shifts are potentially irreversible with great impacts on ecosystems (Madin *et al.*, 2012; Wernberg *et al.*, 2016a). Additionally, species where there is no suitable habitat at their cold range limits will be particularly vulnerable to warming as they can only contract, but not expand their range as no new colonization is possible (Burrows *et al.*, 2011, 2014). This also poses the risk of range contractions leading to extinctions where endemic species run out of habitat. This is a particularly important issue in the southern hemisphere where there are no sub-Antarctic landmasses (Wernberg *et al.*, 2011b). An often overlooked consequence of range-contractions is the risk of losing genetic diversity. Several European seaweeds have a disproportionally large fraction of their genetic diversity concentrated at their warm range-edge (a consequence of glacial refugia) (Provan and Maggs, 2012).These unique genetic linages are threatened by local extinctions of the species. For example, while the persistence of the canopy-forming seaweed *Bifurcaria bifurcata* is not threatened, local extinction in Morocco, which is expected by the end of the century, would cause a reduction in global genetic diversity of this species (Neiva *et al.*, 2015). Another example is the seaweed *Fucus vesiculosus*, where local extinctions at its southern range edge in the eastern Atlantic have been documented over the past 30 years, causing the loss of several genetic lineages (Assis *et al.*, 2014). Similarly, for the red seaweed *Chondrus crispus*, where a unique genetic diversity in rear-edge populations in Iberia are in danger of local extinction due to ongoing warming, thus affecting their overall genetic diversity (Provan and Maggs, 2012). All studies concluded that loss of unique lineages, reducing the genetic pool of the seaweeds, compromises their adaptive potential to respond to future warming and interactive stressors (Provan and Maggs, 2012; Assis and Perrin, 2014; Neiva *et al.*, 2015).

A critical problem is that information on species' range boundaries is scarce and largely qualitative due to lack of baseline information and regular surveys (Wernberg *et al.*, 2011a; Bates *et al.*, 2015; Marcelino and Verbruggen, 2015; Straub *et al.*, 2016).

3.3.4 Conclusions and recommendations

There is overwhelming evidence that seaweeds are impacted by ocean warming globally, affecting species as well as associated communities, altering whole ecosystems with likely substantial impacts on valuable ecosystem services.

Effects include direct physiological limitations of metabolism and reproduction as well as indirect effects mediated through changes in ecological interactions such as herbivory and competition. The relative importance of direct physiological effects and indirect effects through other abiotic pathways and species interactions is still poorly understood. It is also clear that warming often compounds effects of other natural and anthropogenic stressors magnifying their effects. Still, only relatively few studies have tested the effects on seaweeds of warming in combination with other factors and rarely has the vulnerability of all life stages been tested. It is recommended that more studies attempt to isolate the mechanisms that drive changes in seaweed populations, especially to distinguish direct from indirect effects of warming and the role of multiple stressors. It is also recommended that more studies adopt a complete life-cycle approach to identify which life stages will be limiting the distribution and performance of seaweed populations in the future.

There is substantial evidence from several continents that warming affects the biogeography of seaweeds, but changes in distribution are often hard to establish due to lack of consistent high resolution baseline information. Some regions, such as South America, are greatly under-represented. This is likely a consequence of data deficiency. It is recommended that more effort is directed to establishing and monitoring species abundances and boundaries to enable early detection of changes.

The long-term ecological and economic consequences of warming are still to be realized for most seaweed dominated systems. The impacts are, however, likely to be substantial considering the array of ecological functions and ecosystem services provided by seaweeds. There are however substantial knowledge-gaps around the variety of ecological services seaweed systems provide and, in particular, the values these services contribute to local and regional economies. It is recommended that more studies establish the nature and value of ecological functions seaweeds provide to better understand the flow-on effects on humans of warming-mediated changes in seaweed communities.

To date there has been limited focus on solutions and mitigation options. It is recommended that more studies focus on solutions by investigating opportunities for maintaining ecological functions through species replacements (i.e. establish ecological redundancy among different seaweeds) or boosting resilience of cool-adapted populations through assisted *a priori* breeding with warm-adapted populations. Similarly, the viability of reducing impacts of warming by managing additional local stressors such as eutrophication, pollution and overfishing requires more attention. Finally, it is recommended that rehabilitation programmes be developed and their viability tested.

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Causes, scale, effects and consequences

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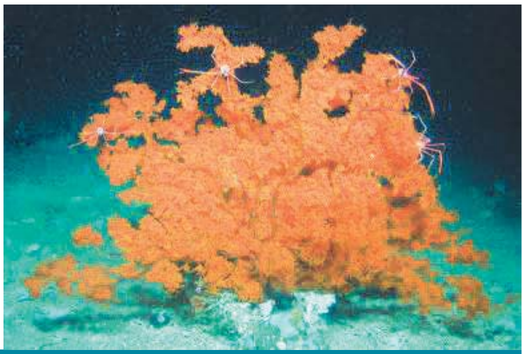

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