

Macroalgae and Temperate Rocky Reefs

Thomas Wernberg¹, Dan A. Smale^{1,7}, Adriana Vergés^{2,3}, Alexandra H. Campbell^{2,3},
Bayden D. Russell⁴, Melinda A. Coleman⁵, Scott D. Ling⁶, Peter D. Steinberg^{2,3},
Craig R. Johnson⁶, Gary A. Kendrick¹ and Sean D. Connell⁴

¹UWA Oceans Institute and School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, Perth 6009, Australia. thomas.wernberg@uwa.edu.au

²Centre for Marine Bio-Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia, 2052

³Sydney Institute of Marine Sciences, Chowder Bay road, Mosman, NSW, 2088
Evolution and Ecology Research Centre, University of New South Wales, Sydney NSW, 2052

⁴Southern Seas Ecology Laboratories, School of Earth and Environmental Sciences, DX650 418, University of Adelaide, South Australia 5005, Australia.

⁵NSW Marine Parks Authority, 9 Burrawang St, Narooma, NSW, 2546, Australia

⁶Institute for Marine & Antarctic Studies, University of Tasmania, Hobart, Tasmania 7001, Australia.

⁷Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, PL1 2PB

Wernberg, T. et al. (2012) Macroalgae and temperate rocky reefs. In *A Marine Climate Change Impacts and Adaptation Report Card for Australia 2012* (Eds. E.S. Poloczanska, A.J. Hobday and A.J. Richardson). <<http://www.oceanclimatechange.org.au>>. ISBN: 978-0-643-10928-5

What is happening

A recent analysis of herbarium records back to the 1940s suggests temperate seaweeds on both east and west coasts of Australia have retreated south 10-50 km per decade as waters have warmed. A recent extreme warming event (marine heatwave) in Western Australia caused substantial changes to seaweed habitats, including a reduction in large habitat forming species. In eastern Tasmania, a substantial decline in algal habitat is associated with southward expansion of a grazing sea urchin aided by the strengthening of the East Australian Current and warmer temperatures.

What is expected

Warming will reduce the resilience of macroalgal habitats to other stressors such as pollution. Temperate species will contract their ranges southwards and tropical species expand their ranges further south. Many temperate species, found only in Australia, are at risk of extinction in the next 50-100 years. Extreme events (storms, heat waves, etc) will increase in frequency and magnitude and drive shifts in species' distributions and interactions.

Macroalgae

What we are doing about it

IMOS Autonomous Underwater Vehicle Facility will provide long-term monitoring of water properties and temperate reefs at key locations in Qld, NSW, Tas and WA. Several research projects focusing on climate change and temperate macroalgae are under way. These focus both on establishing the range of impacts as well as the mechanistic relationships which drive impacts of climate change.

Introduction

The Australian continent is bounded to the south by a temperate coastline more than twice the length of the Great Barrier Reef. It straddles three biogeographic provinces (Waters et al. 2010) where rocky reefs dominated by macroalgae (seaweeds) are a defining feature throughout (e.g., Underwood et al. 1991, O'Hara 2001, Wernberg et al. 2003, Connell and Irving 2008, Smale et al. 2010).

Australia has one of the most species rich and endemic temperate algal floras in the world (Bolton 1994, Kerswell 2006), and it contributes substantially to the unique biodiversity of the Australian continent. Climatic stability over geological time has been one of the key conditions mediating the evolution of this unique algal flora (Phillips 2001, Kerswell 2006), and given the current rate of global climate change there is now serious concern for its continued existence (Johnson et al. 2011, Wernberg et al. 2011b). However, it is not only the biodiversity of algae themselves that is under threat; macroalgae are foundation species that facilitate the existence of a myriad of equally unique associated marine life (Connell 2003, Wernberg et al. 2005, Coleman et al. 2007, Ling 2008, Tuya et al. 2008). Impacts of climate change on macroalgae are therefore likely to have disproportionately large ecological consequences across entire temperate marine ecosystems.

The previous assessment concluded that there is clear evidence that organisms on temperate rocky reefs are vulnerable to the direct and indirect impacts of climate change, and that observed responses to date are largely consistent with increasing ocean temperature (Wernberg et al. 2009). In particular, it was found that the poleward extension of the East Australian Current and associated increasing water temperatures have caused a poleward range shift for sea urchins, leading to overgrazing and loss of algal habitat (high confidence), habitat forming algae (low confidence) and invasive species (low confidence) in eastern Australia. Very few changes attributable to climate change had been recorded on the south and west coasts (low confidence). These changes were discussed in more detail in Johnson et al. (2011) and Wernberg et al. (2011b). Here we update these assessments, reporting on observed changes in temperate marine macroalgae and their interacting ecological systems, directly or indirectly related to climate change.

Observed impacts

Multiple stressors

A key finding of the previous assessment was that almost all observed impacts possibly related to climate change in temperate Australia (and internationally) involved multiple stressors. For example, losses or declines of habitat forming macroalgae over the past decades were attributed to historical overfishing of herbivore predators (Ling et al. 2009), pollution and reduced water quality associated

Macroalgae

with urbanization (Coleman et al. 2008, Connell et al. 2008). Similarly, changes to the distribution and abundance of fishes in southeastern Tasmania have been attributed to a combination of climate change and fishing pressure (Last et al. 2011). While all of these changes have been observed over a period of intense warming (Pearce & Feng 2007, Ridgway 2007), the direct link to climate change is circumstantial in all cases except for overgrazing by range-shifting urchins in Tasmania. As highlighted in recent reviews (Johnson et al. 2011, Wernberg et al. 2011b, Russell & Connell 2012), the lack of strong links to climate change is possibly due to a combination of the fact that multiple stressors, interacting across disparate spatial and temporal scales, have been increasing in intensity concomitantly and that climate change rarely is the proximate cause of impact. Compounding this is the fact that, relative to many other regions of the world, historical baseline data span short time scales, and so provides only a partial picture of scales of natural temporal variability. To that end, understanding how climate change might have altered underlying ecological patterns and processes remains a challenge. Spatially-extensive surveys conducted across temperate Australia in the last two decades will help to alleviate these difficulties in the future (e.g., Stuart-Smith et al. 2009) as will the long-term continuation of recently established broad-scale monitoring programs (cf. the AUV program mentioned in section 9. Current and planned research effort).

A recent study in Western Australia showed how physiological adjustments (an individual-level effect) in habitat-forming kelps (*Ecklonia radiata*) in warm water resulted in lower resilience of the kelp bed (a habitat-level effect) to additional perturbations (Wernberg et al. 2010). This study is important because it provides a mechanistic framework for understanding how climate change, through sub-lethal stress associated with slightly elevated mean temperature, can increase ecosystem vulnerability to multiple stressors.

Temperature

The best documented environmental change is that temperatures have increased substantially over the past ~5 decades (Pearce & Feng 2007, Ridgway 2007). Despite these well documented physical changes, there is still relatively little consistent evidence for impacts on macroalgae and associated temperate reef organisms. Previously, Millar (2007, 2009) suggested that several species of large brown algae had retreated south on the east coast of Australia in response to warming. A more recent quantitative analysis of temperate macroalgae on both sides of the continent supported this contention, and indicated flora-wide changes at the tropical-temperate boundary on both coasts as well as median southward shifts across the temperate flora in the order of ~10-50 km per decade (Wernberg et al. 2011a). The findings of Millar and Wernberg et al. are, however, based on anecdotal evidence and herbarium records, and need verification by field collections (see also 6.1 Amount of evidence). In any case, the latter study also highlighted how the east-west orientation of Australia's temperate coastline predisposes flora and fauna to potential species extinctions from southward shifting isotherms. Importantly, this applies not only to macroalgae but all organisms associated with temperate, shallow subtidal habitats.

Intertidal invertebrates, which can interact with and potentially control the abundance and distribution of macroalgae, have also been found to shift south at a rate of ~30 km decade around Tasmania (Pitt et al. 2010). In contrast, no or only few changes were seen towards the northern end of the temperate zone on the east coast (Poloczanska et

Macroalgae

al. 2011). Several species of herbivorous fishes (*Girella tricuspidata*, *G. elevata*, *G. tricuspidata*, *G. zebra*, *Aplodactylus lophodon* and *Kyphosus sydneyanus*) have also shifted south around Tasmania, some up to 200 km (Stuart-Smith et al. 2009, Last et al. 2011).

A key unknown, however, relates to the fact that increases in temperature are often associated with changes in other environmental variables, such as decreased nutrients or increased salinity. This is particularly relevant for southeastern Australia, where a strengthening of the East Australia Current has led to decreased nitrate concentrations and increased salinity, in conjunction with increased temperature (see Johnson et al. 2011). Thus, teasing apart the effects of multiple drivers, and examining interaction effects and possible synergies, is crucial for mechanistic understanding of ecological change.

Atmospheric CO₂, pH and aragonite saturation state, sea- level rise and other climate change factors

Factors other than increasing ocean temperatures have had no observed impacts on macroalgae and other temperate marine organisms in Australia. This lack of observed impacts may stem from two issues. First, there is a general lack of both historical and contemporary data on how ecological processes relate to ocean pH *in situ*. This means there is no base-line with which to assess if changes have already occurred, and a new baseline is not being established for the assessment of future changes. Second, under future climate change scenarios, ocean pH is predicted to drop another 0.3-0.4 units by 2100. Given that many marine organisms appear unaffected by changes of this magnitude, at least in the short term (Hendriks et al. 2010, Wernberg et al. 2012a), the direct effects of ocean acidification on temperate marine ecosystems may not be realised for the next 40-100 years.

Calcifying algae such as encrusting or articulated coralline algae are among the most abundant and widespread organisms on subtidal rocky reefs (Steneck 1986). On the temperate coast of southern Australia, crusts occupy up to 80% of hard substrate, dominating space beneath canopies (Melville & Connell 2001). Recent experimental work in Australia has shown that acidification associated with conservative projections of future CO₂ concentrations (550 ppm) will have negative effects on the growth and recruitment of coralline algae (Russell et al. 2009, Russell et al. 2011). Furthermore, increased [CO₂] and temperature have greater negative effects in combination (~ 700 ppm and 3°C, respectively) than in isolation (Mediterranean coralline algae, Martin & Gattuso 2009). However, more study on temperate coralline algae and macroalgae is required because recent work on some tropical algae suggests that the effects of declining pH are likely to be species-specific and related to mineral composition of the algae, morphology, metabolic processes and environmental characteristics such as light conditions and water flow (Hepburn et al. 2011, Hurd et al. 2011, Nash et al. 2011, Cornwall et al. 2012).

In contrast to coralline algae, elevated [CO₂] may have little negative or even positive effects on non-calcareous algae (Beardall et al. 1998, Connell & Russell 2010, Russell et al. 2011). There is still debate on whether increasing [CO₂] will enhance productivity in marine algae. Most marine algae have carbon concentrating mechanisms (CCMs) which allow them to use bicarbonate for photosynthesis, meaning that photosynthesis is carbon saturated at current concentrations. In the past,

Macroalgae

general consensus within the literature was that algae with CCMs will not increase productivity under future conditions (see review by Beardall et al. 1998), but there are an increasing number of studies showing that ephemeral, fast growing algae respond positively to increased $[\text{CO}_2]$ when in combination with other factors (e.g., temperature, Connell & Russell 2010, elevated nutrients, Russell et al. 2009, Falkenberg et al. 2012). If these normally ephemeral algae become persistent, the likelihood that they will displace larger canopy-forming algae is increased in locations in which these are susceptible to bloom (Harley & Connell 2009). In any case, there are substantial knowledge-gaps in our understanding of how macroalgae might respond to changes in ocean pH, including the role of metabolically driven short-term fluctuations in pH in buffering or exacerbating climate induced changes (Hurd et al. 2011).

In addition to direct effects, ocean acidification can also result in strong indirect effects via alterations on species interactions. For instance, ocean acidification can interfere with chemically-mediated interactions between coralline algae and settling corals (Doropoulos et al. 2012), or inhibit kelp (Connell & Russell 2010) which suggests that future recruitment of habitat forming species may be impaired by CO_2 concentrations predicted to be reached this century. Since temperate invertebrates such as sea urchins and abalone also respond to chemical cues from coralline algae, these taxa are also expected to be influenced by acidification, and this is likely to have cascading effects to algal-dominated communities. In addition, alterations to herbivory may cause restructuring of systems such that alterations to consumption are unlikely to occur independently of production (Connell et al. 2011). These combinations are likely to cause synergies between factors that remain largely unexplored, but for which we have some insights (Connell et al. 2011).

Finally, trophic dynamics in temperate algal communities can also be strongly influenced by acidification through alterations to the detrital food chain. For example, higher CO_2 conditions can indirectly inhibit marine decay processes, delaying access to recycled trace nutrients, which may be disruptive to the seasonal regrowth of algae and/or higher trophic levels of nearshore ecosystems (Swanson & Fox 2007). Moreover, any losses of subtidal canopy species will have important cascading effects on other communities subsidized by algal detritus (Bishop et al. 2010).

Storm-driven waves

Storm-driven waves are an important source of disturbances to temperate reef communities (e.g., Seymour et al. 1989, Reed et al. 2011), and wave exposure is well known to control macroalgal habitats, productivity and community structure (e.g., Phillips et al. 1997, Goldberg & Kendrick 2004, Wernberg & Connell 2008, Vanderklift et al. 2009, Reed et al. 2011, Thomson et al. 2012). Overall, wave heights have increased significantly over the past decades at several locations off Australia's temperate coastline (Young et al. 2011, Bosserelle et al. 2012) however to date, there have been no reported observations of impacts attributable to these changes. It is possible, to some extent, to predict the structure of ecological communities under intensified wave action by examining existing exposure gradients (e.g., Hill et al. 2010), although altered frequency and magnitude of 'extreme events' are likely to affect communities in non-linear ways. International studies suggest that climate-driven loss of macroalgal canopies to waves may have cascading effects on associated ecosystems and food webs (Byrnes et al. 2011). Community-wide impacts of loss of

Macroalgae

temperate macroalgal canopies can linger for many years even without climatic stressors (e.g., >8 years, Schiel & Lilley 2011), and increasing temperatures are likely to exacerbate these effects by suppressing recovery further (Wernberg et al. 2010).

Extreme events

Climate change not only causes changes to the mean conditions, but also the magnitude of variation around the mean: the frequency of extreme climatic events (droughts, floods, heat waves, etc.) has been increasing globally as a consequence of climate change, and this trend is expected to continue and intensify (Kerr 2011). A recent global analysis of sea surface temperatures from the past 30 years has revealed a 38% increase in extremely hot days in coastal waters (Lima & Wetthey 2012). Such heat waves have also been evident in temperate Australia: during the early parts of 2011 southwestern Australia experienced a ‘marine heat wave’ of unprecedented magnitude and duration. Ocean temperatures along >1,000 km of coastline soared to 3-5 °C above normal and remained substantially elevated for several weeks (Pearce et al. 2011). For example, in Cockburn Sound – one of the largest and most valuable embayments in Australia – significant warming to depths of 20 m persisted for ~8 weeks, while dissolved oxygen levels were also depleted (Rose et al. 2012). The event, which caused the highest thermal stress anomalies in at least 140 years (Wernberg et al. 2012b), was driven by exceptionally strong La Niña conditions superimposed onto a longer-term trend of increasing temperatures in the region, and affected only Western Australia. During and immediately after the event there were many anecdotal observations from temperate waters of species (primarily fishes and conspicuous animals such as turtles) outside their normal ranges (Pearce et al. 2011) but so far only limited systematic and quantitative observations have been carried out. Visual observations made by an Automated Underwater Vehicle (AUV) at the Houtman Abrolhos Islands (28.43 °S), at the transition between tropical and temperate waters, indicated negative effects on both corals (bleaching) and temperate seaweeds (kelps, *Ecklonia radiata*), which were covered extensively by epibiotic fouling (presumably encrusting coralline algae) (Fig. 1, Smale & Wernberg 2012, Smale et al. 2012). There were also reports of die-offs of abalone along the central west coast (Pearce et al. 2011), and ongoing work suggests ecosystem-wide impacts with declines in canopy-forming algae (both kelps and fucoids) and shifts in fish communities towards more warm-affinity species (Wernberg et al. 2012b). Diebacks of canopy-forming roalgae in Australia have previously been associated with warm water events: unusually high summer temperatures for an extended period during summer 2000/2001 caused a substantial decline in *Ecklonia radiata* and *Phyllospora comosa* canopies in Tasmania (Valentine & Johnson 2004). The dieback facilitated the establishment of the invasive macroalgae *Undaria pinnatifida*. Interestingly, only small disturbed areas recovered to native algae whereas large areas showed no signs of recovery (Valentine & Johnson 2004). This example demonstrates how temperature-induced disturbances can mediate additional impacts (e.g., species invasions) and how the scale of impact has important implications to resilience and recovery.

Macroalgae

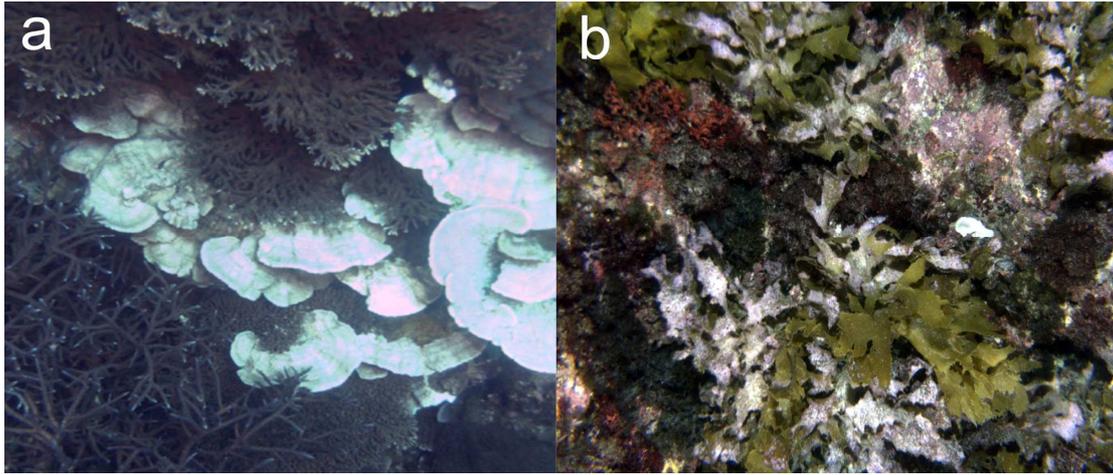


Figure 1. Bleached coral (a, *Montipora* sp.) and heavy biofouling of kelp (b, *Ecklonia radiata*) was observed at the Houtman Abrolhos Islands in April 2011, following a severe marine heat wave off the west coast of Australia (images modified from Smale & Wernberg 2012).

Access to existing databases from government-funded monitoring programs would provide a unique opportunity for rigorous ‘before-after’ evaluations of the impacts of an extreme event. Given the unprecedented temporal and spatial scale of this extreme event, such comparisons would be extremely informative and this should be considered an immediate priority.

Ocean currents and population connectivity

A critical, yet understudied component of climate change is how predicted changes to ocean circulation patterns will influence connectivity of marine organisms. Ocean currents are key factors driving patterns of dispersal and connectivity of marine organisms including macroalgae (e.g., Banks et al. 2010, White et al. 2010, Alberto et al. 2011, Coleman et al. 2011a, Coleman et al. 2011b) and predicted changes in current strength, extent and meso-scale features under future scenarios of climate change will have significant implications for how populations of marine organisms are connected in our oceans.

Australia’s boundary current systems are predicted to change in contrasting ways under future scenarios of climate change and these variations in oceanographic-biological coupling will have critical implications for connectivity of macroalgae and other marine organisms. The Leeuwin Current and its extension has weakened by 10-30 % in the past 50 years (Feng et al. 2004) and is predicted to weaken a further 15% by 2060 (Sun et al 2012), although strong decadal variation has been observed in the current system (Feng et al. 2010). In contrast, the East Australian Current has been steadily increasing in strength (Ridgway 2007, Hill et al. 2008) and is predicted to further increase by 12% in the core transport, and 35% in the poleward extension by 2060 (Sun et al. 2012). Given that macroalgal connectivity is correlated with current strength (Coleman et al. 2011b), this is likely to result in even greater genetic connectivity along the east coast and further decreasing connectivity along the western and southern coastlines (Coleman et al. 2009, Coleman & Kelaher 2009, Coleman et al. 2011a, Coleman et al. 2011b). This will have implications for critical population parameters such as genetic diversity, inbreeding and adaptive ability which, combined with concurrent climate induced stressors such as increases in sea surface temperature and acidification and current-mediated range expansion of grazers (Banks

Macroalgae

et al. 2010) may compromise the dynamics and functioning of populations of marine macroalgae along Australia's temperate coastlines (Wernberg et al. 2011b).

Climate change and species interactions

Evidence increasingly shows that some of the most severe consequences of global change are not caused by direct effects on individual species, but rather by changes to ecological processes and interactions between species (Traill et al. 2010, van der Putten et al. 2010, Kordas et al. 2011). Climate-mediated changes in biotic interactions often occur as a consequence of shifts in species ranges, which either disrupt existing interactions or create new ones when species differ in their ability to track a changing climate through dispersal (Berg et al. 2010, Gilman et al. 2010). Since climate-mediated rates of spread of marine species are over a magnitude greater than for terrestrial species (Sorte et al. 2010), marine communities are especially vulnerable to shifts in species interactions. This is compounded by the fact that higher trophic levels are often more sensitive to climate change than lower levels, leading to important alterations to food-web structure and ecosystem function (Voigt et al. 2003). For example, increasing temperature increases per capita interaction strength between *Sargassum* and amphipod grazers, reversing the positive direct effect of temperature on plant growth (O'Connor 2009).

In temperate algal forests, alterations in herbivore-algae interactions have already mediated some of the most dramatic impacts of climate change observed to date. Two examples stand out here: one is the spread of the warm temperate sea urchin *Centrostephanus rodgersii* into Tasmanian kelp forests, driven by the intensification of the East Australian Current and concurrent over-fishing of urchin predators (rock lobster, *Jasus edwardsii*) (Johnson et al. 2005, Ling et al. 2008) and resulting in the deforestation of large sections of Tasmanian coast as described above. A second stand out example is the westward spread of herbivorous tropical fish into the Mediterranean, which has led to the large-scale disappearance of canopy-forming algae from much of the benthos of the eastern Mediterranean (Sala et al. 2011). In intertidal systems, temperature-mediated changes in the community composition of grazers have also been recorded in the British Isles, and models based on these observations similarly predict a decrease in primary production by canopy-forming fucoids mediated by changes in species interactions (Hawkins et al. 2009).

Of concern for macroalgal forests in the future is the range expansion into temperate areas of tropical herbivorous fishes, which are renowned for having high consumption rates and keeping coral reefs largely free of significant stands of macroalgae. For example, the unicorn fish *Naso unicornis*, one of the main consumers of algae in Indo-Pacific reefs (Hoey & Bellwood 2009), is now found in the temperate shores of Japan (Soeparno et al. 2012) and Australia (Booth et al. 2007). Critically, the poleward movement of tropical herbivorous fishes appears to be occurring at a much faster rate than any poleward retraction of seaweed communities (Wernberg et al. 2011a), with some tropical fish on the east coast of Australia now found more than 1,000 km south of the northern limits (SE Queensland) of the dominant habitat-forming temperate kelp, *Ecklonia radiata* (Womersley 1987). Similarly, on the west coast, the 2011 warming event led to an increase relative abundance of warm-water herbivorous fish (Wernberg et al. 2012b). More work is needed on the susceptibility of temperate seaweeds to grazing by tropical fish, but changes in species interactions

Macroalgae

in a warming ocean may impact temperate macroalgal communities much sooner than direct physiological effects.

Disease

In addition to well-studied species interactions such as herbivory and competition, marine organisms also interact with microorganisms, which are abundant and ubiquitous in seawater (millions of cells per milliliter, Reinheimer 1992). Climate change can influence disease dynamics by altering the virulence, abundance or distribution of pathogens and/or by (simultaneously) affecting host susceptibility. Indeed, the incidence of diseases affecting natural populations appears to be increasing and this has been linked to climate change and other anthropogenic impacts (Harvell et al. 2002). Many symptoms of algal diseases have been described (Correa et al. 1993, Correa et al. 1994, Correa et al. 1997, Faugeton et al. 2000) but the ecological consequences of these infections or any relationships between outbreaks and environmental variables have rarely been assessed. Disease has been suggested, although not confirmed, as a possible cause of episodic declines of large, habitat-forming macroalgae around Australia and New Zealand in the past (Cole & Babcock 1996, Easton et al. 1997, Cole & Syms 1999, Coleman et al. 2008).

Recently, a bleaching phenomenon affecting the chemically-defended macroalga *Delisea pulchra* was described as a temperature-mediated bacterial disease (Campbell et al. 2011, Case et al. 2011, Fernandes et al. 2011). In this case, high water temperatures were linked to a depletion of the alga's chemical defenses (which inhibit surface colonisation by many bacteria) and an increase in the frequency of bleaching in natural populations (Campbell et al. 2011). Bleaching was induced in the laboratory under high temperatures in the presence of ambient seawater microorganisms and was reduced through treatment with antibiotics (Campbell et al. 2011). Several specific bacterial strains can cause bleaching in *D. pulchra* in laboratory studies, but only when the seaweed's production of chemical defences is experimentally inhibited and temperatures elevated (Campbell et al. 2011, Fernandes et al. 2011). In one of these pathogens (*Nautella* sp. R11), virulence genes have been identified and are under continued investigation (Fernandes et al. 2011) and virulence appears to be induced or increased at higher water temperatures (Case et al. 2011). Additionally, metagenomic analyses of bacterial DNA from *D. pulchra*'s biofilm suggest that many bacterial strains may contain genes that allow them to 'switch' to a pathogenic lifestyle under appropriate conditions (Fernandes et al. 2011).

Although the ways in which increasing temperatures affect host defenses and bacterial virulence are likely to be complex and species-specific, these findings present an alarming scenario, in which warming waters may reduce the resilience of hosts (e.g., Wernberg et al. 2010) whilst simultaneously enhancing or inducing the virulence of pathogens. This is particularly the case given that opportunistic pathogens are likely ubiquitous in these systems, that is, no changes in distribution are needed for them to have an impact. Moreover, diseases are also likely to have substantial indirect ecological effects, for example where non-lethal infections mediate the formation of wounds. Indeed, small wounds are abundant on macroalgae, and they greatly increase the susceptibility to mechanical damage and mortality from waves (de Bettignies et al. 2012).

Macroalgae

Far more attention has been given to understanding how climate change affects interactions between coral hosts and their diverse microbial pathogens (see reviews by (Harvell et al. 2002, Rosenberg & Ben-Haim 2002). A similarly focused effort is required to understand host-pathogen interactions involving macroalgae, the temperate, habitat-forming equivalents to corals.

Confidence assessment: observed impacts

Amount of evidence (theory, observations, models)

As a whole, the evidence for impacts of climate change on marine macroalgae and temperate rocky reef organisms in Australia is limited (reviewed in Wernberg et al. 2011b). There are however a few robust examples from Tasmania such as the range-shift of sea urchins and subsequent decimation of kelp forests, and dramatic decline in the extent of dense *Macrocystis* stands as a unique habitat type correlated with ocean climate change (Johnson et al. 2011).

Overall, the majority of observed impacts relate to shifts in species distributions. These observations have been made for a broad variety of temperate reef organisms including macroalgae, invertebrates and fishes, and for most temperate species, the observed shifts have been reasonably similar in magnitude. Additionally, these changes match well with a large and growing body of literature that document changes of similar magnitude across spatial temperature gradients for macroalgal habitat structure (Connell & Irving 2008, Wernberg et al. 2011c), macroalgal species composition (Wernberg et al. 2003, Smale et al. 2010), and fish communities (Tuya et al. 2011, Langlois et al. 2012). While these correlative studies do not constitute robust evidence for cause-effect pathways, the level of correlative agreement supports the idea of changing climatic conditions as a common underlying driver. Increased research effort is required to experimentally test the causal links between climate change factors and biological responses, particularly for temperate macroalgae and species interactions (Wernberg et al. 2012a).

The biggest challenge to detecting impacts of climate change in temperate Australia is the lack of historical base line data on both physical and biological conditions. This issue is further compounded by the scale and remoteness of the coastline – there are simply no existing observations – historical or contemporary - from large swaths of Australia's temperate marine environments.

Several different approaches have been taken to reconstruct historical baselines where no readily accessible data were available for comparisons with contemporary data. For example, Connell et al. (2008) successfully retrieved data on macroalgal canopies in South Australia from late-career or retired researchers. This study highlighted issues with data storage (even electronic media) as a barrier to transferring data through time, and demonstrated how imperative it is to capture information in a permanent and accessible form (Connell et al. 2008). Other studies have used anecdotal evidence and natural history collections to inform on both past and present distributions (Millar 2007, Last et al. 2011, Wernberg et al. 2011a). Even if a sophisticated analytical framework exists (Shaffer et al. 1998, Tingley & Beissinger 2009), the use of such data is not without problems and the results must be interpreted cautiously. Despite this, such data can nevertheless be useful by providing unique indications of potential change that will allow tests of specific hypotheses to be tested

Macroalgae

through targeted experiments and surveys. While capturing these coarse-scale historical data is important, just as important to robust interpretation of responses to climate change is a clear indication of ‘natural’ medium to long-term temporal variability in macroalgal community structure in the absence of anthropogenically mediated change in environmental conditions. There are few, if any, sites in Australia where these data are available.

The experimental evidence for how climate change might affect marine organisms has been growing exponentially in the past decade, but it is clear that the collective body of evidence is highly biased (Wernberg et al. 2012a). For example, <20% of all experiments tested possible impacts on macrophytes including macroalgae. This is a serious bias considering the ecological importance of macroalgae as food, habitat and shelter for associated organisms. Similarly, it is also clear that the experimental evidence is highly artificial, with very few studies based on field conditions (Wernberg et al. 2012a). There is also a growing realization that studies must consider all major ecosystem components, interactions and/or life stages of key organisms such as habitat forming macroalgae if we are to accurately predict impacts of climate change (Russell et al. 2012). Additional field based work is also necessary to elucidate interactions between climate change effects and other anthropogenic ‘forcings’ (Wernberg et al. 2012a) such as fishing (Ling et al. 2009), introduced species (Valentine & Johnson 2004), and eutrophication (Connell & Russell 2010). Further, attention to differences in scale of origin of pressure and impact of pressure is needed to reconcile apparently idiosyncratic differences in the strength and direction of climate impacts (Russell & Connell 2012).

Degree of consensus (high level of statistical agreement, model confidence)

The general consensus about the overall impacts and projections for the future is high. However, due to the limited direct and unequivocal evidence (cf. 6.1) for specific climate driven impacts, expert opinion has a large weight in this assessment. This consensus is evident from recent publications, widely co-authored among the major researchers and research groups working on marine climate change issues in temperate Australia (Poloczanska et al. 2007, Johnson et al. 2011, Wernberg et al. 2011b).

Confidence level

The direct evidence for impacts unequivocally attributable to climate change is limited, but there is a high degree of consensus among researchers about the overall changes that have occurred/are occurring, and there is therefore medium confidence in what has already happened and what will happen in the future.

Potential impacts by 2030 (and/or 2100)

- A major threat to eastern, southern and western Australia is the loss of diversity in macroalgae that are endemic to this region. Temperate species will contract and tropical species expand. Many temperate species are at risk of extinction in the next 50-100 years.

Macroalgae

- Increasing temperatures are likely to reduce the resilience of macroalgal habitats to other perturbations (pollution, fishing, exotic species, disturbance), exacerbating impacts of non-climate drivers.
- Loss of canopy, especially the kelp *Ecklonia radiata*, and shifts in canopy species from the endemic Fucales to subtropical and tropical species of *Sargassum* will affect benthic community structure that may have flow on effects for commercially important benthic fishery species.
- Connectivity of macroalgal populations will decline on the west coast and increase on the east coast with forecast changes to boundary currents. This will result in potential flow-on effects to population level parameters and macroalgal persistence.
- Increasing temperatures and acidification, decreased nutrient often associated with warming due to shifts in ocean circulation, and other stressors may affect the susceptibility of organisms to disease, or affect the virulence, abundance or distribution of microbial pathogens, both of which can alter host-pathogen dynamics.
- Diseases affecting natural populations in general are predicted to increase with frequency and severity as a consequence of climate change.
- An increase in herbivory mediated by the range expansion of warm-water species may reduce the abundance of canopy-forming algae, with cascading effects on the communities they support.
- Ocean acidification may reduce the capacity of coralline algae to recruit and grow, having implications for invertebrate settlement
- Increasing [CO₂] is likely to increase productivity in naturally ephemeral species of macroalgae, leading them to increasingly dominate space at the expense of habitat forming species (e.g. kelps).

Recent marine heat waves and urchin invasions suggest national monitoring (e.g., using the IMOS AUV facility) should be budgeted fully for decades to create the time series required to assess change and its drivers. To complement this national resource, regional inshore studies on temperate reef ecosystems that cover degrees of latitude need also to be fully funded.

Confidence assessment: projected impacts

So far, there have been very few projections of future conditions relating directly to macroalgae and the amount of explicit evidence is very limited. Moreover, predictive modelling for other organisms in temperate Australia such as fishes and invertebrates (e.g., Cheung et al. 2009, Brown et al. 2010, Cheung et al. 2010) is only just starting to emerge. Based on evidence from elsewhere and expert experience, there is a reasonably high consensus that species distributions will continue to shift south, with potential declines in the abundance of ecologically important temperate species (e.g., giant kelp, *Macrocystis*) and a loss of biodiversity through (local) extinctions. So far, however, solid evidence is still lacking but scientists are working quickly to fill this information gap.

Macroalgae

Current and planned research effort

Several projects which focus on climate change and temperate macroalgae are currently under way. Here we list project titles, and short summaries.

Impacts of climate change on biogenic habitat-forming seaweeds in southeast Australia (Australian Research Council, DP1096573, *Johnson & Wright, 2010-2012*): Will examine the synergistic effects of changes in both temperature and nutrient levels for three key habitat-forming seaweeds on rocky reefs in SE Australia. Will assess whether performance of individuals in warmer parts of species' ranges is helpful in predicting responses to climate change in colder parts of a range and, estimate the heritability of key traits and thus the potential to adapt to climate change.

Effects of climate change on temperate benthic assemblages on the continental shelf in eastern Australia (Australian Research Council, FS110200029, *Johnson, Holbrook, Barrett, Steinberg, 2011-2013*): Will determine present patterns of physical parameters on the continental shelf in SE Australia, and predict changes in both the trend and variability of the temperature and nutrient signal on the shelf. These data will be combined with observations of benthic communities 0-200 m depth to, for the first time, develop bioclimate models to predict changes in key habitats important for major fisheries and as areas of high biodiversity. Unique data from experiments will enable testing the efficacy of current approaches to bioclimate prediction.

Understanding the global impacts and implications of range-shifting species in marine systems (Australian National Network in Marine Science, *Fruscher, Pecl, Wernberg, Smale, Tobin, 2011-2013*): Will synthesise available data on biological responses and subsequent human impacts (economic, social and governance) across marine hotspots (including SE and SW Australia) globally and provide a comprehensive assessment of the dynamics and implications (including socio-economic) of range-shifting species.

Climatic forcing of ecological function in temperate marine habitats: bridging the gaps (Australian Research Council, FT110100174, *Wernberg, 2011-2015*): Will integrate work on past, present and future ecological change in response to climatic forcing in temperate marine ecosystems to build capacity and expand the theoretical framework needed for successful conservation and sustainable use of marine resources in a changing climate.

Long-term changes in the phenology of Australia's temperate marine macroalgae: has climate change impacted the world's most diverse algal flora? (Australian Research Council, LP120100023, *Wernberg & Gurgel, 2012-2015*): Will use herbarium specimens to reconstruct a ~100-year baseline of reproductive timing in dozens of seaweed species to generate knowledge critically needed to identify and prioritize vulnerable species.

Stress, virulence and bacterial disease in seaweeds: The rise of the microbes (Australian Research Council DP 1096464, *Steinberg, Kjelleberg, Thomas, Egan & Coleman, 2009-2012*): Will test how bacterial pathogens interact with anthropogenic stressors to impact kelps and other habitat-forming macroalgae and assess if the growing impact of anthropogenic stressors in coastal systems is in fact

Macroalgae

due to the effects of common, opportunistic pathogens acting on stressed plants and animals.

Connectivity and Climate Change in a hotspot of ocean warming (Environmental Trust Grant, Coleman, Roughan and Kelaher, 2012): Will meld oceanographic modelling with ecology to predict future changes to coastal connectivity providing decision makers the ability to implement early and informed adaptation responses to climate change in the ocean.

Long term monitoring of temperate reefs in Australia using the IMOS Autonomous Underwater Vehicle Facility (Nation-wide collaboration between Universities [USyd, UNSW, UTas, UWA], national research providers [CSIRO, AIMS], and State Government Departments [TAFI, NSW Parks and Wildlife, FisheriesWA], 2008-): Will design and test long term monitoring of temperate reefs in Australia using the IMOS Autonomous Underwater Vehicle Facility (AUV). The IMOS AUV facility will provide precisely navigated time series measurements of water column parameters and benthic imagery using AUVs at selected reference stations at key locations in Queensland, New South Wales, Tasmania and Western Australia. Until now, monitoring has supplied data on climate change effects on temperate reefs, including the urchin invasion of Tasmania and the 2011 marine heat wave of Western Australia.

References

- Alberto, F., Raimondi, P., Reed, D., Watson, J., Siegel, D., Mitarai, S., Coelho, N. and Serrao, E. (2011) Isolation by oceanographic distance explains genetic structure for *Macrocystis pyrifera* in the Santa Barbara Channel. *Molecular Ecology* 20:2543–2554
- Banks, S.C., Ling, S.D., Johnson, C.R., Piggott, M.P., Williamson, J.E. and Beheregaray, L.B. (2010) Genetic structure of a recent climate change-driven range extension. *Molecular Ecology* 19:2011-2024
- Beardall, J., Beer, S. and Raven, J.A. (1998) Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Botanica Marina* 41:113-123
- Berg, M., Kiers, E., Driessen, G., van der Heijden, M., Kooi, B., Kuenen, F., Liefting, M., Verhoef, H. and Ellers, J. (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16:587-598
- Bishop, M., Coleman, M. and Kelaher, B. (2010) Cross-habitat impacts of species decline: response of estuarine sediment communities to changing detrital resources. *Oecologia* 163:517-525
- Bolton, J.J. (1994) Global seaweed diversity: patterns and anomalies. *Botanica Marina* 37:241-245
- Booth, D., Figueira, W., Gregson, M., Brown, L. and Beretta, G. (2007) Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current. *Estuarine, Coastal and Shelf Science* 72:102-114
- Bosserelle, C., Pattiaratchi, C. and Haigh, I. (2012) Inter-annual variability and longer-term changes in the wave climate of Western Australia between 1970 and 2009. *Ocean Dynamics* 62:63-76

Macroalgae

- Brown, C., Fulton, E. and Hobday, A. (2010) Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Global Change Biology* 16:1194-1212
- Byrnes, J.E., Reed, D.C., Cardinale, B.J., Cavanaugh, K.C., Holbrook, S.J. and Schmitt, R.J. (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biology* 17:2513-2524
- Campbell, A., Harder, T., Nielsen, S., Kjelleberg, S. and Steinberg, P. (2011) Climate change and disease: bleaching of a chemically defended seaweed. *Global Change Biology* 17:2958-2970
- Case, R., Longford, S., Campbell, A., Steinberg, P.D. and Kjelleberg, S. (2011) Temperature induced bacterial virulence and bleaching disease in a chemically defended marine macroalga. *Environmental Microbiology* 13:529-537.
- Cheung, W., Lam, V., Sarmiento, J., Kearney, K., Watson, R., Zeller, D. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* 16:24-35
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10:235-251
- Cole, R.G. and Babcock, R.C. (1996) Mass mortality of a dominant kelp (Laminariales) at Goat Island, North-eastern New Zealand. *Marine and Freshwater Research* 47:907-911
- Cole, R.G. and Syms, C. (1999) Using spatial pattern analysis to distinguish causes of mortality: An example from kelp in north-eastern New Zealand. *Journal of Ecology* 87:963-972
- Coleman, M.A., Chambers, J., Knott, N.A., Malcolm, H.A., Harasti, D., Jordan, A. and Kelaher, B.P. (2011a) Connectivity within and among a Network of Temperate Marine Reserves. *PLoS ONE* 6:e20168
- Coleman, M.A., Gillanders, B.M. and Connell, S.D. (2009) Dispersal and gene flow in the habitat-forming kelp, *Ecklonia radiata*: relative degrees of isolation across an east-west coastline. *Marine and Freshwater Research* 60:802-809
- Coleman, M.A. and Kelaher, B.P. (2009) Connectivity among fragmented populations of a habitat-forming alga, *Phyllospora comosa* (Phaeophyceae, Fucales) on an urbanised coast. *Marine Ecology Progress Series* 381:63-70
- Coleman, M.A., Kelaher, B.P., Steinberg, P.D. and Millar, A.J.K. (2008) Absence of a large brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for historical decline. *Journal of Phycology* 44:897-901
- Coleman, M.A., Roughan, M., Macdonald, H.S., Connell, S.D., Gillanders, B.M., Kelaher, B.P. and Steinberg, P.D. (2011b) Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. *Journal of Ecology* 99:1026-1032
- Coleman, M.A., Vytupil, E., Goodsell, P.J., Gillanders, B.M. and Connell, S.D. (2007) Diversity and depth-related patterns of mobile invertebrates associated with kelp forests. *Marine and Freshwater Research* 58:589-595
- Connell, S., Russell, B. and Irving, A. (2011) Can strong consumer and producer effects be reconciled to better forecast 'catastrophic' phase-shifts in marine ecosystems? *Journal of Experimental Marine Biology and Ecology* 400:296-301
- Connell, S.D. (2003) Negative effects overpower the positive of kelp to exclude invertebrates from the understory community. *Oecologia* 137:97-103

Macroalgae

- Connell, S.D. and Irving, A.D. (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *Journal of Biogeography* 35:1608-1621
- Connell, S.D. and Russell, B.D. (2010) The direct effects of increasing CO₂ and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proceedings of the Royal Society B* 277:1409-1415
- Connell, S.D., Russell, B.D., Turner, D.J., Shepherd, S.A., Kildea, T., Miller, D., Airoidi, L. and Cheshire, A. (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Marine Ecology Progress Series* 360:63-72
- Cornwall, C.E., Hepburn, C.D., Pritchard, D., Currie, K.I., McGraw, C.M., Hunter, K.A. and Hurd, C.L. (2012) Carbon-use strategies in macroalgae: differential responses to lowered pH and implications for ocean acidification. *Journal of Phycology* 48:137-144
- Correa, J.A., Buschmann, A., Retamales, C. and Beltran, J. (1997) Infectious diseases of *Mazella laminarioides* (Rhodophyta): changes in infection prevalence and disease expression associated with season, locality and within-site location. *Journal of Phycology* 33:344-352
- Correa, J.A., Flores, V. and Garrido, J. (1994) Green patch disease in *Iridaea laminarioides* (Rhodophyta) caused by *Endophyton* sp. (Chlorophyta). *Diseases of Aquatic Organisms* 19:203-213
- Correa, J.A., Flores, V. and Sanchez, P. (1993) Deformative disease in *Iridaea laminarioides* (Rhodophyta): Gall development associated with an endophytic cyanobacterium. *Journal of Phycology* 29:853-860
- de Bettignies, T., Thomsen, M.S. and Wernberg, T. (2012) Wounded kelps: patterns and susceptibility to breakage. *Aquatic Biology* in press
- Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O. and Mumby, P. (2012) Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecology Letters* 15:338-346
- Easton, L.M., Lewis, G.D. and Pearson, M.N. (1997) Virus-like particles associated with dieback symptoms in the brown alga *Ecklonia radiata*. *Diseases of Aquatic Organisms* 30:217-222
- Falkenberg, L., Russell, B. and Connell, S. (2012) Strong species interactions resist the synergistic effects of local and global pollution in kelp forests. *PLoS One* 7:e33841
- Faugeron, S., Martinez, E.A., Sanchez, P.A. and Correa, J.A. (2000) Infectious diseases in *Mazella laminarioides* (Rhodophyta): estimating the effect of infections on host reproductive potential. *Diseases of Aquatic Organisms* 42:143-148
- Feng, M., Li, Y. and Meyers, G. (2004) Multidecadal variations of Fremantle sea level: footprint of climate variability in the tropical Pacific. *Geophysical Research Letters* 31:L16302
- Feng, M., McPhaden, M.J. and Lee, T. (2010) Decadal variability of the Pacific subtropical cells and their influence on the southeast Indian Ocean. *Geophysical Research Letters* 37:L09606
- Fernandes, N., Case, R., Longford, S., Seyedsayamdost, M., Steinberg, P., Kjelleberg, S. and Thomas, T. (2011) Genomes and virulence factors of novel bacterial pathogens causing bleaching disease in the marine red alga *Delisea pulchra*. *PLoS ONE* 6:e27387

Macroalgae

- Gilman, S., Urban, M., Tewksbury, J., Gilchrist, G. and Holt, R. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25:325-331
- Goldberg, N.A. and Kendrick, G.A. (2004) Effects of island groups, depth, and exposure to ocean waves on subtidal macroalgal assemblages in the Recherche Archipelago, Western Australia. *Journal of Phycology* 40:631-641
- Harley, C.D.G. and Connell, S.D. (2009) *Shifts in abiotic variables and consequences for diversity*. In: Wahl M (ed) Marine hard bottom communities: patterns, dynamics, diversity and change, Vol 206. Springer, Berlin, p 257-268
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. and Samuel, M.D. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158-2162
- Hawkins, S., Sugden, H., Mieszkowska, N., Moore, P., Poloczanska, E., Leaper, R., Herbert, R., Genner, M., Moschella, P., Thompson, R., Jenkins, S., Southward, A. and Burrows, M. (2009) Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series* 396:245-259
- Hendriks, I.E., Duarte, C.M. and Álvarez, M. (2010) Vulnerability of marine biodiversity to ocean acidification: A meta-analysis. *Estuarine, Coastal and Shelf Science* 86:157-164
- Hepburn, C.D., Pritchard, D.W., Cornwall, C.E., McLeod, R.J., Beardall, J., Raven, J.A. and Hurd, C.L. (2011) Diversity of carbon use strategies in a kelp forest community: implications for a high CO₂ ocean. *Global Change Biology* 17:2488-2497
- Hill, K.L., Rintoul, S.R., Coleman, R. and Ridgway, K.R. (2008) Wind-forced low frequency variability of the East Australian Current. *Geophysical Research Letters* 35:L08602
- Hill, N., Pepper, A., Puotinen, M., Hughes, M., Edgar, G., Barrett, N., Stuart-Smith, R. and Leaper, R. (2010) Quantifying wave exposure in shallow temperate reef systems: applicability of fetch models for predicting algal biodiversity. *Marine Ecology Progress Series* 417:83-95
- Hoey, A. and Bellwood, D. (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12:1316-1328
- Hurd, C.L., Cornwall, C.E., Currie, K., Hepburn, C.D., McGraw, C.M., Hunter, K.A. and Boyd, P.W. (2011) Metabolically induced pH fluctuations by some coastal calcifiers exceed projected 22nd century ocean acidification: a mechanism for differential susceptibility? *Global Change Biology* 17:3254-3262
- Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling, K.M. and Taw, N. (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* 400:17-32
- Johnson, C.R., Ling, S.D., Ross, J., Shepherd, S. and Miller, K. (2005) *Establishment of the long-spined sea urchin (Centrostephanus rodgersii) in Tasmania: first assessment of potential threats to fisheries*, FRDC Final Report. Project No. 2001/044. Deakin West, ACT, Australia.

Macroalgae

- Kerr, R.A. (2011) Humans are driving extreme weather; Time to prepare. *Science* 334:1040
- Kerswell, A.P. (2006) Global biodiversity patterns of benthic marine algae. *Ecology* 87:2479-2488
- Kordas, R.L., Harley, C.D.G. and O'Connor, M.I. (2011) Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology* 400:218-226
- Langlois, T.J., Radford, B.T., Van Niel, K.P., Meeuwig, J.J., Pearce, A.F., Rousseaux, C.S.G., Kendrick, G.A. and Harvey, E.S. (2012) Consistent abundance distributions of marine fishes in an old, climatically buffered, infertile seascape. *Global Ecology and Biogeography* 21:886-897.
- Last, P.R., White, W.T., Gledhill, D.C., Hobday, A.J., Brown, R., Edgar, G.J. and Pecl, G. (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography* 20:58-72
- Lima, F.P. and Wetthey, D.S. (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications* 3:704
- Ling, S. (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156:883-894
- Ling, S.D., Johnson, C.R., Frusher, S. and King, C.K. (2008) Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology* 14:907-915
- Ling, S.D., Johnson, C.R., Frusher, S.D. and Ridgway, K.R. (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America* 106:22341-22345.
- Martin, S. and Gattuso, J.-P. (2009) Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biology* 15:2089-2100
- Melville, A.J. and Connell, S.D. (2001) Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecology* 26:102-108
- Millar, A. (2009) Are seaweed distributions changing due to global warming? *Phycologia*, abstracts for papers presented at the 9th International Phycological Congress 48:83
- Millar, A.J.K. (2007) *Flindersian and Peronian provinces*. In: *Algae of Australia: Introduction*. Australian Biological Resources Study, Canberra, p 554-559
- Nash, M., Troitzsch, U., Opdyke, B., Trafford, J., Russell, B. and Kline, D. (2011) Biomineralization of dolomite and magnesite discovered in tropical coralline algae: a biological solution to the geological dolomite problem. *Biogeosciences* 8:3331-3340
- O'Connor, M.I. (2009) Warming strengthens an herbivore-plant interaction. *Ecology* 90:388-398
- Pearce, A. and Feng, M. (2007) Observations of warming on the Western Australian continental shelf. *Marine and Freshwater Research* 58:914-920
- Pearce, A., Lenanton, R., Jackson, G., Moore, J., Feng, M. and Gaughan, D. (2011) *The "marine heat wave" off Western Australia during the summer of 2010/11.*

Macroalgae

- Fisheries Research Report No 222 Department of Fisheries, Western Australia:40pp
- Phillips, J.A. (2001) Marine macroalgal biodiversity hotspots: Why is there high species richness and endemism in southern Australian marine benthic flora? *Biodiversity & Conservation* 10:1555-1577
- Phillips, J.C., Kendrick, G.A. and Lavery, P.S. (1997) A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. *Marine Ecology Progress Series* 153:125-138
- Pitt, N.R., Poloczanska, E.S. and Hobday, A.J. (2010) Climate-driven range changes in Tasmanian intertidal fauna. *Marine and Freshwater Research* 61:963-970
- Poloczanska, E.S., Babcock, R.C., Butler, A., Hobday, A., Hoegh-Guldberg, O., Kunz, T.J., Matear, R., Milton, D.A., Okey, T.A. and Richardson, A.J. (2007) Climate change and Australian marine life. *Oceanography and Marine Biology* 45:407-478
- Poloczanska, E.S., Smith, S., Fauconnet, L., Healy, J., Tibbetts, I.R., Burrows, M.T. and Richardson, A.J. (2011) Little change in the distribution of rocky shore faunal communities on the Australian east coast after 50 years of rapid warming. *Journal of Experimental Marine Biology and Ecology* 400:145-154
- Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P. and Siegel, D.A. (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* 92:2108-2116
- Reinheimer, G. (1992) *Aquatic Microbiology*, Vol 4th edition. Wiley, New York
- Ridgway, K.R. (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters* 34: L13613
- Rose, T., Smale, D. and Botting, G. (2012) The 2011 marine heatwave off southwest Australia. *Ocean Science Discussions* 9:1691-1703.
- Rosenberg, E. and Ben-Haim, Y. (2002) Microbial diseases of corals and global warming. *Environmental Microbiology* 4:318-326
- Russell, B. and Connell, S. (2012) Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. *Marine Biology*:1-7 doi:10.1007/s00227-011-1863-8
- Russell, B.D., Harley, C.D.G., Wernberg, T., Mieszkowska, N., Widdicombe, S., Hall-Spencer, J.M. and Connell, S.D. (2012) Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biology Letters* 8:164-166
- Russell, B.D., Passarelli, C.A. and Connell, S.D. (2011) Forecasted CO₂ modifies the influence of light in shaping subtidal habitat. *Journal of Phycology* 47:744-752
- Russell, B.D., Thompson, J.-A.I., Falkenberg, L.J. and Connell, S.D. (2009) Synergistic effects of climate change and local stressors: CO₂ and nutrient-driven change in subtidal rocky habitats. *Global Change Biology* 15:2153-2162
- Sala, E., Kizilkaya, Z., Yildirim, D. and Ballesteros, E. (2011) Alien marine fishes deplete algal biomass in the eastern Mediterranean. *Plos One* 6 e17356
- Schiel, D.R. and Lilley, S.A. (2011) Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *Journal of Experimental Marine Biology and Ecology* 407:108-115

Macroalgae

- Seymour, R.J., Tegner, M.J., Dayton, P.K. and Parnell, P.E. (1989) Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. *Estuarine, Coastal and Shelf Science* 28:277-292
- Shaffer, H.B., Fisher, R.N. and Davidson, C. (1998) The role of natural history collections in documenting species declines. *Trends in Ecology & Evolution* 13:27-30
- Smale, D. and Wernberg, T. (2012) Ecological observations associated with an anomalous warming event at the Houtman Abrolhos Islands, Western Australia. *Coral Reefs* 31:441-441
- Smale, D.A., Kendrick, G.A., Harvey, E.S., Langlois, T.J., Hovey, R.K., Van Niel, K.P., Waddington, K.I., Bellchambers, L.M., Pember, M.B., Babcock, R.C., Vanderklift, M.A., Thomson, D.P., Jakuba, M.V., Pizarro, O. and Williams, S.B. (2012) Regional-scale benthic monitoring for Ecosystem-Based Fisheries Management (EBFM) using an Autonomous Underwater Vehicle (AUV). *ICES Journal of Marine Science* doi:10.1093/icesjms/fss082.
- Smale, D.A., Kendrick, G.A. and Wernberg, T. (2010) Assemblage turnover and taxonomic sufficiency of subtidal macroalgae at multiple spatial scales. *Journal of Experimental Marine Biology and Ecology* 384:76-86
- Soeparno, N., Nakamura, Y., Shibuno, T. and Yamaoka, K. (2012) Relationship between pelagic larval duration and abundance of tropical fishes on temperate coasts of Japan. *Journal of Fish Biology* 80:346-357.
- Sorte, C.J.B., Williams, S.L. and Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography* 19:303-316
- Steneck, R. (1986) The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics* 17:273-303
- Stuart-Smith, R.D., Barrett, N.S., Stevenson, D.G. and Edgar, G.J. (2009) Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology* 16:122-134.
- Sun, C., Feng, M., Matear, R.J., Chamberlain, M.A., Craig, P., Ridgway, K.R. and Schiller, A. (2012) Marine downscaling of a future climate scenario for Australian boundary currents. *Journal of Climate* 25:2947-2962
- Swanson, A.K. and Fox, C.H. (2007) Altered kelp (Laminariales) phlorotannins and growth under elevated carbon dioxide and ultraviolet-B treatments can influence associated intertidal food webs. *Global Change Biology* 13:1696-1709
- Thomson, D.P., Babcock, R.C., Vanderklift, M.A., Symonds, G. and Gunson, J.R. (2012) Evidence for persistent patch structure on temperate reefs and multiple hypotheses for their creation and maintenance. *Estuarine, Coastal and Shelf Science* 96:105-113
- Tingley, M.W. and Beissinger, S.R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution* 24:625-633
- Truill, L., Lim, M., Sodhi, N. and Bradshaw, C. (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology* 79:937-947
- Tuya, F., Wernberg, T. and Thomsen, M.S. (2008) The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats. *Estuarine, Coastal and Shelf Science* 78:774-782

Macroalgae

- Tuya, F., Wernberg, T. and Thomsen, M.S. (2011) The relative influence of local to regional drivers of variation in reef fishes. *Journal of Fish Biology* 79:217-234
- Valentine, J.F. and Johnson, C.R. (2004) Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. *Marine and Freshwater Research* 55:223-235
- van der Putten, W., Macel, M. and Visser, M. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2025-2034
- Vanderklift, M.A., Lavery, P.S. and Waddington, K.I. (2009) Intensity of herbivory on kelp by fish and sea urchins differs between inshore and offshore reefs. *Marine Ecology Progress Series* 376:203–211
- Voigt, W., Perner, J., Davis, A., Eggers, T., Schumacher, J., Bahrmann, R., Fabian, B., Heinrich, W., Kohler, G., Lichter, D., Marstaller, R. and Sander, F. (2003) Trophic levels are differentially sensitive to climate. *Ecology* 84:2444-2453
- Waters, J., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., Sanderson, C., West, J.A. and Gurgel, C.F. (2010) Australia's marine Biogeography revisited: back to the future. *Austral Ecology* 35: 988-992.
- Wernberg, T., Campbell, A., Coleman, M.A., Connell, S.D., Kendrick, G.A., Moore, P.J., Russell, B.D., Smale, D. and Steinberg, P.D. (2009) *Macroalgae and temperate rocky reefs*. In: Poloczanska ES, Hobday AJ, Richardson AJ (eds) Report Card of Marine Climate Change for Australia; detailed scientific assessment. NCCARF Publication 05/09, Hobart, p 128-146
- Wernberg, T. and Connell, S.D. (2008) Physical disturbance and subtidal habitat structure on open rocky coasts: effects of wave exposure, extent and intensity. *Journal of Sea Research* 59:237–248
- Wernberg, T., Kendrick, G.A. and Phillips, J.C. (2003) Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Diversity and Distributions* 9:427-441
- Wernberg, T., Kendrick, G.A. and Toohey, B.D. (2005) Modification of the physical environment by an *Ecklonia radiata* (Laminariales) canopy and implications for associated foliose algae. *Aquatic Ecology* 39:419-430
- Wernberg, T., Russell, B., Thomsen, M., Gurgel, C., Bradshaw, C., Poloczanska, E. and Connell, S. (2011a) Seaweed communities in retreat from ocean warming. *Current Biology* 21:1828-1832
- Wernberg, T., Russell, B.D., Moore, P.J., Ling, S.D., Smale, D.A., Campbell, A., Coleman, M.A., Steinberg, P.D., Kendrick, G.A. and Connell, S.D. (2011b) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology* 400:7-16
- Wernberg, T., Smale, D.A. and Thomsen, M.S. (2012a) A decade of climate change experiments on marine organisms: procedures, patterns and problems. *Global Change Biology* 18:1491-1498
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., Bettignies, Td., Bennett, S. and Rousseaux, C.S. (2012b) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* DOI: 10.1038/NCLIMATE1627
- Wernberg, T., Thomsen, M.S., Tuya, F. and Kendrick, G.A. (2011c) Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology* 400:264-271

Macroalgae

- Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A and Toohey, B.D. (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecology Letters* 13:685-694
- White, C., Selkoe, K.A., Watson, J., Siegel, D.A., Zacherl, D.C. and Toonen, R.J. (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B* 277:1685-1694
- Womersley, H.B.S. (1987) *The marine benthic flora of southern Australia - Part II*, Vol. South Australian Government Printing Division, Adelaide
- Young, I.R., Zieger, S. and Babanin, A.V. (2011) Global trends in wind speed and wave height. *Science* 332:451-455