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Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming

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ABSTRACT

Temperate Australia is a global hotspot for marine biodiversity and its waters have experienced well-above global average rates of ocean warming. We review the observed impacts of climate change (e.g. warming, ocean acidification, changes in storm patterns) on subtidal temperate coasts in Australia and assess how these systems are likely to respond to further change. Observed impacts are region specific with the greatest number of species responses attributable to climate change reported in south-eastern Australia, where recent ocean warming has been most pronounced. Here, a decline of giant kelp (*Macrocystis pyrifera*) and poleward range extension of a key herbivore (sea urchin) and other trophically important reef organisms has occurred. Although, evidence of changes on other coastlines around Australia is limited, we suggest that this is due to a lack of data rather than lack of change. Because of the east–west orientation of the south coast, most of Australia's temperate waters are found within a narrow latitudinal band, where any southward movement of isotherms is likely to affect species across very large areas. Future increases in temperature are likely to result in further range shifts of macroalgae and associated species, with range contractions and local extinctions to be expected for species that have their northern limits along the southern coastline. While there is currently no evidence of changes attributable to non-temperature related climate impacts, potentially due to a lack of long-term observational data, experimental evidence suggests that ocean acidification will result in negative effects on calcifying algae and animals. More importantly, recent experiments suggest the combined effects of climate change and non-climate stressors (overharvesting, reduced water quality) will lower the resilience of temperate marine communities to perturbations (e.g. storms, diseases, and introduced species), many of which are also predicted to increase in frequency and/or severity. Thus climate change is likely to, both by itself and in synergy with other stressors, impose change to southern Australian coastal species, including important habitat-forming algae and the associated ecological functioning of temperate coasts. Management of local and regional-scale stresses may increase the resistance of temperate marine communities to climate stressors and as such, provides an attractive tool for building resilience in temperate systems.

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1. Introduction

Global biodiversity is under increasing pressure from environmental change caused by human activities. Despite recent attention towards defining the biological impacts of climate change (e.g. Southward et al., 1995; Parmesan and Yohe, 2003; Harley et al., 2006; Helmuth et al., 2006a,b), the effects of this global physical forcing on marine organisms and ecosystems are still poorly understood (Richardson and Poloczanska, 2008; Rosenzweig et al., 2008).

Australia's marine biodiversity is globally unique. With 30–40% of the world's species of macroalgae, the algal flora of southern Australia is the most speciose in the world (Bolton, 1994; Kerswell, 2006), and up to 50% of its species are estimated to be endemic (Phillips, 2001). Rates of endemism in Australia are similarly high for predominantly marine invertebrates such as echinoderms (31%), molluscs (38%), annelids (67%), and marine sponges (56%) (Cork et al., 2006), with endemism being even higher for some temperate species. For example, southern Australia has 2–3 times as many species of molluscs as any other temperate coast in the world (Crame, 2000), and in some places up to 60% of these are endemic (Benkendorff and Davis, 2002). The evolution of this globally unique biodiversity has been attributed to a combination of the extensive rocky coasts, the unique oceanography associated with Australia's boundary currents (cf. Fig. 1), and climatic stability over geological time scales (Adey and Steneck, 2001; Phillips, 2001; Kerswell, 2006).

A characteristic feature of the Australian continent is that it is bound to the south by the longest east–west running coastline in the world. Together with the east and west coasts south of $\sim 27^{\circ}\text{S}$, the temperate coastline of Australia covers >3000 km. It straddles three biogeographic provinces (Waters et al., 2010) and includes some of the most pristine temperate coast in the world, as well as several areas which are heavily populated. Rocky reefs dominated by macroalgae (seaweeds) are a defining feature across these coasts (e.g., Underwood et al., 1991; O'Hara, 2001; Wernberg et al., 2003; Connell and Irving, 2008; Smale et al., 2010a,b). Because of its east–west orientation, Australia's temperate coastline is found within a narrow latitudinal band where even a small southward shift in isotherms will affect a very large area. Indeed, because of the lack of habitat to the south of the Australian mainland, most species will have limited opportunity to shift their geographical ranges poleward in response to warming, resulting in a narrowing of geographical ranges if distribution limits shift poleward.

Southern Australia has experienced some of the fastest increases in ocean temperatures globally, but climate signals have been variable within the region. In south-eastern Australia, strengthening of the East Australian Current has caused warming at a rate of $0.023^{\circ}\text{C year}^{-1}$ which is approximately four times the global ocean warming average (Ridgway, 2007). Coastal waters in south-western Australia have also

warmed appreciably, increasing by $0.013^{\circ}\text{C year}^{-1}$ since 1951 (Pearce and Feng, 2007), while south coast waters have warmed $\sim 0.011^{\circ}\text{C year}^{-1}$ since 1950 (Suppiah et al., 2006). Warming of Australia's temperate coasts is set to continue with another 1–3 $^{\circ}\text{C}$ predicted for the coming century (Lough, 2009). In addition, compounding stressors such as increasing pressure from human populations, changes to storm and rainfall patterns, terrestrial based inputs (e.g. nutrients and turbidity) and fishing will reduce the resilience of desirable ecosystem states (Ling et al., 2009b; Wernberg et al., 2010).

There is now great concern for the continued existence of Australia's unique temperate marine biodiversity under current rates of global climate change. Thus, relative to temperate rocky shores elsewhere, its unique evolutionary history and high levels of endemism, occurring within a relatively narrow climate envelope, make the biota of southern Australia highly vulnerable in terms of potential for total species losses as the marine environment warms, the seas become more acidic, storm patterns change, sea levels rise or consumers shift their distributions. Here, we review the current evidence for impacts of climate change across Australia's temperate rocky coasts and consider future needs for understanding ecological change (see also Johnson et al., 2011-this issue; Poloczanska et al., 2011-this issue). In recognition of the need to understand the range of potential impacts even if providing unequivocal evidence is near impossible, we have included a broad range of published, unpublished and anecdotal evidence across southern Australia. We first recognise known changes that may have been forced by climate and then forecast future change that may be managed by policy. Much of this review is based on the idea that large scale process such as climate change cannot be studied or prepared for unless the compounding or mediating effects of local scale influences (e.g. eutrophication, over-fishing) on climate change responses are also recognised (see also Philippart et al., 2011-this issue; Schiel, 2011-this issue).

2. Observed responses and impacts

Southern Australia is particularly under-represented in terms of documented responses to climate change in marine systems (Poloczanska et al., 2007; Rosenzweig et al., 2008). A lack of long-term data against which to assess change has been identified as one of the primary reasons for this paucity of documented impacts. However, warming over the past ~ 50 years has been identified as a primary or contributing cause of a number of ecological changes.

2.1. Range contractions

Perhaps the most visible impact has been the decline of the surface-canopy of the giant kelp *Macrocystis pyrifera*. Archival aerial photographs, admiralty charts and anecdotal accounts by fishermen and

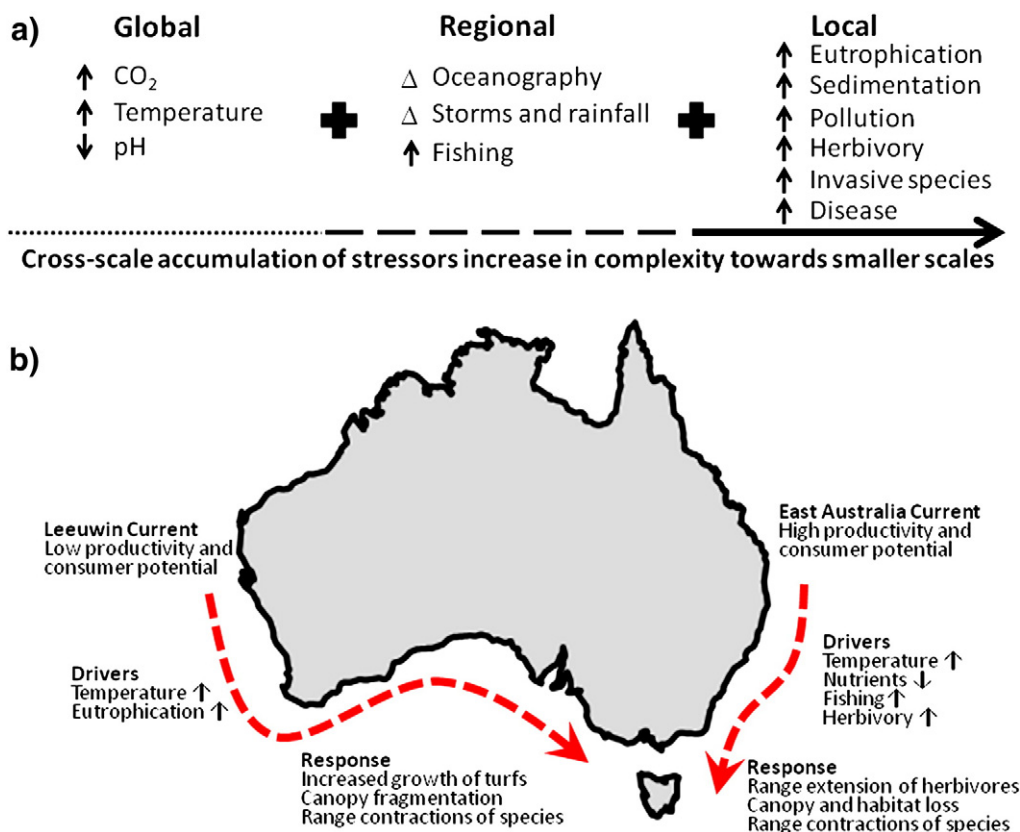


Fig. 1. Drivers of ecological change accumulate differently across global to regional to local scales (a). Different stressors tend to be associated with particular scales, albeit often these are not well defined and little understanding of their explicit scales of expression remains. Recognition of regional-scale influences (e.g. oceanography) may provide a framework for understanding how local stressors (e.g. eutrophication and herbivory) interact with global stressors to provoke ecological change (b). For example, responses in coastal systems lacking strong herbivore effects have tended to focus on climate interactions with water quality (e.g. kelp forests of the Leeuwin Current; Russell et al., 2009; Wernberg et al., 2010). Conversely, on rocky coasts with strong consumer control (i.e. East Australian Current), concerns for kelp persistence focusses on climate interactions with recruitment and fishing of lobsters (i.e. kelp forests of the East Australian Current, Ling et al., 2009a).

marine naturalists document that previously widespread *M. pyrifera* forests have disappeared from many sites in eastern Tasmania (Edyvane, 2003; Johnson et al., 2011-this issue). Ocean warming and an associated influx of nutrient poor water driven by a strengthening of the East Australian Current appears the most plausible cause of this decline (Johnson et al., 2011-this issue).

The distribution of other large macroalgae may also have been affected. Herbarium records suggest that the distribution of the three habitat-forming species *Ecklonia radiata*, *Phyllospora comosa* and *Durvillaea potatorum* have shifted southwards on the east coast over recent decades (Millar, 2007). Massive declines of large habitat-forming algae have also been recorded around urban centres, such as for *P. comosa* around Sydney (Coleman et al., 2008) and *E. radiata* around Adelaide (Connell et al., 2008). The processes responsible for these changes are currently under study but are likely to be directly or indirectly driven by climate and local anthropogenic stressors such as reduced water quality (Connell, 2007; Connell et al., 2008). For example, an unusual dieback of *P. comosa* and *E. radiata* in eastern Tasmania in 2001 was attributed to above-average seawater temperatures coupled with nutrient stress during calm sea conditions (Valentine and Johnson, 2004).

2.2. Range extensions

The barren-forming sea urchin *Centrostephanus rodgersii* has extended its range poleward by ~160 km decade⁻¹ over the past 40 years, from New South Wales to eastern Tasmania (Ling et al., 2009b). There is strong evidence that a strengthening of the East Australia Current and associated ocean warming (Ridgway, 2007) has

been responsible for this southward range extension as ocean temperatures across much of eastern Tasmania now exceed the 12 °C threshold for successful development of *C. rodgersii* larvae (Ling et al., 2008). *C. rodgersii* is a voracious grazer, and in New South Wales ~50% of all near-shore rocky reefs are urchin barrens where urchins have eaten most erect vegetation, leaving behind bare rock (Andrew and Byrne, 2007; Connell and Irving, 2008). In the three decades since its arrival, previously absent urchin barrens are now extensive throughout north-eastern Tasmania, and these are expected to expand further (Johnson et al., 2005). This habitat transition has been estimated to cause a minimum local loss of ~150 taxa associated with macroalgal beds (Ling, 2008).

Similar southern (poleward) range expansion has also been documented for 16 intertidal species in south-eastern Australia, including the giant rock barnacle *Austromegabalanus nigrescens* which has expanded into Tasmania, albeit with a slower mean expansion rate of ~29 km decade⁻¹ since the 1950s (Pitt et al., 2010).

Southward (poleward) range extensions have been documented for 45 species of fish on the south-east coast (Last et al., 2011). These represent ~15% of coastal fishes in temperate southeastern Australia and include several herbivorous, territorial and predatory species with the potential to significantly influence macroalgal habitats. For example, the damselfish *Parma microlepis*, known to influence other organisms by defending local territories (e.g., Buckle and Booth, 2009), was extremely rare in north-eastern Tasmania in the early 2000s, where it now constitutes one of the most conspicuous benthic fishes, particularly on *C. rodgersii* barrens (S. Ling, pers. obs). Of the predators, the Port Jackson shark (*Heterodontus portusjacksoni*) and the eastern blue grouper (*Acherodus viridis*) have extended their

ranges into north-eastern Tasmania, although both are still rare. Both species are known predators of *C. rodgersii* (Andrew and Byrne, 2007), but at their present densities and size structure it is unlikely that they are impacting on sea urchin populations.

While increasing frequency of sightings of south-eastern Australian mainland marine species has occurred in north-eastern Tasmania, predicted range contractions of southern seaweed-associated species appear more cryptic and trophic consequences more uncertain. For example, sightings of red velvet fish (*Gnathanacanthus goetzei*) have declined over the past 16 years, which may be a response to climate-driven decline in its primary habitat, *Macrocystis pyrifera* habitat (G. Edgar, unpub. data).

2.3. Reduced recruitment

In Western Australia (WA) there have been no explicit reports of ecological effects on temperate coasts as a result of recent climate change (Pearce and Feng, 2007). The longest biological dataset in WA concerns the distribution, abundance and recruitment of the commercially important western rock lobster (*Panulirus cygnus*). Western rock lobsters are conspicuous consumers of small invertebrates and calcareous algae, and it is possible that they influence floral and faunal assemblage structure (Edgar, 1990). Historical recruitment data for *P. cygnus* have shown a strong correlation between the strength of the Leeuwin Current and the magnitude of puerulus larval settlement. However, very low recruitment of *P. cygnus* has been recorded in the last three years, despite seemingly favourable conditions. Whether this decline is due to reduced brood stock through overharvesting or changes in physical environmental factors (i.e. ocean currents and eddies, temperature) is currently unknown, but recent analyses indicate that recruitment and migration patterns of rock lobster may have changed in response to rising temperature over the last 35 years (Caputi et al., 2010). Similarly, ocean warming in eastern Tasmania appears to be exacerbating the impacts of fishing on southern rock lobsters (*Jasus edwardsii*) by negatively influencing recruitment patterns of this species, but seemingly increasing the recruitment of the con-generic eastern rock lobster (*Jasus verreauxii*), typical of waters further north (Pelc et al., 2009).

2.4. Interactions with non-climate stressors

2.4.1. Fishing and harvesting

Superimposed on the climate-driven incursion of *Centrostephanus rodgersii* to eastern Tasmania is the heavy exploitation of marine predators. Long-term changes to species inside Marine Protected Areas (MPAs) relative to adjacent fished sites show that fishing has a major impact on the abundance and size structure of major target species in Tasmania (Barrett et al., 2009). This increase in abundance includes the important sea urchin predator, the spiny lobster *Jasus edwardsii*, that must reach a size of 140 mm carapace length to be an effective predator of *C. rodgersii* (Ling et al., 2009b). Indeed, intensive fishing for well over a century is estimated to have reduced the stock of legal-sized lobsters (110 mm carapace length) on eastern Tasmanian coasts to approximately 2–8% of pre-fished biomass by the 1990s (Frusher, 1997; Ling et al., 2009b).

2.4.2. Introduced species

Anthropogenic introduction of exotic species poses substantial threat to patterns of global biodiversity. While increasing invasions are not directly climate related, climate change has often been proposed to facilitate the establishment, further spread and impact of invasive exotic species in temperate marine systems (Stachowicz et al., 2002). In Australia, the introduced alga *Undaria pinnatifida* established dense mono-specific stands following the temperature-related dieback of native canopy-species in eastern Tasmania in 2001 (Valentine and Johnson, 2004).

It has also been suggested that the spread of the European green shore crab *Carcinus maenas* from Victoria into Tasmania has been facilitated by increasing ocean temperatures in response to a strengthening of the East Australia Current (Thresher et al., 2003). *C. maenas* is a voracious predator in intertidal and shallow subtidal habitats where it is capable of exerting strong top-down control of marine communities (Bertness and Ewanchuk, 2002). Impacts of *C. maenas* on rocky coasts remain undocumented in eastern Tasmania, but impacts on soft sediment communities have been recorded in Tasmania (Ross et al., 2004).

3. Expected impacts this century

It is difficult to unambiguously attribute ecological changes to anthropogenic climate change because of the potential for other co-occurring mechanisms to explain the observed patterns. The number of cases where climate change can reasonably be linked to an impact is, however, compelling. It is clear that macroalgal-dominated coasts in southern Australia are vulnerable to the direct and indirect impacts of climate change. Interestingly, there have not been any reported changes directly or indirectly attributed to climate change factors other than increasing temperatures. This could, perhaps, reflect that little or no data is available to document changes on other environmental factors (e.g., ocean acidification). Nevertheless, warming appears to be the primary climate-related pressure of concern for the immediate future (see also discussion on ocean acidification in Section 3.3). It is, however, likely that the influence of additional factors will increase as the environmental changes continue to manifest.

3.1. Temperature

The projected temperature increase for temperate Australian marine waters is in the order of ~1 °C and 1.5–3.0 °C by 2030 and 2070 respectively (Lough, 2009). Existing temperature gradients of this magnitude in southern Australia (e.g., Smale and Wernberg, 2009) are associated with considerable differences in physiology (Stæhr and Wernberg, 2009; Wernberg et al., 2010), species distributions of algae, invertebrates and fish (O'Hara and Poore, 2000; Wernberg et al., 2003, 2010; Tuya et al., 2008a,b; Smale et al., 2010b), population structure and dynamics (Ling, 2008; Wernberg and Goldberg, 2008), and habitat structure (Connell et al., 2008) of temperate marine species. For example, along the west coast the cool-adapted and endemic canopy-forming brown alga *Scytothalia dorycarpa* increases in abundance with increasing latitude (Smale et al., 2010b; Wernberg et al., 2010, 2011-this issue). Conversely, the relative abundance of warm temperate and tropical foliose brown algae such as *Padina* spp. and *Dictyota* spp., are inversely related to latitude (Smale et al., 2010b). It seems, therefore, very likely that the forecasted temperature increase would lead to a redistribution of flora and fauna equivalent to these latitudinal patterns (Hawkins et al., 2009). For most temperate species, this will imply range contractions as their northern (warm) range limits contract poleward while their southern limits can shift no farther south.

Continued ocean warming is likely to affect the successful recruitment, growth and productivity of prominent coastal organisms. For example, thermal thresholds are known for *C. rodgersii* larval survival (12 °C, Ling et al., 2008) and for growth and productivity of *E. radiata* (18.5 °C, Kirkman, 1984). A negative relationship between recruitment success and water temperature has also been shown for *E. radiata* (Wernberg et al., 2010). Similarly, the distribution of the turbinid gastropod *Turbo torquatus* shows signs that elevated temperatures may limit recruitment success; populations in warmer waters at northern latitudes are strongly dominated by a single cohort which recruited during a period of relatively cool ocean conditions, whereas populations in cooler waters at southern latitudes have multiple cohorts representing continuous successful recruitment (Wernberg et al., 2008). Increasing temperatures, therefore, may put marginal populations under further pressure and at risk of eventual collapse.

3.2. Trophodynamics

Increasing ocean temperatures are likely to affect herbivores and their foraging activities both directly and indirectly. Rates of herbivory may be enhanced as a direct result of temperature-driven increases in the metabolic rate of herbivores (Kordas et al., 2011-this issue), as demonstrated in laboratory experiments for temperate sea urchins (Siikavuopio et al., 2008) and amphipods (O'Connor, 2009; Sotka and Giddens, 2009). At the same time, the nutritional value of available food sources may change, either as a consequence of shifting species composition or as a consequence of altered biochemistry of existing species. Studies from Western Australia indicate that physiological adaptation and acclimatisation of *Ecklonia radiata* to warmer environments are associated with substantial changes in tissue nutrients and pigments, such that the nitrogen content (an important determinant of nutritional value) of kelp tissue decreases by $\sim 15\% \text{ } ^\circ\text{C}^{-1}$ temperature increase (Stæhr and Wernberg, 2009). This, in turn, can influence the ecological performance and fecundity of invertebrates that rely on kelp and other algal food sources (Foster et al., 1999; Kraufvelin et al., 2006), many of which are trophically important as herbivores or prey items for higher order consumers. Complex climate-driven interactions between key herbivores (e.g. the sea urchin *C. rodgersii*), reduced nutrient levels caused by shifting currents and strong impacts on higher trophic levels as a result of intense harvesting, will likely conspire to sway trophic dynamics in favour of increased herbivory in some areas (e.g., Tasmania) and thus strong impacts on ecologically important seaweed communities.

3.3. Ocean acidification

Ocean pH has dropped by 0.1 units since the industrial revolution and is predicted to drop by a further 0.3–0.4 units by 2100 (Meehl et al., 2007). Although most experimental studies on ocean acidification to date have focussed on tropical assemblages, recent work has shown that effects of ocean acidification on temperate marine systems may be equally complex and deleterious (Hall-Spencer et al., 2008; Martin and Gattuso, 2009; Russell et al., 2009).

Calcified coralline algae occupy up to 80% of hard substrate on the temperate coast of southern Australia, where they play an important ecological role as competitors for space and settlement cues for invertebrates (Steneck, 1986). Recent experimental work in Australia has shown that acidification associated with conservative projections of future CO_2 concentrations (550 ppm) is likely to have negative effects on the growth and recruitment of coralline algae, and this effect is compounded by increased temperature (Russell et al., 2009) and altered light regimes (Russell et al., 2011). In contrast to coralline algae, ocean acidification may have little negative or even positive direct effects on non-calcareous algae (Beardall et al., 1998; Russell et al., 2009; Connell and Russell, 2010).

Even if changes to ocean pH may be occurring much more rapidly than originally anticipated (Wootton et al., 2008), the evidence pointing to direct effects of ocean acidification on temperate marine ecosystems in the near future is ambiguous, and it is possible that these will not be realised for the next 50–100 years. For example, recent work on early larval development suggests that impacts in the next century are unlikely for the sea urchin *Heliocidaris erythrogramma* (Byrne et al., 2009) whereas increased larval mortality may be a consequence for abalone (Crim et al., 2011-this issue). Regardless, as with changes in temperature, ocean acidification is likely to initially result in increasing sublethal effects (e.g. slower growth rates, susceptibility to disease, and reduced reproductive capabilities) on a wide range of processes and species and these may combine to produce unforeseen indirect effects.

It is not surprising that research into the effects of ocean acidification in marine environments has a disproportionate focus on the negative effects on organisms that form calcareous structures (i.e. coral reefs, Hoegh-Guldberg et al., 2007; Anthony et al., 2008; Dupont et al., 2008;

Fabry et al., 2008; Kuffner et al., 2008; Parker et al., 2009). However, this preoccupation fails to identify the potential positive effects of increased CO_2 for both calcareous (e.g. echinoderm growth and feeding rates, Gooding et al., 2009; Dupont et al., 2010) and non-calcareous species (e.g. turf-forming algae, Russell et al., 2009). It is important to recognise that such positive effects could act as perturbations in ecological systems. For example, filamentous turf-forming algae form a natural component of the early post-disturbance successional stages of seaweed-dominated landscapes (Wernberg, 2006; Wernberg and Connell, 2008), yet under altered environmental conditions turfs can expand and inhibit the recruitment of kelp, potentially eroding resilience of kelp forests under future conditions (Connell and Russell, 2010).

3.4. Changes in storm patterns

Projections suggest that the frequency and/or the intensity of severe storms and waves may increase in the future (Poloczanska et al., 2007). This will cause increased intensity of physical disturbance on most coasts (e.g. localised loss of seaweed canopies, Seymour et al., 1989; Thomsen et al., 2004) which could be of great ecological significance. Physical disturbance regulates species richness and community structure, and disturbance regime plays an important role in maintaining diversity and driving patch dynamics in temperate marine communities in Australia (Kennelly, 1987a; Kendrick et al., 1999, 2004; Toohey et al., 2007; Wernberg and Connell, 2008; Wernberg and Goldberg, 2008). Studies have shown that increased wave energy correlates well with larger gaps in (i.e. fragmentation of) the seaweed canopy (Kennelly, 1987a; Farrell, 1989; Wernberg and Connell, 2008), which has implications for local diversity, productivity and overall community structure (Kennelly, 1987b; Kendrick et al., 1999; Wernberg, 2006; Wernberg and Goldberg, 2008). Exactly how temperate marine community structure will be affected by increasing frequency and/or intensity of physical disturbance remains uncertain, but evidence from elsewhere suggests that chronically disturbed habitats generally support species poor assemblages (Sousa, 1979; Hughes and Connell, 1999; Barnes and Conlan, 2007). In addition, systematic changes to weather patterns, and thus swell conditions, are likely to influence a range of ecologically important processes. For example, high wave exposure suppresses the natural post-disturbance recovery of *Ecklonia radiata* canopies (Wernberg et al., 2003). Moreover, increasing disturbance regimes will interact with, and compound, the negative effects of elevated ocean temperature on the recruitment and recruit performance of kelps, compromising the ability of kelp canopies to withstand and recover from disturbances (Wernberg et al., 2010).

3.5. Rainfall, run-off and nutrients

Climate change is predicted to alter rainfall patterns, but these changes will differ regionally (CSIRO, 2007); rainfall will be further reduced in regions of low rainfall, and therefore less sediment and nutrient run-off will occur, while the converse will be true in areas of higher annual rainfall. Experience from urbanised coasts shows that elevated sediments and nutrients generally benefit small, more opportunistic species of algae (Pedersen and Borum, 1996; Worm et al., 1999; Gorgula and Connell, 2004; Russell and Connell, 2005), leading to shifts from canopy to turfing algal dominated systems (e.g., Worm et al., 1999; Eriksson et al., 2002; Connell et al., 2008). Therefore, increases in sediment and nutrient inputs would generally have a negative impact on algal-dominated reef assemblages. However, such effects will vary within the regional oceanographic and biological context. For example, where declining nutrient levels caused by changes in oceanography are likely to cause negative impacts on *Macrocystis* kelp beds in Tasmania (Johnson et al., 2011-this issue), increasing nutrient levels are likely to have large negative effects in regions of more

oligotrophic waters, such as those in southern Australia (Russell et al., 2005). Further, eastern Australia has greater grazing pressure that may counter any negative effects of terrestrially derived nutrients by consuming bloom forming algae (Connell, 2007; Connell and Irving, 2008). Independent of nutrient driven effects, there are also likely to be changes to inshore reefs as a result of increased frequency of extreme rainfall events. For example, hyposaline conditions have been observed to cause a major shift in reef habitat mediated by extensive mortality of *Centrostephanus rodgersii* following major flood events in 1986 and 1988 in Botany Bay (New South Wales), whereby rapid re-colonisation of seaweed habitat occurred on reefs that were previously urchin barrens (Andrew, 1991).

3.6. Disease

There is considerable concern globally that predicted warming and other anthropogenic stressors may increase the spread of pathogens and enhance their virulence as well as decrease the resilience of host organisms including sea urchins (Lester et al., 2007) and macroalgae (Jackson et al., 2001; Lafferty et al., 2004). For example, massive declines (40–100%) of the kelps *Ecklonia radiata* in New Zealand (Cole and Babcock, 1996; Cole and Syms, 1999) and *Laminaria religiosa* in Japan (Vairappan et al., 2001) have been attributed to outbreaks of disease. Moreover, complex interactions between bacterial pathogens, seaweed chemical defences and environmental factors, such as temperature, have been shown to be important in determining the extent to which a common red alga in southeastern Australia (*Delisea pulchra*) suffers from bacterial disease which can result in death of the alga (Case et al., 2011).

3.7. Expected patterns of impact

Given that the impacts of climate and non-climate stressors will vary considerably among regions, ecological impacts are likely to manifest heterogeneously across temperate Australia (Fig. 1). Such impacts will be greatest where large scale southward flowing currents (e.g. East Australian and Leeuwin Currents) transport additional warm water poleward, and around population centres where additional stressors are strongest, but may be delayed by local oceanic features providing refuge habitats, such as zones of upwelling of relatively cool and nutrient rich water masses or deeper water refuges (e.g., Graham et al., 2007). Importantly, impacts may not be gradual. For example, despite evidence for concurrent warming and major ecological changes prior to their study, Stuart-Smith et al. (2009) found relatively few changes in Tasmanian coastal communities over a 10–15 year period, and suggested that this reflected a period of relative stability following major abrupt community reorganisation (see also Hsieh et al., 2005). Physiological acclimatisation may offset the immediate translation of environmental change into distributional change of temperate marine organisms (Wernberg et al., 2010). In addition, range shifts may be obscured by habitat buffering, where complex interactions between habitat-forming and modifying species, coastal topography and environmental conditions create benign micro-habitats, maintaining the latitudinal extent of a species in a mosaic of micro-refugia (Helmuth et al., 2006a,b; Hawkins et al., 2008).

4. Management and adaptation responses

Management actions focussed on reducing the risk of major shifts in ecosystems, and potential loss of high numbers of species, are particularly urgent given predictions of continued and further accelerating warming. However, a fundamental consideration in assessing and managing impacts of climate change on temperate marine communities is the broad spectrum of anthropogenic pressures operating at global (climate), regional (changes to oceanography, overharvesting) and local (eutrophication, non-native species, coastal development, point-source

pollution, aquaculture) scales that interact to drive unprecedented and complex changes in marine systems (Harley et al., 2006; Harley and Connell, 2009) (Fig. 1).

Direct climate change can only be managed in a global international context and, except for supporting international initiatives, is outside the reach of national and state governments. However, since reduced resilience of marine systems will be driven by interactions between global climate and regional and local scale pressures (Ling et al., 2009b, 2009b; Russell and Connell, 2009; Wernberg et al., 2010), adaptive strategies focussed at these smaller scales may be better placed to ameliorate the negative impacts of an inevitably changing climate (Falkenberg et al., 2010). Recognition of this, in combination with greater attention to the anticipation and prevention of socially-undesirable regime shifts, has led to more proactive management of local stressors in some regions. For example in South Australia, local government has encouraged research into the processes that either increase or weaken resilience, and of the socio-economic drivers and governance that regulate modification of the physical environment (e.g. water quality) and their biota (e.g. fisheries). South Australian managers now recognise global–local connections of future change, recently implementing long-term policy solutions for the sea (policy on reducing wastewater discharge) that also act as solutions for the land (policy on establishing new sources of water that do not rely entirely on rainfall). Upgrades to wastewater treatment plants, to produce recycled water for residential and industrial use, not only reduces reliance on rainfall for fresh water supplies, but also reduces the nutrient rich discharge that has primarily contributed to phase shifts on metropolitan coasts from kelp to turf-dominated ecosystems (Connell et al., 2008). Similarly in Tasmania, managers are recognising the need to reduce risk of climate-driven impacts of overgrazing on coastal ecosystems by supporting a program of rebuilding predator biomass to reduce the risk of overgrazing by the range-extending sea urchin *C. rodgersii* (Ling et al., 2009b). Networks of marine reserves that are being established along temperate coasts Australia-wide that serve to minimise both top-down and bottom-up impacts, may increase the resilience of marine communities to climate change.

Indeed, efforts to reduce the compounding influence of multiple stressors may reduce the frequency and extent to which ecological systems change to unexpected states (Paine et al., 1998; Scheffer and Carpenter, 2003). If multiple perturbations reduce the resilience of a system, then local management may be effective in reducing the effects of climate change (Hughes et al., 2007; Russell and Connell, 2009). If local impacts are driving local system shifts (e.g., Gorman et al., 2009), removal of these stressors may increase the resilience of natural systems to climate change (Russell et al., 2009; Ling et al., 2009a). Reduction of such stressors may assist restoration through actions akin to terrestrial re-forestation. For example, it may be possible to reverse observed shifts from kelp to turf dominated systems by re-seeding kelp forests with recruits from populations in cooler water.

5. Future directions

Improving predictions of responses to variation in biotic and abiotic variables has been a persistent challenge in ecology. Consequently, there is a considerable history on the advantages and disadvantages of alternate approaches, with general agreement centring on the need for multiple approaches combining the use of good natural history, rigorous tests of spatial and temporal patterns and experimental assessments of the combinations of factors that drive them. In this regard, it will continue to be useful to assess past changes as a function of known climate change. While these assessments are necessary, their use in forecasting relies on integrating experimentally derived knowledge of the relevant combinations of processes most responsible for accelerating (e.g. synergistic processes) or resisting ecological change (e.g. counter-balancing processes).

Reconstruction of past patterns of ecosystem diversity and composition has direct relevance to predicting the consequences of climate change because it provides information about how ecosystem may respond in the future. However, it is important that such data are treated as a 'null models' as additional factors such as fishing and eutrophication also lead to changes in ecosystem dynamics. In the same way that climate can be related to ecological variation through time, it can be related to ecological variation in space. Studies of the ways in which key species respond to various environmental and ecological conditions across existing gradients of temperature (Pennings and Silliman, 2005; Wernberg et al., 2010) and pH (Hall-Spencer et al., 2008) have provided important insights into how species or systems may respond to changing climate conditions. The gradual temperature gradients, such as those along the tropical-temperate transitions of the Australian eastern and western coastlines (Smale and Wernberg, 2009), offer strong opportunities for combining observational and experimental studies (comparative experiments sensu Menge et al., 2002) to quantify the subtle effects of climate on the response of systems to additional perturbations (e.g. Wernberg et al., 2010).

There are relatively few observed examples of species responding to climate change within Australian temperate waters, in part due to the paucity of large-scale long-term baseline data. It is, however, very likely that a large number of species, including conspicuous habitat formers, have experienced range shifts or changes in their population structure in response to recent warming, but these changes have gone unrecorded (Edgar et al., 2005; Richardson and Poloczanska, 2008). Therefore, there is an immediate need to initiate programs that will enable impacts on species, assemblages and ecosystem functioning to be documented, subsequently allowing appropriate management plans to be designed and implemented (Hobday et al., 2006). For some species, use of sediment cores or the fossil record as a natural baseline for species biogeographic range and turnover may be applicable (e.g., Greenstein and Pandolfi, 2008). Due to the number of biogeographical provinces in Australian temperate marine systems (Waters et al., 2010), and the high levels of biodiversity and endemism, it is not possible to monitor all species. Therefore, efforts should be made to identify climate indicator species as has been done by the MarClim project in the United Kingdom (Mieszkowska et al., 2005). Indeed, development of cost-effective indicators to detect changes in ecosystem health and ecological responses to climate change is currently underway in Western Australia, following substantial funding from the State (e.g., Smale et al., 2010a,b).

Experiments that follow these observational assessments will need to focus on meaningful combinations of local and global stressors, ensuring that predictions of future shifts in ecological diversity are not underestimated by any false impression created by summing single drivers. Such experiments may be particularly powerful for predicting context-dependencies (cf. Fig. 1) associated with local needs of management. While the link between human activity and abiotic changes often appears obvious in hindsight, ecologists continue to be surprised by the ecological outcomes (Paine et al., 1998). These surprises occur as a product of synergies between abiotic and biotic drivers which cannot be predicted by simply 'adding up' the effects of single drivers. As progress is made in identifying the conditions leading to major biotic shifts, there will be a need to assess the parameters most responsible for ecological changes and the scales at which they operate. Experimental assessments can empower local managers because they show that policies of reducing local stressors (e.g. nutrient pollution) can reduce the effects of global stressors not under their governance (e.g. ocean acidification) (Russell et al., 2009).

Forecasts of habitat loss often centre on change to primary productivity or the strength of herbivory (Connell et al., 2011-this issue). Indeed, the balance between production and consumption of species that provoke ecosystem change is often altered by local influences that are contingent on middle-scale influences (e.g. oceanography) and together are mediated by climate (Fig. 1). Regional-scale differences (e.g. Leeuwin Current versus East Australian Current) drive

contrasting forecasts of loss and fragmentation of kelp forests. On coasts lacking strong herbivory (i.e. within the Leeuwin Current, Connell and Irving, 2008), concerns about future climate tends to focus on interactions with water quality (Russell et al., 2009; Wernberg et al., 2010). Conversely, on rocky coasts with strong consumer control (i.e. within the East Australian Current), change in consumer abundance has strong effects on kelp loss (i.e. kelps-to-barrens, Andrew, 1991; Ling and Johnson, 2009) and concerns for kelp persistence focuses on recruitment and fishing of consumers and their predators (Ling et al., 2009b). Recognition of such middle-scale influences (e.g. regional scales of biogeography and oceanography) may provide a framework for interpreting how local stressors (e.g. nutrient pollution and fishing) interact with global stressors to provoke change (Fig. 1).

6. Conclusions

This review recognises that the world's oceans have changed naturally at timescales ranging from days to decades to millennia, but we highlight the directional changes that overlay this natural variation as a result of human activities. A recurring theme is the context-dependency of climate change impacts that result from the mediating affects of meso-scale and local scale influences (Fig. 1). Such cross-scale interactions mean that the abiotic conditions at any one location will reflect the combined influence of meso-scale (e.g. oceanography and storm frequency) and local scale interactions (e.g. catchment type \times coastal morphology). The novel environmental conditions generated by climate change (e.g. increases in temperature and CO₂ concentrations) are likely to drive greater change in localities that have lower resilience (e.g. nutrient pollution on oligotrophic coasts or heavily fished reefs) to combinations of global and local stressors. The largest climate driven changes are, therefore, a product of their local–regional settings.

Documented cases of climate-driven change in the temperate waters of Australia are currently dominated by range shifts (both contraction and expansion) driven by increasing temperature. In Tasmania this has precipitated substantial habitat-level changes, with the loss of kelp forests and associated species. In combination with the climate-driven addition and loss of functionally important marine species at higher latitudes, altered rates of ecosystem processes will continue to result in major changes to the structure and function of local temperate coasts. While the only true way to mitigate climate change is to reduce the reliance on carbon-based sources of energy (Russell and Connell, 2010), research is needed to assess where it may be possible to ameliorate the effects of climate through management of local stressors (e.g. reduction of nutrient pollution, MPA legislation) or biological communities (e.g. MPAs and kelp re-seeding to increase resilience).

Future patterns of diversity will include the outcome of local processes and reflect the influence of climate operating across many spatial scales. The future range shifts or changes to current mosaics will represent individual species responses to spatial heterogeneity which is continually modified by temporal change. The ecological challenge is to interface local complexity into successively larger scales. While this pursuit has been a fundamental activity in ecology, the need has become more difficult to ignore if our research is to maintain its relevance as a forecasting tool. Future patterns of species diversity, and their individual functions, will be a product of the temporal modification of spatial opportunities and constraints for colonisation and persistence. Ecological research into climate change has its own opportunity to diversify its approach and integrate where previous constraints hamper a more comprehensive understanding of diversity in the past, present and future.

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