



Conserving potential coral reef refuges at high latitudes

Maria Beger^{1,2*}, Brigitte Sommer², Peter L. Harrison³, Stephen D.A. Smith^{4,5} and John M. Pandolfi²

¹Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, Brisbane, Qld 4072, Australia, ²Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane, Qld 4072, Australia, ³Marine Ecology Research Centre, Southern Cross University, Lismore, NSW 2480, Australia, ⁴National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia, ⁵Marine Ecology Research Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia

*Correspondence: Maria Beger, Australian Research Council Centre of Excellence for Environmental Decisions and Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane Qld 4072, Australia.
E-mail: m.beger@uq.edu.au

ABSTRACT

Aim High-latitude coral reef communities composed of tropical, subtropical and temperate species are heralded as climate change refuges for vulnerable tropical coral reef species, giving them high, but as yet unrealized, conservation priority. We review the ecology of subtropical reefs in the context of climate change and evaluate management strategies ensuring both their own continuity and their potential to act as refuges for tropical species.

Location Global high-latitude coral reef environments.

Methods We review the literature about refuges management, high-latitude reefs, climate change effects on reef organisms and the conservation of reefs.

Results High-latitude coral reef systems are functionally different from their tropical counterparts, characterized by unique biogeographical overlap of taxa at their range margins, endemic species and strong seasonality in species composition. They are shaped by marginal environmental conditions, which are predicted to undergo greater changes than reefs at lower latitudes, resulting in community re-assembly through range shifts, altered dispersal patterns, survivorship and habitat loss. The combined impact of these changes, however, is difficult to assess, as some effects may be antagonistic. Climate change conservation options include passive management strategies such as no-take reserves that aim to minimize local disturbances, and active strategies such as relocating populations to refuge sites. Success of active intervention relies on the long-term persistence of relocated populations, which is unlikely for high-latitude populations once source tropical populations at lower latitudes are locally extinct.

Main conclusion High-latitude reefs are poised for rapid modification under climate change. Management should anticipate these changes by setting up no-take reserves on suitable subtropical reefs now to foster ecosystem resilience through reduced anthropogenic impacts. Given the uncertainty over which species will arrive or depart and lack of knowledge about the history of most subtropical reef development, active management is presently not the best use of management resources.

Keywords

Climate change management, high-latitude reefs, range shifts, reef conservation, subtropical reefs, transitional biogeographical zones.

INTRODUCTION

Transitions between biogeographical zones along environmental gradients often have the potential to function as centres of heightened evolutionary activity (Kark *et al.*, 2007; Kawecki, 2008; Conover *et al.*, 2009; Gibson *et al.*, 2009).

Communities in transition zones contain many species located in marginal environments, where selective pressures can drive speciation and adaptive diversity (Doebeli & Dieckmann, 2003; Haak *et al.*, 2010). These marginal environments often contain both species' range edges and rare species with potentially unique adaptive genetic and phenotypic

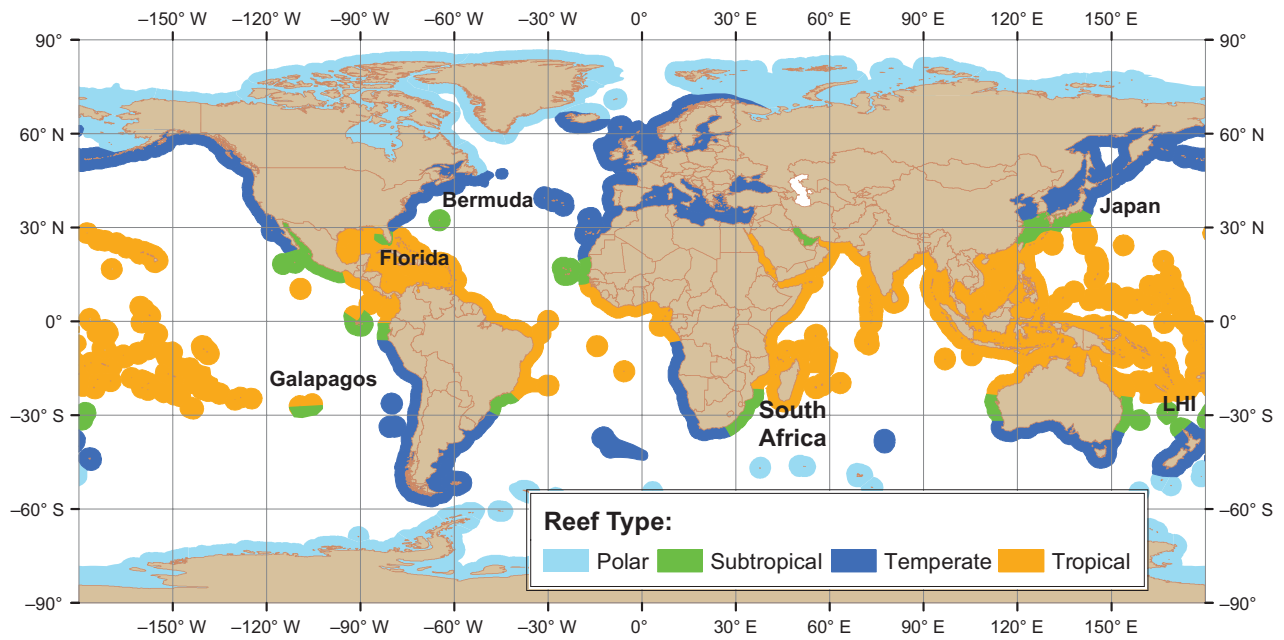


Figure 1 Locations of marine bioregions that include subtropical non-accreting reefs supporting scleractinian corals or where tropical and temperate reef biota overlap (modified after Spalding *et al.*, 2007). Reef occurrences in black. LHI – Lord Howe Island, Australia.

characteristics (Smith *et al.*, 2001; Kark *et al.*, 2007; Beatty *et al.*, 2008; Kawecki, 2008). They are characterized by high species turnover or rapid gradients of species richness (Williams *et al.*, 1999). In these biogeographical transition zones, the effects on community structure from climate change might be particularly acute, as community re-assembly will result from range shifts, altered dispersal patterns and survivorship, and habitat loss. In addition, transition zones potentially provide environmental stepping stones for species movements during climate-driven range shifts (Gibson *et al.*, 2009). These characteristics plus their inherent biodiversity values make transitional environments high conservation priorities (Smith *et al.*, 2001; Gibson *et al.*, 2009; Budd & Pandolfi, 2010; Haak *et al.*, 2010).

Here, we focus on transitional high-latitude, subtropical coral reef communities that have been heralded as potential refuges for tropical taxa during climate change (Riegl, 2003; Riegl & Piller, 2003). They form distinct marine ecoregions (Spalding *et al.*, 2007) (Fig. 1), and their transitional communities with overlapping tropical, subtropical and temperate species ranges (Harrison & Booth, 2007) are differentiated from tropical coral reefs in terms of their community structure and ecological dynamics (Harriott *et al.*, 1994; Harriott & Banks, 2002; Sommer *et al.*, 2013 in press) (Fig. 2). For example, in Australia, high-latitude coastal reefs include scleractinian corals at or close to their southern range limits, the canopy-forming kelp *Ecklonia radiata* (Agardh 1848) at its northern range limit, high abundance of other invertebrate taxa with temperate distributions including sea urchins, barnacles and ascidians (Harriott *et al.*, 1994; Harriott & Banks, 2002), and tropical, subtropical and temperate species of fish (Booth *et al.*, 2007;

Malcolm *et al.*, 2010) and molluscs (Harrison & Smith, 2012). High-latitude coral communities are sometimes distinguished from coral reefs based on their inability to accrete calcium carbonate reefs (Buddemeier & Smith, 1999), although subtropical coral reefs are well developed in some regions. In contrast to some tropical systems with relatively low ranges of environmental conditions, transitional ecosystems often support populations at species' thresholds of environmental tolerance both in terms of the magnitude of anomalies and variability in physicochemical environmental conditions.

The idea that subtropical reefs are important future refugia is consistent with the evidence that they have been instrumental in the survival of coral reef organisms through geological time (Kiessling, 2009), acting as refuges for tropical corals (Halfar *et al.*, 2005; Greenstein & Pandolfi, 2008). As tropical coral reefs are in critical decline worldwide from over-exploitation and changing environmental conditions (Hughes *et al.*, 2010; Pandolfi *et al.*, 2011), understanding marginal communities will facilitate predictions about future tropical reefs that may become marginal under climate change (Kleypas *et al.*, 1999; Guinotte *et al.*, 2003). For example, corals living in variable temperature regimes exhibit high thermal tolerance (Oliver & Palumbi, 2011) that may enhance their resistance to climate change (Pandolfi *et al.*, 2011). Where currents from the tropics to higher latitudes facilitate larval transport (Harrison & Booth, 2007; Beger *et al.*, 2011), shifts in species ranges away from tropical habitats to cooler regions may provide a mechanism for species' preservation. Range expansions are already evident in eastern Australia and in Japan, where species of tropical fish and hard coral are establishing populations increasingly

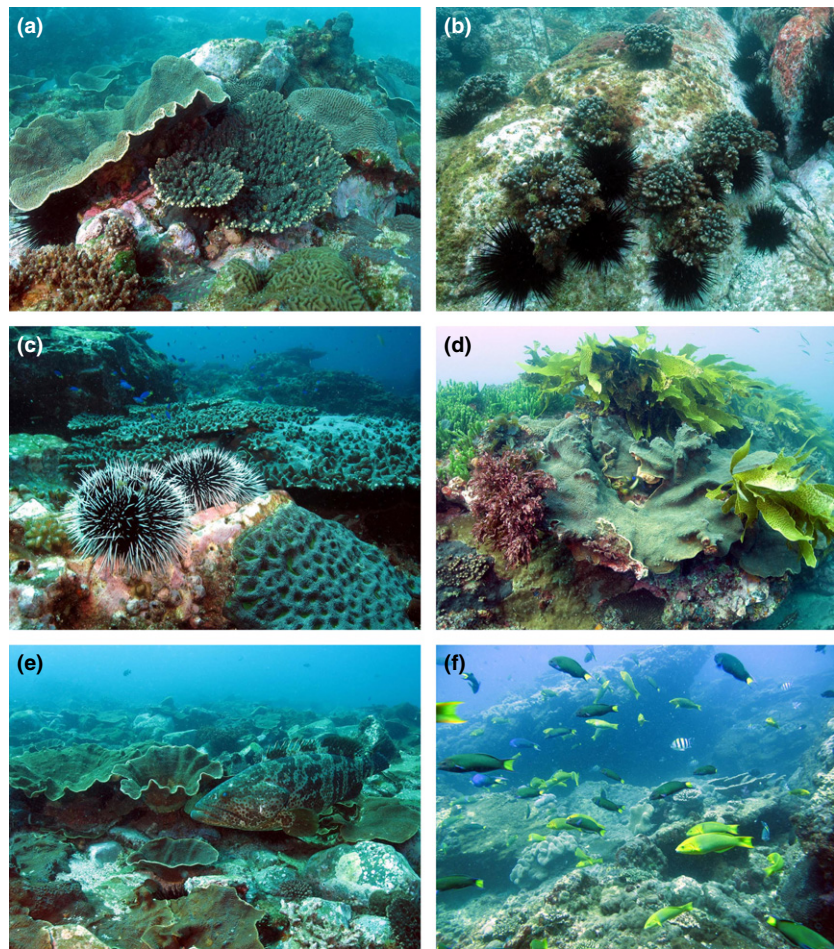


Figure 2 Subtropical reefs of eastern Australia: (a) diverse coral assemblage in the Solitary Islands Marine Park (30°S latitude); (b) the endemic species *Pocillopora aliciae* Schmidt-Roach *et al.*, 2013 growing in *Centrostephanus rodgersii* urchin barrens in Port Stephens and Great Lakes Marine Park (32°S); (c) subtropical reef assemblage in the Solitary Islands Marine Park; (d) coral – kelp habitat in the Solitary Islands Marine Park; (e) *Epinephelus daemeli* at Solitary Islands Marine Park; and (f) aggregation of *Thalassoma lunare* and *T. lutescens* at Flinders Reef, Queensland (27°S). Photos A-E by B. Sommer, F by M. Beger.

further polewards (Booth *et al.*, 2007; Figueira & Booth, 2010; Yamano *et al.*, 2011; Baird *et al.*, 2012). However, like other reef systems, subtropical reefs are increasingly threatened by local and global scale impacts (Schleyer *et al.*, 2008; Beger *et al.*, 2011). Greater geographical isolation and smaller population sizes (Hughes *et al.*, 2002), greater projected changes in sea surface temperatures and lower aragonite saturation state of cooler water (Guinotte *et al.*, 2003; Doney *et al.*, 2009; Kroeker *et al.*, 2011) may render subtropical corals particularly vulnerable to climate change.

Climate change is likely to shift the geographical extent of transitional communities and re-assemble communities during range and abundance shifts of constituent species (Gibson *et al.*, 2009; Haak *et al.*, 2010). Range shifts may cause such species to move out of reserves that currently enhance their survival (Araujo *et al.*, 2004), underpinning the need to focus conservation efforts towards appropriate refuges (Araujo *et al.*, 2004; Graham *et al.*, 2008). The high levels of uncertainty in predictions of future conditions (Beger *et al.*, 2011; Lybolt *et al.*, 2011; McDonald-Madden *et al.*, 2011; Wintle *et al.*, 2011) complicate conservation and management decision-making. While a forward-thinking approach to conservation is clearly required to maximize future biodiversity and productivity outcomes, political

support for precautionary management and strategic research to enhance coral reef persistence is severely hampered by this prediction uncertainty. Current conservation efforts protect substantial areas of subtropical reefs from fishing, particularly in Australia, South Africa, Florida, Bermuda and New Zealand (UNEP-WCMC 2010) (Fig. 1). As static conservation areas will not protect shifting species (Hobday, 2011) or dynamic ecosystem responses (Pressey *et al.*, 2007), they may not be sufficient for dealing with threats associated with climate change, necessitating strategic adaptation of conservation approaches. It has been argued that the management of climate change refuges may involve a three-step process, with first the identification of sites most likely to persist under changing climatic conditions (climate refuges) (Shoo *et al.*, 2011), followed by intensive management of these refuges to maintain or restore habitats (Shoo *et al.*, 2011). Then, if refuge health declines, no alternative habitats for species taking refuge at that location are available, and there is a high likelihood of success, the final step is the application of active management such as captive breeding or assisted migration (McDonald-Madden *et al.*, 2011). Active management methods often apply at smaller spatial scales and may aim to restore habitats (e.g. replantations) (Shoo *et al.*, 2011), facilitate processes that are interrupted by human activity or

geography (e.g. creating movement corridors across roads) (Rout *et al.*, 2009), or apply technology (e.g. shading the reef from intense sunlight (Rau *et al.*, 2012)). The suitability of these approaches to coral reefs in general and subtropical coral communities in particular, however, has not yet been discussed or evaluated.

Here, we review what is known of the ecology of subtropical transitional reef communities in the context of global warming and ocean acidification and evaluate how this information might underpin management strategies to ensure both their own continuity and their potential to act as refuges for tropical coral reef species.

THE ECOLOGY OF SUBTROPICAL REEFS

Community structure

The biodiversity of transition zones results from the presence of species that are overlapping at their range edges, as well as endemic taxa (Kark *et al.*, 2007). Subtropical reef transitional communities are characterized by a biogeographical overlap of tropical and temperate species at the limits of their range, subtropical species that tend to be rare or absent at lower latitudes (such as the coral *Acropora solitaryensis* Veron and Wallace, 1984 with southern and northern antitropical populations), and some endemic species with narrow geographic ranges (Harriott & Banks, 1995). Endemism is known to occur at several isolated islands (such as Lord Howe Island, Galapagos Islands, St Helena) with little potential for these taxa to migrate elsewhere and has mostly been reported for fishes (Francis *et al.*, 1999; Edgar *et al.*, 2010; van der Meer *et al.*, 2012a), scleractinian corals (Schmidt-Roach *et al.*, 2013) and zooxanthellate coral symbionts (Wicks *et al.*, 2010b). In most taxa, species turnover, especially of tropically affiliated species, may be high, reflecting variable larval supply and recruitment, and periodic high variability in physicochemical conditions (Wallace *et al.*, 2009; Harrison *et al.*, 2011; Smith, 2011).

Species richness and composition vary along latitudinal gradients (Floeter *et al.*, 2005; Smith *et al.*, 2008; Olbers *et al.*, 2009) but trends can differ for different taxa. While coral cover on high-latitude reef patches is frequently similar to that of tropical coral reefs (Harrison *et al.*, 1998; Harriott & Banks, 2002; Wallace *et al.*, 2009; Thomson & Frisch, 2010), reef accretion and development are often limited due to cumulative stress from a combination of physical and biological factors (Kleypas *et al.*, 1999; Harriott & Banks, 2002). Instead, coral colonies in the subtropics often form low-relief veneers encrusting rocky substrata (Fig. 2). Coral species richness generally declines with increasing latitude (Harriott & Banks, 2002), and at high latitudes, the benthos is more frequently dominated by macroalgae, soft corals and other sessile invertebrates such as ascidians, sponges and barnacles (Harriott *et al.*, 1994; Schleyer *et al.*, 2008; Olbers *et al.*, 2009; Wicks *et al.*, 2010a). Similarly, the diversity and abundance of fish communities decline with increasing

latitude (Booth *et al.*, 2007). A poleward decline in diversity, however, is by no means universal among invertebrates. While some taxa such as bivalve and gastropod molluscs (Roy *et al.*, 2000), and ascidians (Shenkar & Swalla, 2011) show reduced diversity with increasing latitude, there is no such trend in decapods (Pohle *et al.*, 2011), or it may even be reversed, as in peracarid crustaceans (Rivadeneira *et al.*, 2011).

Marginal environmental conditions

High-latitude scleractinian coral communities exist in close proximity to their environmental limits of temperature, salinity and aragonite saturation (Kleypas *et al.*, 1999). They are exposed to high rates and magnitudes of fluctuating environmental conditions (Guinotte *et al.*, 2003) and resulting in chronic disturbance regimes. Although some tropical coral species occur at high latitudes, they are generally locally distributed and rare, and form communities distinct from their tropical counterparts. For example, coral communities on high-latitude coastal reefs of eastern Australia are typified by widely distributed, generalist and stress-tolerant coral species with horizontal morphologies (Sommer *et al.*, 2013 in press).

Subtropical reefs occur where major boundary current systems facilitate larval transport from the tropics to subtropical shallow-water reefs (Booth *et al.*, 2007), as elsewhere the lack of transport may hinder the establishment or maintenance of populations (Harrison, 2011). For example, populations forming remote island communities, such as those at the world's southernmost coral reef, Lord Howe Island (Australia), have limited gene flow and recruitment from intermittent long-distance larval dispersal in more widespread species of fishes (Patterson & Swearer, 2007; van der Meer *et al.*, 2012a) and corals (Noreen *et al.*, 2009). For tropical reef fishes along the southeast coast of Australia, such recruitment events are highly variable among years (Booth *et al.*, 2007), and, given the rarity of individuals with strong genetic affinity to tropical source populations in fishes (van der Meer *et al.*, 2012b) and corals (Ayre & Hughes, 2004; Noreen *et al.*, 2009), this is likely to be the case for other taxa.

Similarly, temperature dynamics play an important role in marginal communities, as lower mean and minimum sea surface temperatures as well as temperature changes over relatively short temporal scales (Guinotte *et al.*, 2003; Malcolm *et al.*, 2011), may limit the settlement of organisms (Nozawa & Harrison, 2007; Schleyer *et al.*, 2008) or the establishment of viable populations (Figueira & Booth, 2010). For example, the proportion of tropical and temperate fish species in subtropical fish communities varies with season, with recruitment of tropical species in summer, and the subsequent demise of some species in winter (Booth *et al.*, 2007). Harriott *et al.* (1994) argued that the frequency of storm events causes coastal coral communities of eastern Australia to be best developed on leeward sides of islands and headlands. Similarly, high-latitude coral communities in Japan are

located in embayments and off sheltered headlands (Nozawa *et al.*, 2008).

Ecosystem function

Shifts in the functional ecology of marginal reefs occur over latitudinal gradients, including changes in the relative contribution of different functional groups of taxa towards ecological processes (Ferreira *et al.*, 2004; Floeter *et al.*, 2005). For example, there is a shift in the relative contribution to grazing by fishes and invertebrates. Herbivorous fishes are the primary grazers on low-latitude reefs but, possibly because of temperature-related physiological constraints (Floeter *et al.*, 2005), sea urchins play a much stronger role in grazing at higher latitudes (Ferreira *et al.*, 2004). Urchin grazing determines the structure of benthic habitats on some high-latitude reefs, and the poleward range extension of one key grazer, *Centrostephanus rodgersii*, (Agassiz 1863), together with other local factors, has played a significant role in the decline of *Macrocystis* giant kelp communities on Australia's temperate eastern coast (Ling *et al.*, 2009), highlighting how shifts in the distribution and abundance of organisms in this zone of biogeographical overlap can have broad ecological consequences.

CLIMATE CHANGE EFFECTS ON PROCESSES SHAPING SUBTROPICAL REEFS

Changes in environmental parameters induced by oceanographic climate change are likely to redefine the characteristics of subtropical coral reef communities in the future, partly by driving range expansions and contractions of tropical, temperate and endemic species, but also through altering biogenic habitats (e.g. through large-scale bleaching, changes in macroalgal cover and calcification) (Schleyer *et al.*, 2008; Harrison *et al.*, 2011; Yamano *et al.*, 2011) and changes in ecosystem function. These changes include both factors that reduce the fitness of reef organisms (threats), and also those that enhance productivity and provide opportunities for new species to become established (benefits). Therefore, a threat to some organisms, such as raised temperature to subtropical corals, may provide benefits to others, by opening up new habitat to tropical species able to disperse to higher latitude refuges.

Climate change will pose multidimensional complex threats to coral reefs (Pandolfi *et al.*, 2011), including: (1) higher mean, and more variable temperature, altering physiology of organisms and causing stress responses such as coral bleaching (Harrison *et al.*, 2011); (2) ocean acidification that alters calcification rates (Fabricius *et al.*, 2011; Pandolfi *et al.*, 2011; Cooper *et al.*, 2012) and dispersal and recruitment abilities (O'Connor *et al.*, 2007; Munday *et al.*, 2009a; Byrne *et al.*, 2011); and (3) greater rates of damage from higher and more frequent wave and wind extremes (Young *et al.*, 2011). Although the magnitude and rate of these changes are likely to be spatially, temporally and taxonomically variable,

resulting in differential species and reef responses (Hurd *et al.*, 2011; Pandolfi *et al.*, 2011), tropical coral reef species may not be able to persist abundantly in their current core ranges and may require refuges at higher latitudes. But these climate change threats also affect high latitudes and may be particularly severe on subtropical reefs, which are in regions projected to experience higher rates of temperature change (Burrows *et al.*, 2011) and higher magnitudes of change than in the tropics, at least in eastern Australia (Hobday & Lough, 2011). This may exacerbate direct impacts on the organisms and indirect impacts on community structure and ecosystem function on high-latitude reefs.

Temperature

Rising mean temperatures have already facilitated the poleward expansion of modern coral species groups in Japan, Florida and Australia (Precht & Aronson, 2004; Yamano *et al.*, 2011; Baird *et al.*, 2012), fish (Figueira & Booth, 2010), and for the urchin *Centrostephanus rodgersii* (Ling *et al.*, 2009) in Australia. As warming continues, the resultant changes in community structure of subtropical reefs may be more pronounced as subtropical endemics may decline, more tropical species become established and more abundant by dispersing poleward (Riegl & Piller, 2003; Greenstein & Pandolfi, 2008; Funk *et al.*, 2012), and range contractions of habitat-forming temperate species occur (Wernberg *et al.*, 2011b; Smale & Wernberg, 2013). A further fundamental difference between subtropical and tropical reef communities is that marginal populations of both tropical and temperate species found on subtropical reefs can become almost locally extinct as a result of one extreme event (e.g. temperate kelp diminished from a single marine heat wave (Smale & Wernberg, 2013)) or may establish populations further poleward in one extreme season (Figueira & Booth, 2010).

Observed and projected strengthening of warm poleward flowing boundary currents and the associated downstream warming (Wu *et al.*, 2012) may accelerate rates of change in environmental conditions and consequently in the geographic ranges of species in high-latitude regions (Greenstein & Pandolfi, 2008; Figueira & Booth, 2010; Yamano *et al.*, 2011). However, the associated altered spatial trajectories of these currents may also cool some high-latitude reefs through upwelling or path changes (Malcolm *et al.*, 2011; Suthers *et al.*, 2011). Although higher temperatures result in elevated developmental growth rates in some taxa such as echinoderms (Gooding *et al.*, 2009), changed food and habitat availability may limit survival (Przeslawski *et al.*, 2008). Increased temperatures facilitate increased fish herbivory with consequent competition for resources (Floeter *et al.*, 2005), a pattern that may be exacerbated by shifts in the distribution of important macroalgal species (Wernberg *et al.*, 2011a). On the other hand, high-latitude populations of marine species can outperform their low-latitude counterparts when tested in experiments at temperatures above the local

environmental means (Conover *et al.*, 2009; Gardiner *et al.*, 2010). This effect could be attributed to possible greater phenotypic plasticity in high-latitude populations that are acclimatized or adapted to greater thermal variability than tropical populations and may indicate that some subtropical populations are more resistant to altered environmental conditions.

Ocean acidification

Globally, current anthropogenic changes in ocean alkalinity and associated aragonite saturation exceed natural variability in most habitat types (Doney *et al.*, 2009; Kroeker *et al.*, 2011; Friedrich *et al.*, 2012), with variable effects on calcifying organisms (Hendriks *et al.*, 2010; Kroeker *et al.*, 2011). For example, lowered seawater pH-values decrease successful settlement in fish (due to disorientation (Munday *et al.*, 2009b)), and corals (Doropoulos *et al.*, 2012), and can reduce deposition rates in calcifying organisms (Byrne *et al.*, 2011; Gaylord *et al.*, 2011). These reduced calcification rates in turn decrease the growth and recruitment success of calcifying corals and shelled invertebrates (Przeslawski *et al.*, 2008; Byrne *et al.*, 2011). Compared with temperature-related effects, the response and adaptation potential of marine organisms to ocean acidification is less understood (Doney *et al.*, 2009; Kroeker *et al.*, 2011), particularly for subtropical domains. However, it is likely that many of the underlying physiological mechanisms causing these effects also apply to subtropical populations and taxa.

There is mounting evidence that both the dynamics of ocean acidification and organism responses are highly variable. Recent experimental evidence suggests that internal pH-values in both invertebrate and calcifying algae bodies exceed those predicted as future ambient pH-values (Hurd *et al.*, 2011; McCulloch *et al.*, 2012) and that pH-value has little effect on the larval development of some invertebrates (Byrne *et al.*, 2009). Increased calcification rates observed for massive *Porites* in cool high-latitude waters of Western Australia suggest that changes in coral calcification are not spatially uniform within species and that calcification might be more sensitive to temperature than to ocean acidification in some species (Cooper *et al.*, 2012). Local diurnal and seasonal fluctuation in pH-values measured *in situ* are highly variable among locations, with some present values exceeding those predicted under the most severe projections for ocean acidification (Hofmann *et al.*, 2011). Among regions, systems influenced by colder water masses had higher amplitudes of local variability (Hofmann *et al.*, 2011). It is therefore likely that subtropical reefs similarly experience high diurnal and seasonal fluctuations in pH-value and aragonite saturation state. Given the differential vulnerability of tropical coral reef species to aragonite saturation states and heat stress (Pandolfi *et al.*, 2011), we hypothesize that decreasing alkalinity and carbonate saturation interacting with thermal stress will act as selective processes on species range shifts, favouring broad ranging species that are adapted to wide thermal and

biochemical ranges to establish viable populations on high-latitude reefs.

Environmental thresholds

The increasing rates of change in oceanographic climate (Kump *et al.*, 2009; Burrows *et al.*, 2011) may result in more frequent or more severe extreme temperature, wind and wave events (Young *et al.*, 2011), thereby increasing stress regimes on subtropical reefs (Harrison *et al.*, 2011). Many species maintain populations under marginal conditions, and relatively small changes in the environment may be detrimental to their survival. For example, storm events reduced the survival probability of a subtropical population of the giant clam *Tridacna maxima* Röding, 1798 in the Solitary Islands, Australia (Smith, 2011). With increasing temperature, decreasing alkalinity, and increased wind and wave frequency in the future (Young *et al.*, 2011), environmental thresholds for subtropical species may be exceeded. For example, the upper temperature threshold for growth of the Australian subtropical endemic anemone fish *Amphiprion latezonatus* Waite, 1900 has been estimated at 28 °C (Rushworth *et al.*, 2011), and Australian subtropical white syndrome, a disease affecting a range of coral species, increases in prevalence at temperatures ≥ 26 °C (Dalton *et al.*, 2010). Increasing water temperatures alter the timing of processes influencing recruitment (e.g. gonad development and spawning times), and result in shorter pelagic larval durations and higher larval mortality (Nozawa & Harrison, 2007; Przeslawski *et al.*, 2008; Byrne *et al.*, 2009). Together with changed ocean circulation patterns (although unknown in magnitude, frequency and scale), this is likely to cause profound changes in connectivity (O'Connor *et al.*, 2007), with unpredictable effects on already fragmented subtropical coral reef communities.

CONSERVING SUBTROPICAL REEFS FOR AN UNCERTAIN FUTURE

Subtropical transitional coral reef communities contain the range edges of many tropical species, underpinning the notion that tropical species will find refuge at high latitudes (Halfar *et al.*, 2005). But how robust are these reef communities to support the influx of tropical species and facilitate the survival of viable populations? Which management actions will support refuges best? The choices of management actions will depend on our understanding of their likelihood of success, based on technical feasibility, ecological and societal context, and the ecological history of the reef community in question (Fig. 3). In general, climate change threats to biodiversity and ecosystem services can be addressed with passive and active management actions. Passive management reduces local impacts to facilitate more robust responses to change, while active management implements or facilitates change that is predicted to occur naturally but under circumstances in which the processes driving the change are hampered by human development or geography.

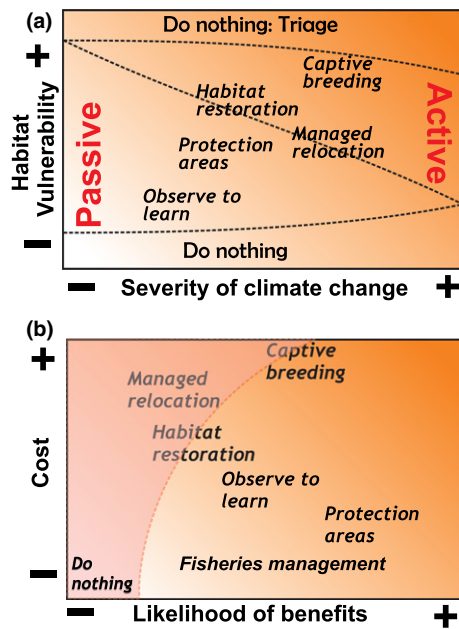


Figure 3 Diagram assessing a suite of management actions to combat the effects of climate change in their (a) suitability to address habitat vulnerability relative to the severity of climate change (after Koehn *et al.*, 2011); and (b) cost benefits in terms of financial cost, degree of difficulty to implement and likelihood of success. The red dotted mask indicates the space where cost is high and benefits are low.

Passive conservation and management

In marine environments, reducing local impacts through passive conservation and management (for example in marine protected area networks) is currently considered to be the most promising way to mitigate the increasing threats of climate change locally (Hughes *et al.*, 2010; Pandolfi *et al.*, 2011; Rau *et al.*, 2012), together with mitigating climate change drivers by reducing greenhouse gas emissions (Peterson *et al.*, 2008; Bellard *et al.*, 2012). Identifying and conserving climate refuges is a priority management goal for coral reefs (Halfar *et al.*, 2005; Graham *et al.*, 2008; Ban *et al.*, 2012), including prioritizing resilient and resistant reefs, protecting source reefs, and protecting processes such as dispersal connectivity to assist recruitment across space and through time (McLeod *et al.*, 2009; Beger *et al.*, 2010). Identifying areas of low environmental stress (McClanahan *et al.*, 2011), or relative climatic stability (Iwamura *et al.*, 2010), and high social and environmental adaptability (Cinner *et al.*, 2011) are considered critically important. For these criteria to aid effective planning for site prioritization, conservation practitioners rely on identifying the spatial representation of biodiversity and the processes that underpin these, socioeconomic information, and predictions of future trends in these factors (Pressey *et al.*, 2007; McLeod *et al.*, 2009; Carvalho *et al.*, 2011). The approaches identified above also apply to high-latitude reefs. In subtropical coral reef environments experiencing fluctuations in species assemblages and habitat types,

however, conservation decisions require an additional insurance factor (Allison *et al.*, 2003) to account for these dynamic changes in community structure and ecosystem function.

Active management

Active interventions have been proposed as alternatives and complements to marine reserves and fisheries management (Rau *et al.*, 2012) and have been widely debated in a climate change context (Bellard *et al.*, 2012). Active management interventions are often species specific, targeting taxa with low dispersal capabilities, discrete habitat boundaries or extremely low numbers of individuals, and include managed relocation, habitat restoration, captive breeding programmes and seed banks (Vallee *et al.*, 2004) (Fig. 3). Among active management strategies for climate change impacts, the pros and cons of assisted migration are particularly debated (Richardson *et al.*, 2009). In cases in which the environmental niches of species or species groups move, but barriers prevent the organisms adjusting their ranges accordingly, extinction may be prevented by artificially relocating individuals to sites where environmental conditions are still or may become favourable for their survival (Hoegh-Guldberg *et al.*, 2008; Shoo *et al.*, 2011), including high-latitude reefs. Criticisms of this approach tend to highlight that given uncertain or low probabilities of persistent new populations establishing, and the high cost to conduct relocation programmes, the benefit is doubtful (Richardson *et al.*, 2009). In most cases, the impact of novel species on the local ecology of recipient locations and the follow-on effects are unclear and may create more problems than benefits.

Active restoration of coral reefs (Rinkevich, 2008; Briggs, 2009; Riegl *et al.*, 2011) is hampered by the need to develop better technologies for translocating corals as the major structural group to aid large-scale active management. On local scales, restoration of reefs with farmed coral is used to mitigate impacts of coastal development (Shaish *et al.*, 2010); but translocation of corals across large distances or to higher latitudes has not yet been attempted. Even if techniques are developed to scale up local coral gardening, transplanted coral is unlikely to survive in adverse environmental conditions (Shaish *et al.*, 2010) at sites where naturally dispersing corals are unable to establish viable populations despite larval supply: this questions the overall benefits of this approach (Fig. 3). Captive breeding of marine species may be possible for those for which larval rearing techniques have been developed (Nozawa & Harrison, 2007; Moorhead & Zeng, 2010), particularly fishes. However, the prominent cases of introducing bluestripe snapper *Lutjanus kasmira* (Forsskål, 1775) to Hawaii (Randall, 1987) and lionfish *Pterois volitans* (Linnaeus, 1758) to the Caribbean (Albins & Hixon, 2008) highlight how potential novel ecological interactions can act to the detriment of local species (Albins & Hixon, 2008; Green *et al.*, 2012; Gaither *et al.*, 2013).

Understanding historical patterns of marine biodiversity (Greenstein & Pandolfi, 2008) and how they relate to today's

ecological processes can help identify the reefs more likely to persist, or act as refuges, and appropriate management decisions. At the high-latitude coral reefs of Moreton Bay, Australia, subtle changes in sea level and intensification of ENSO events led to marked variability in the capacity for reef development over the past 7000 yrs (Lybolt *et al.*, 2011). Reef development corresponded with times of enhanced reef expansion at southern Great Barrier Reef areas (Perry & Smithers, 2011), supporting the probable dependence of Moreton Bay reefs on receiving propagules from ecologically connected subtropical and tropical reefs (Harrison *et al.*, 1998). If this dependence of some subtropical reef communities on tropical sources can be generalized, it is tempting to conclude that translocating populations of tropical or heat-adapted corals to higher latitudes (Riegl *et al.*, 2011) may not ensure their establishment in the new location if sources are lost. The current lack of understanding about how to implement such active management measures and their potential economic and ecological costs mean that these are not realistic management options for subtropical reefs at present (Ricciardi & Simberloff, 2009).

Conserving coral reef refuges

Stringent protection of suitable reef habitat appears to be the most promising avenue to enhance the persistence of subtropical coral reef communities, and their ability to act as refuges for tropical coral reef species. An urgent priority is to establish conservation areas on currently unprotected subtropical reefs and to prioritize sites that enhance connectivity along dispersal routes. This will ensure that suitable habitat corridors are available to account for altered dispersal patterns and smaller habitat patches (Bellard *et al.*, 2012).

The management of subtropical refuges for climate change, such as other adaptation measures, must be considered in conjunction with other environmental and societal issues (Koehn *et al.*, 2011; Wintle *et al.*, 2011) (Fig. 3). To maximize the management effectiveness, reef managers will inevitably require increased reserve network area (Beger *et al.*, 2010) and, at least in the short-term, decreased fisheries effort and pollution pressures. The development of mechanisms to trade-off conflicting conservation objectives, management costs, model uncertainty and social considerations presents a considerable challenge. For example, as predictions of future ecological responses to climate change are highly uncertain, how should they be weighted in the decision-making process compared with current habitat distributions and socioeconomic benefits?

Conservation decisions are inevitably based on limited knowledge about coral reef ecosystems. Consequently, to avoid costly management mistakes (Fig. 3b), there is a critical need for research that improves our capacity for decision-making about the conservation of subtropical reef communities. In particular, we need information about traits associated with new species, the potential fate of endemics (Beger *et al.*, 2011), changes to complex interactions such as

food webs or co-extinctions, and possible indirect effects (Bellard *et al.*, 2012). Similarly, the role of active management techniques, and the potential ecological impact of such interventions (Ricciardi & Simberloff, 2009), should be investigated empirically, as well as in a decision-theoretic framework addressing when, and where to implement such actions (Richardson *et al.*, 2009; McDonald-Madden *et al.*, 2011). The limited area of subtropical reef and increasing use of coastal resources are likely to intensify the conflict between conservation objectives and exploitative human activities (Smith *et al.*, 2008). Therefore, the management of subtropical reefs for climate change must consider potential consequences of management actions, and other environments and potential user groups, as well as changing societal values and expectations in the future (Koehn *et al.*, 2011).

ACKNOWLEDGEMENTS

We appreciate discussions with scientists and managers concerned with the future of high-latitude reefs. We acknowledge the Australian Research Council (ARC) Centre of Excellence (CoE) for Coral Reef Studies grant to JMP and others. Additionally, MB was supported by an ARC Linkage project (LP0774850), and a Discovery Early Career Research Award to the ARC CoE for Environmental Decisions (CE110001014). BS was supported by an Australian Postgraduate Award.

REFERENCES

- Albins, M.A. & Hixon, M.A. (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral reef fishes. *Marine Ecology Progress Series*, **367**, 233–238.
- Allison, G.W., Gaines, S.D., Lubchenco, J. & Possingham, H.P. (2003) Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecological Applications*, **13**, S8–S24.
- Araujo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618–1626.
- Ayre, D.J. & Hughes, T.P. (2004) Climate change, genotypic diversity and gene flow in reef-building corals. *Ecology Letters*, **7**, 273–278.
- Baird, A.H., Sommer, B. & Madin, J.S. (2012) Pole-ward range expansion of *Acropora* spp. along the east coast of Australia. *Coral Reefs*, **31**, 1063.
- Ban, N.C., Pressey, R.L. & Weeks, S. (2012) Conservation objectives and sea-surface temperature anomalies in the Great barrier reef objetivos de conservación y anomalías en la temperatura de la superficie del mar en la gran barrera arrecifal. *Conservation Biology*, **26**, 799–809.
- Beatty, G.E., McEvoy, P.M., Sweeney, O. & Provan, J. (2008) Range-edge effects promote clonal growth in peripheral

- populations of the one-sided wintergreen *Orthilia secunda*. *Diversity and Distributions*, **14**, 546–555.
- Beger, M., Simon, L., Game, E., Ball, I., Treml, E., Watts, M. & Possingham, H.P. (2010) Incorporating functional ecological connectivity into spatial decision making for conservation. *Conservation Letters*, **3**, 359–368.
- Beger, M., Babcock, R., Booth, D.J. *et al.* (2011) Research challenges to improve the management and conservation of subtropical reefs to tackle climate change threats. *Ecological Management & Restoration*, **12**, e7–e10.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.
- Booth, D.J., Figueira, W.F., Gregson, M.A., Brown, L. & 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.
- Briggs, J. (2009) Atlantic coral reefs: the transplantation alternative. *Biological Invasions*, **11**, 1845–1854.
- Budd, A.F. & Pandolfi, J.M. (2010) Evolutionary novelty is concentrated at the edge of coral species distributions. *Science*, **328**, 1558–1561.
- Buddemeier, R.W. & Smith, S.V. (1999) Coral adaptation and acclimatization: a most ingenious paradox. *American Zoologist*, **39**, 1–9.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C.J., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.J., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.
- Byrne, M., Ho, M., Selvakumaraswamy, P., Nguyen, H.D., Dworjanyn, S.A. & Davis, A.R. (2009) Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *Proceedings of the Royal Society B*, **276**, 1883–1888.
- Byrne, M., Ho, M., Wong, E., Soars, N.A., Selvakumaraswamy, P., Shepard-Brennan, H., Dworjanyn, S.A. & Davis, A.R. (2011) Unshelled abalone and corrupted urchins: development of marine calcifiers in a changing ocean. *Proceedings of the Royal Society B*, **278**, 2376–2383.
- Carvalho, S.B., Brito, J.C., Crespo, E.G., Watts, M.E. & Possingham, H.P. (2011) Conservation planning under climate change: toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biological Conservation*, **144**, 2020–2030.
- Cinner, J.E., Folke, C., Daw, T. & Hicks, C.C. (2011) Responding to change: using scenarios to understand how socio-economic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. *Global Environmental Change-Human and Policy Dimensions*, **21**, 7–12.
- Conover, D.O., Duffy, T.A. & Hice, L.A. (2009) The covariance between genetic and environmental influences across ecological gradients reassessing the evolutionary significance of countergradient and cogeographic variation. *Annals of the New York Academy of Sciences*, **1168**, 100–129.
- Cooper, T.F., O'Leary, R.A. & Lough, J.M. (2012) Growth of Western Australian corals in the Anthropocene. *Science*, **335**, 593–596.
- Dalton, S.D., Smith, S.D.A., Harrison, M., Carroll, A., Pereg, L. & Cairns, S.C. (2010) Spatial and temporal patterns of Australian subtropical white syndrome at representative subtropical reefs in eastern Australia. Host range, prevalence, and progression of tissue necrosis. In: *Handbook of Disease Outbreaks: Prevention, Detection and Control*. (ed. by A. Holmgren and G. Borg), pp. 187–210. NOVA Science Publishers, Hauppauge, NY.
- Doebeli, M. & Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.
- Doney, S.C., Fabry, V.J., Feely, R.A. & Kleypas, J.A. (2009) Ocean acidification: the other CO₂ problem. *Annual Review of Marine Science*, **1**, 169–192.
- Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O. & Mumby, P.J. (2012) Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecology Letters*, **15**, 338–346.
- Edgar, G.J., Banks, S.A., Brandt, M., Bustamante, R.H., Chiriboga, A., Earle, S.A., Garske, L.E., Glynn, P.W., Grove, J.S., Henderson, S., Hickman, C.P., Miller, K.A., Rivera, F. & Wellington, G.M. (2010) El Niño, grazers and fisheries interact to greatly elevate extinction risk for Galapagos marine species. *Global Change Biology*, **16**, 2876–2890.
- Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. & Lough, J.M. (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, **1**, 165–169.
- Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P. & Joyeux, J.C. (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *Journal of Biogeography*, **31**, 1093–1106.
- Figueira, W.F. & Booth, D.J. (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, **16**, 506–516.
- Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddock, M.J. & Horn, M.H. (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, **147**, 1435–1447.
- Francis, M.P., Worthington, C.J., Saul, P. & Clements, K.D. (1999) New and rare tropical and subtropical fishes from northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **33**, 571–586.
- Friedrich, T., Timmermann, A., Abe-Ouchi, A., Bates, N.R., Chikamoto, M.O., Church, M.J., Dore, J.E., Gledhill, D.K., Gonzalez-Davila, M., Heinemann, M., Ilyina, T., Jungclauss, J.H., McLeod, E., Mouchet, A. & Santana-Casiano, J.M. (2012) Detecting regional anthropogenic trends in ocean acidification against natural variability. *Nature Climate Change*, **2**, 167–171.

- Funk, W.C., McKay, J.K., Hohenlohe, P.A. & Allendorf, F.W. (2012) Harnessing genomics for delineating conservation units. *Trends in Ecology & Evolution*, **27**, 489–496.
- Gaither, M.R., Aeby, G.M.V., Meguro, Y.-i., Rigby, M., Runyon, C., Toonen, R.J., Wood, C.L. & Bowen, B.W. (2013) An invasive fish and the time-lagged spread of its parasite across the Hawaiian Archipelago. *PLoS ONE* **8**, e56940.
- Gardiner, N.M., Munday, P.L. & Nilsson, G.E. (2010) Counter-gradient variation in respiratory performance of coral reef fishes at elevated temperatures. *PLoS ONE*, **5**, e13299.
- Gaylord, B., Hill, T.M., Sanford, E., Lenz, E.A., Jacobs, L.A., Sato, K.N., Russell, A.D. & Hettlinger, A. (2011) Functional impacts of ocean acidification in an ecologically critical foundation species. *Journal of Experimental Biology*, **214**, 2586–2594.
- Gibson, S.Y., Van der Marel, R.C. & Starzomski, B.M. (2009) Climate change and conservation of leading-edge peripheral populations. *Conservation Biology*, **23**, 1369–1373.
- Gooding, R.A., Harley, C.D.G. & Tang, E. (2009) Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proceedings of the National Academy of Sciences USA*, **106**, 9316–9321.
- Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S., Chabanet, P., Clark, S., Spalding, M.D., Letourneur, Y., Bigot, L., Galzin, R., Oehman, M.C., Garpe, K.C., Edwards, A.J. & Sheppard, C.R.C. (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS ONE*, **3**, e3039.
- Green, S.J., Akins, J.L., Maljković, A. & Côté, I.M. (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE*, **7**, e32596.
- Greenstein, B.J. & Pandolfi, J.M. (2008) Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. *Global Change Biology*, **14**, 513–528.
- Guinotte, J.M., Buddemeier, R.W. & Kleypas, J.A. (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs*, **22**, 551–558.
- Haak, A.L., Williams, J.E., Neville, H.M., Dauwalter, D.C. & Colyer, W.T. (2010) Conserving peripheral trout populations: the values and risks of life on the edge. *Fisheries*, **35**, 530–549.
- Halfar, J., Godinez-Orta, L., Riegl, B., Valdez-Holguin, J.E. & Borges, J.M. (2005) Living on the edge: high-latitude *Porites* carbonate production under temperate eutrophic conditions. *Coral Reefs*, **24**, 582–592.
- Harriott, V.J. & Banks, S.A. (1995) Recruitment of Scleractinian Corals in the Solitary Islands Marine Reserve, a high-latitude coral dominated community in Eastern Australia. *Marine Ecology Progress Series*, **123**, 155–161.
- Harriott, V.J. & Banks, S.A. (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs*, **21**, 83–94.
- Harriott, V.J., Smith, S.D.A. & Harrison, P.L. (1994) Patterns of coral community structure of subtropical reefs in the Solitary Islands Marine Reserve, Eastern Australia. *Marine Ecology-Progress Series*, **109**, 67–76.
- Harrison, P.L. (2011) Sexual reproduction of scleractinian corals. *Coral reefs: an ecosystem in transition* (ed. by Z. Dubinsky and N. Stambler), pp. 59–85. Springer Publishers, The Netherlands.
- Harrison, P.L. & Booth, D.J. (2007) Coral reefs: naturally dynamic and increasingly disturbed ecosystems. *Marine ecology* (ed. by S.D.C.A.B.M. Gillanders), pp. 316–377. Oxford University Press, Melbourne.
- Harrison, M.A. & Smith, S.D.A. (2012) Cross-shelf variation in the structure of molluscan assemblages on shallow, rocky reefs in subtropical, eastern Australia. *Marine Biodiversity*, **42**, 203–216.
- Harrison, P.L., Harriott, V.J., Banks, S.A. & Holmes, N.J. (1998) The coral communities of Flinders Reef and Myora Reef in the Moreton Bay Marine Park, Queensland, Australia. *Moreton bay and catchment* (eds by I.R. Tibbetts, N.J. Hall and W.C. Dennison), pp. 525–536. School of Marine Science, The University of Queensland, Brisbane.
- Harrison, P.L., Dalton, S.J. & Carroll, A.G. (2011) Extensive coral bleaching on the world's southernmost coral reef at Lord Howe Island, Australia. *Coral Reefs*, **30**, 775.
- Hendriks, I.E., Duarte, C.M. & Alvarez, M. (2010) Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine Coastal and Shelf Science*, **86**, 157–164.
- Hobday, A.J. (2011) Sliding baselines and shuffling species: implications of climate change for marine conservation. *Marine Ecology-an Evolutionary Perspective*, **32**, 392–403.
- Hobday, A.J. & Lough, J.M. (2011) Projected climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, **62**, 1000–1014.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345–346.
- Hofmann, G.E., Smith, J.E., Johnson, K.S., Send, U., Levin, L.A., Micheli, F., Paytan, A., Price, N.N., Peterson, B., Takeshita, Y., Matson, P.G., Crook, E.D., Kroeker, K.J., Gambi, M.C., Rivest, E.B., Frieder, C.A., Yu, P.C. & Martz, T.R. (2011) High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS ONE*, **6**, e28983.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Harriott, V.J., Moltschanivskyj, N.A., Pratchett, M.S., Tanner, J.E. & Willis, B.L. (2002) Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. *Ecology*, **83**, 436–451.
- Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J. & Steneck, R.S. (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*, **25**, 633–642.
- Hurd, C.L., Cornwall, C.E., Currie, K., Hepburn, C.D., McGraw, C.M., Hunter, K.A. & 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.
- Iwamura, T., Wilson, K.A., Venter, O. & Possingham, H.P. (2010) A climatic stability approach to prioritizing global conservation investments. *PLoS ONE*, **5**, e15103.
- Kark, S., Allnutt, T.F., Levin, N., Manne, L.L. & Williams, P.H. (2007) The role of transitional areas as avian biodiversity centres. *Global Ecology and Biogeography*, **16**, 187–196. doi:10.1111/j.1466-8238.2006.00274.x.
- Kawecki, T.J. (2008) Adaptation to marginal habitats. *Annual Review of Ecology Evolution and Systematics*, **39**, 321–342.
- Kiessling, W. (2009) Geologic and Biologic Controls on the Evolution of Reefs. *Annual Review of Ecology Evolution and Systematics*, **40**, 173–192.
- Kleypas, J.A., McManus, J.W. & Menez, L.A.B. (1999) Environmental limits to coral reef development: where do we draw the line? *American Zoologist*, **39**, 146–159.
- Koehn, J.D., Hobday, A.J., Pratchett, M.S. & Gillanders, B.M. (2011) Climate change and Australian marine and freshwater environments, fishes and fisheries: synthesis and options for adaptation. *Marine and Freshwater Research*, **62**, 1148–1164.
- Kroeker, K.J., Micheli, F., Gambi, M.C. & Martz, T.R. (2011) Divergent ecosystem responses within a benthic marine community to ocean acidification. *Proceedings of the National Academy of Sciences USA*, **108**, 14515–14520.
- Kump, L., Bralower, T. & Ridgwell, A. (2009) Ocean acidification in deep time. *Oceanography*, **22**, 94–107.
- Ling, S.D., Johnson, C.R., Ridgway, K., Hobday, A.J. & Hadson, M. (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology*, **15**, 719–731.
- Lybolt, M.L.M., Neil, D., Zhao, J.X., Feng, Y.X., Yu, K.F. & Pandolfi, J. (2011) Instability in a marginal coral reef: the shift from natural variability to a human-dominated seascape. *Frontiers in Ecology and the Environment*, **9**, 154–160.
- Malcolm, H.A., Jordan, A. & Smith, S.D.A. (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. *Marine Biodiversity*, **40**, 181–193.
- Malcolm, H.A., Davies, P.L., Jordan, A. & Smith, S.D.A. (2011) Variation in sea temperature and the East Australian Current in the Solitary Islands region between 2001–2008. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, **58**, 616–627.
- McClanahan, T.R., Maina, J.M. & Muthiga, N.A. (2011) Associations between climate stress and coral reef diversity in the western Indian Ocean. *Global Change Biology*, **17**, 2023–2032.
- McCulloch, M., Falter, J., Trotter, J. & Montagna, P. (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change*, **2**, 623–627.
- McDonald-Madden, E., Runge, M.C., Possingham, H.P. & Martin, T.G. (2011) Optimal timing for managed relocation of species faced with climate change. *Nature Climate Change*, **1**, 261–265.
- McLeod, E., Salm, R., Green, A. & Almany, J. (2009) Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, **7**, 362–370.
- van der Meer, M.H., Hobbs, J.-P.A., Jones, G.P. & van Herwerden, L. (2012a) Genetic connectivity among and self-replenishment within island populations of a restricted range subtropical reef fish. *PLoS ONE*, **7**, e49660.
- van der Meer, M.H., Jones, G.P., Hobbs, J.P.A. & van Herwerden, L. (2012b) Historic hybridization and introgression between two iconic Australian anemonefish and contemporary patterns of population connectivity. *Ecology and Evolution*, **2**, 1592–1604.
- Moorhead, J.A. & Zeng, C.S. (2010) Development of captive breeding techniques for marine ornamental fish: a review. *Reviews in Fisheries Science*, **18**, 315–343.
- Munday, P.L., Donelson, J.M., Dixon, D.L. & Endo, G.G.K. (2009a) Effects of ocean acidification on the early life history of a tropical marine fish. *Proceedings of the Royal Society B*, **276**, 3275–3283.
- Munday, P.L., Dixon, D.L., Donelson, J.M., Jones, G.P., Pratchett, M.S., Devitsina, G.V. & Doving, K.B. (2009b) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences USA*, **106**, 1848–1852.
- Noreen, A.M.E., Harrison, P.L. & Van Oppen, M.J.H. (2009) Genetic diversity and connectivity in a brooding reef coral at the limit of its distribution. *Proceedings of the Royal Society B*, **276**, 3927–3935.
- Nozawa, Y. & Harrison, P.L. (2007) Effects of elevated temperature on larval settlement and post-settlement survival in scleractinian corals, *Acropora solitaryensis* and *Favites chinensis*. *Marine Biology*, **152**, 1181–1185.
- Nozawa, Y., Tokeshi, M. & Nojima, S. (2008) Structure and dynamics of a high-latitude scleractinian coral community in Amakusa, southwestern Japan. *Marine Ecology-Progress Series*, **358**, 151–160.
- O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. & Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 1266–1271.
- Olbers, J.M., Celliers, L. & Schleyer, M.H. (2009) Zonation of benthic communities on the subtropical Aliwal Shoal, Durban, KwaZulu-Natal, South Africa. *African Zoology*, **44**, 8–23.
- Oliver, T.A. & Palumbi, S.R. (2011) Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs*, **30**, 429–440.
- Pandolfi, J.M., Connolly, S.R., Marshall, D.J. & Cohen, A.L. (2011) Projecting coral reef futures under global warming and ocean acidification. *Science*, **333**, 418–422.
- Patterson, H.M. & Swearer, S.E. (2007) Long-distance dispersal and local retention of larvae as mechanisms of

- recruitment in an island population of a coral reef fish. *Austral Ecology*, **32**, 122–130.
- Perry, C.T. & Smithers, S.G. (2011) Cycles of coral reef ‘turn-on’, rapid growth and ‘turn-off’ over the past 8500 years: a context for understanding modern ecological states and trajectories. *Global Change Biology*, **17**, 76–86.
- Peterson, E.L., Beger, M. & Richards, Z.T. (2008) Thinking outside the reef. *Science*, **319**, 1759.
- Pohle, G., Iken, K., Clarke, K.R., Trott, T., Konar, B., Cruz-Motta, J.J., Wong, M., Benedetti-Cecchi, L., Mead, A., Miloslavich, P., Mieszkowska, N., Milne, R., Tamburello, L., Knowlton, A., Kimani, E. & Shirayama, Y. (2011) Aspects of benthic decapod diversity and distribution from rocky nearshore Habitat at geographically widely dispersed sites. *PLoS ONE*, **6**, e18606.
- Precht, W. & Aronson, R. (2004) Climate flickers and range shifts of reef corals. *Frontiers in Ecology and the Environment*, **2**, 307–314.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in Ecology & Evolution*, **22**, 583–592.
- Przeslawski, R., Ah Yong, S., Byrne, M., Wörheide, G. & Hutchings, P.A.T. (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology*, **14**, 2773–2795.
- Randall, J.E. (1987) Introductions of marine fishes to the Hawaiian Islands. *Bulletin of Marine Science*, **47**, 356–400.
- Rau, G.H., McLeod, E.L. & Hoegh-Guldberg, O. (2012) The need for new ocean conservation strategies in a high-carbon dioxide world. *Nature Climate Change*, **2**, 720–724.
- Ricciardi, A. & Simberloff, D. (2009) Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution*, **24**, 248–253.
- Richardson, D.M., Hellmann, J.J., McLachlan, J.S. *et al.* (2009) Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences USA*, **106**, 9721–9724.
- Riegl, B. (2003) Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs*, **22**, 433–446.
- Riegl, B. & Piller, W.E. (2003) Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences*, **92**, 520–531.
- Riegl, B.M., Purkis, S.J., Al-Cibahy, A.S., Abdel-Moati, M.A. & Hoegh-Guldberg, O. (2011) Present limits to heat-adaptability in corals and population-level responses to climate extremes. *PLoS ONE*, **6**, e24802.
- Rinkevich, B. (2008) Management of coral reefs: we have gone wrong when neglecting active reef restoration. *Marine Pollution Bulletin*, **56**, 1821–1824.
- Rivadeneira, M.M., Thiel, M., Gonzalez, E.R. & Haye, P.A. (2011) An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: out of the deep south. *Global Ecology and Biogeography*, **20**, 437–448.
- Rout, T.M., Hauser, C.E. & Possingham, H.P. (2009) Optimal adaptive management for the translocation of a threatened species. *Ecological Applications*, **19**, 515–526.
- Roy, K., Jablonski, D. & Valentine, J.W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society of London B*, **267**, 293–299.
- Rushworth, K.J.W., Smith, S.D.A., Cowden, K.L. & Purcell, S.W. (2011) Optimal temperature for growth and condition of an endemic subtropical anemonefish. *Aquaculture*, **318**, 479–482.
- Schleyer, M.H., Kruger, A. & Celliers, L. (2008) Long-term community changes on a high-latitude coral reef in the Greater St Lucia Wetland Park, South Africa. *Marine Pollution Bulletin*, **56**, 493–502.
- Schmidt-Roach, S., Miller, K.J. & Andreakis, N. (2013) *Pocillopora aliciae*: a new species of scleractinian coral (Scleractinia, Pocilloporidae) from subtropical Eastern Australia. *Zootaxa*, **3626**, 576–582.
- Shaish, L., Levy, G., Katzir, G. & Rinkevich, B. (2010) Coral reef restoration (Bolinao, Philippines) in the face of frequent natural catastrophes. *Restoration Ecology*, **18**, 285–299.
- Shenkar, N. & Swalla, B.J. (2011) Global diversity of Ascidiacea. *PLoS ONE*, **6**, e20657.
- Shoo, L.P., Storlie, C., Vanderwal, J., Little, J. & Williams, S.E. (2011) Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology*, **17**, 186–193.
- Smale, D.A. & Wernberg, T. (2013) Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B*, **280**, 20122829.
- Smith, S.D.A. (2011) Growth and population dynamics of the giant clam *Tridacna maxima* (Roding) at its southern limit of distribution in coastal, subtropical eastern Australia. *Molluscan Research*, **31**, 37–41.
- Smith, T.B., Kark, S., Schneider, C.J., Wayne, R.K. & Moritz, C. (2001) Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends in Ecology and Evolution*, **16**, 431.
- Smith, S.D.A., Rule, M.J., Harrison, M. & Dalton, S.J. (2008) Monitoring the sea change: preliminary assessment of the conservation value of nearshore reefs, and existing impacts, in a high-growth, coastal region of subtropical eastern Australia. *Marine Pollution Bulletin*, **56**, 525–534.
- Sommer, B., Harrison, P.L., Beger, M. & Pandolfi, J.M. (in press 2013) Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology*. doi:10.1890/13-1445.1.
- Spalding, M.D., Fox, H.E., Halpern, B.S., McManus, M.A., Molnar, J., Allen, G.R., Davidson, N., Jorge, Z.A., Lombana, A.L., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, **57**, 573–583.

- Suthers, I.M., Everett, J.D., Roughan, M., Young, J.W., Oke, P.R., Condie, S.A., Hartog, J.R., Hobday, A.J., Thompson, P.A., Ridgway, K., Baird, M.E., Hassler, C.S., Brassington, G.B., Byrne, M., Holbrook, N.J. & Malcolm, H.A. (2011) The strengthening East Australian Current, its eddies and biological effects - an introduction and overview. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **58**, 538–546.
- Thomson, D.P. & Frisch, A.J. (2010) Extraordinarily high coral cover on a nearshore, high-latitude reef in south-west Australia. *Coral Reefs*, **29**, 923–927.
- UNEP-WCMC (2010) *World Database on Protected Areas*, UNEP-WCMC, Cambridge.
- Vallee, L., Hogbin, T.L.M., Makinson, B., Matthes, M. & Rossetto, M. (2004) *Guidelines for the translocation of threatened plants in Australia*, 2nd edn. Australian Network for Plant Conservation, Canberra.
- Wallace, C.C., Fellegara, I., Muir, P.R. & Harrison, P.L. (2009) The scleractinian corals of Moreton Bay, eastern Australia: high latitude, marginal assemblages with increasing species richness. *Memoirs of the Queensland Museum*, **54**, 1–118.
- Wernberg, T., Thomsen, M.S., Tuya, F. & Kendrick, G.A. (2011a) Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology*, **400**, 264–271.
- Wernberg, T., Russell, B.D., Thomsen, M.S., Gurgel, C.F.D., Bradshaw, C.J.A., Poloczanska, E.S. & Connell, S.D. (2011b) Seaweed communities in retreat from ocean warming. *Current Biology*, **21**, 1828–1832.
- Wicks, L.C., Gardner, J.P.A. & Davy, S.K. (2010a) Spatial patterns and regional affinities of coral communities at the Kermadec Islands Marine Reserve, New Zealand—a marginal high-latitude site. *Marine Ecology-Progress Series*, **400**, 101–113.
- Wicks, L.C., Sampayo, E., Gardner, J.P.A. & Davy, S.K. (2010b) Local endemicity and high diversity characterise high-latitude coral-Symbiodinium partnerships. *Coral Reefs*, **29**, 989–1003.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, **26**, 459–474.
- Wintle, B.A., Bekessy, S.A., Keith, D.A., van Wilgen, B.W., Cabeza, M., Schroder, B., Carvalho, S.B., Falcucci, A., Maiorano, L., Regan, T.J., Rondinini, C., Boitani, L. & Possingham, H.P. (2011) Ecological-economic optimization of biodiversity conservation under climate change. *Nature Climate Change*, **1**, 355–359.
- Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T., McPhaden, M.J., Alexander, M., Qiu, B., Visbeck, M., Chang, P. & Giese, B. (2012) Enhanced warming over the global subtropical western boundary currents. *Nature Climate Change*, **2**, 161–166.
- Yamano, H., Sugihara, K. & Nomura, K. (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters*, **38**, L04601.
- Young, I.R., Zieger, S. & Babanin, A.V. (2011) Global trends in wind speed and wave height. *Science*, **332**, 451–455.

BIOSKETCH

Maria Beger is a Research Fellow at The University of Queensland and interested in identifying patterns of coral reef biodiversity and processes or threats influencing these and developing and benchmarking procedures to efficiently capture these in conservation and management of marine environments. She is based in the Centre of Excellence for Environmental Decisions (www.ceed.edu.au) and collaborates extensively with the Marine Paleoecology Lab (marinepalaeoecology.org) working on the subtropical reefs of eastern Australia. In this review, all authors conceived ideas and collated information, but M.B. led the writing.

Author contributions: All authors conceived the ideas and contributed to the writing; M.B. and B.S. analysed the literature, and M.B. led the writing.

Editor: Robert Cowie