Conserving potential coral reef refuges at high latitudes

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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.

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 refugia 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
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 solitariaensis 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...
likely to be spatially, temporally and taxonomically variable, 
2011). Although the magnitude and rate of these changes are 
and more frequent wave and wind extremes (Young 
et al., 2011; Cooper 
alter calcification rates (Fabricius 
et al., 2012) and dispersal and recruitment 
benefits). Therefore, a threat 
reduce the fitness of reef organisms (threats), and also those 
ecosystem function. These changes include both factors that 
ecological processes (Ferreira et al., 2004; Floeter et al., 2005). For 
example, there is a shift in the relative contribution to graz-
ing by fishes and invertebrates. Herbivorous fishes are the 
고기 과자로 거짓 vietnamesic fššrs 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 deter-
moves 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 SHAPE SUBTROPICAL REEFS

Changes in environmental parameters induced by oceano-
graphic climate change are likely to redefine the characteris-
tics of subtropical coral reef communities in the future, 
partly by driving range expansions and contractions of tropi-
cal, 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 physi-
ology 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 pole-
ward 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 resul-
tant 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 
amost 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 geo-
graphic 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 (Pandolphi 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.
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 (Valle 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. Critics 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; Rieg 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

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**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 (Ginner 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,
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).

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BIOSKETCH

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