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Climate Change, Coral Reef Ecosystems, and Management Options for Marine Protected Areas

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Abstract Marine protected areas (MPAs) provide place-based management of marine ecosystems through various degrees and types of protective actions. Habitats such as coral reefs are especially susceptible to degradation resulting from climate change, as evidenced by mass bleaching events over the past two decades. Marine ecosystems are being altered by direct effects of climate change including ocean warming, ocean acidification, rising sea level, changing circulation patterns, increasing severity of storms, and changing freshwater influxes. As impacts of climate change strengthen they may exacerbate effects of existing stressors and require new or modified management approaches; MPA networks are generally accepted as an improvement over individual MPAs to address multiple threats to the marine environment. While MPA networks are considered a potentially effective management approach for conserving marine biodiversity, they should be established in conjunction with other management strategies, such as fisheries regulations and reductions of nutrients and other forms of land-based pollution. Information about interactions between climate change and more "traditional" stressors is limited. MPA managers are faced with high

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levels of uncertainty about likely outcomes of management actions because climate change impacts have strong interactions with existing stressors, such as land-based sources of pollution, overfishing and destructive fishing practices, invasive species, and diseases. Management options include ameliorating existing stressors, protecting potentially resilient areas, developing networks of MPAs, and integrating climate change into MPA planning, management, and evaluation.

Keywords Marine protected areas · Management options · Climate change · Coral reef ecosystems

Introduction

Human impacts have degraded marine ecosystems primarily through overexploitation and destructive fishing practices, pollution, and climate change. Overfishing and pollution have long histories (Jackson and others 2001; Lotze and others 2006; Roberts 2007), and presumably lower the resistance and resilience of marine ecosystems to further impacts from climate change. Comprehensive recommendations have been made for improving ocean policy in light of these threats (POC 2003; USCOP 2004) and for mitigating impacts of climate change (IPCC 2007c). At the same time, there is a pressing need to provide resource managers with approaches that can help maintain the structure and function of marine ecosystems in the face of climate change impacts.

There is growing recognition among scientists and marine resource managers that ecosystem-based approaches may help sustain the wide array of services provided by marine ecosystems (Rosenberg and McLeod 2005; Levin and Lubchenco 2008; Palumbi and others 2008; Ruckelshaus and others 2008). Marine protected areas (MPAs), particularly no-take marine reserves, can help restore ecosystem structure and function (Palumbi 2002; Sobel and Dahlgren 2004; Mumby and others 2006), and help protect marine biodiversity and associated ecosystem services (Ballantine 1997; NRC 2001; Palumbi 2002, 2004; Roberts and others 2003a; Sobel and Dahlgren 2004; Roberts 2005; Salm and others 2006; Palumbi and others 2009).

MPA networks are generally accepted as an improvement over individual MPAs to address multiple threats to the marine environment (Ballantine 1997; Salm and others 2000; Allison and others 2003; Roberts and others 2003b; Mora and others 2006; McLeod and others 2008b). Networks are more effective than single MPAs because networks spread the risk of reduced viability of a habitat or community type following a large-scale disturbance. Appropriately designed networks are better able to protect both short- and long-distance dispersers than individual MPAs and thus have greater potential to achieve conservation and fishery objectives (Roberts 1997). Networks can utilize local and regional dispersal patterns to enhance larval recruitment, be designed to protect critical life stages, and can protect critical ecological processes and functions such as migration corridors (Gerber and Heppell 2004). Finally, networks allow for protection of marine ecosystems at an appropriate scale; a network of MPAs can encompass a wide range of biogeographic and oceanographic conditions as an alternative to one extremely large area (NRC 2001; Hansen and others 2003).

While MPA networks are considered a critical management tool for conserving marine biodiversity, they must be established in conjunction with other management strategies to be effective (Hughes and others 2003; McLeod and others 2008b). MPAs are vulnerable to activities beyond their boundaries. For example, uncontrolled pollution and unsustainable fishing outside protected areas can adversely affect species and ecosystem functions within protected areas (Kaiser 2005). Therefore, MPA networks should be established considering other forms of resource management (e.g., fishery catch limits and gear restrictions) (Allison and others 1998; Beger and others 2003; Kaiser 2005) and integrated ocean and coastal management to control land-based threats such as pollution and sedimentation (Cho 2005). In the long term, the most effective configuration may be networks of highly protected areas nested within a broader management framework (Salm and others 2006). Such a framework might include an extensive multiple-use area integrated with coastal management regimes that help minimize land-based sources of pollution (e.g., Done and Reichelt 1998; McLeod and others 2008b).

This article is adapted from a preliminary review of management options (termed adaptations) for MPAs in the context of climate change (Keller and others 2008). We briefly discuss climate change stressors on marine ecosystems and interactions of these stressors with “traditional” ones, and then discuss options for MPA management in the context of climate change. We highlight coral reef ecosystems because it was beyond the scope of this review to comprehensively cover all types of marine ecosystems and because severe impacts on coral reefs such as mass bleaching events have been evident for decades and have been a topic of considerable research (e.g., Hoegh-Guldberg and others 2007a; Baker and others 2008).

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Climate Change Stressors

Ocean Warming

An average warming of 0.1°C has occurred in the 0–700 m depth layer of the ocean between 1961 and 2003 (Bindoff and others 2007). Increasing ocean temperatures affect a range of organismal physiological processes (Table 1) and influence ecological processes such as foraging, growth, and larval duration and dispersal, with ultimate impacts on the geographic ranges of species (Table 1). Within marine communities, these temperature changes and range shifts may result in new species assemblages and biological interactions (Table 1).

The IPCC (2007a, b) reported that temperature increases over the last 50 years are nearly twice those for the last 100 years, with projections that global average surface air temperature will rise 1.8–4.0°C (lowest to highest scenarios) by 2090–2099, largely caused by increasing atmospheric carbon dioxide concentrations. Over the last 20 years, an extensive body of literature has conclusively linked anomalously high surface seawater temperatures as the major cause of coral bleaching (Table 1). Increases in sea surface temperature of about 1–3°C are likely to cause more frequent and severe mass coral reef bleaching events (Table 1) and will continue to cause widespread mortality unless thermal adaptation or acclimatization by corals occurs (IPCC 2007a). However, the ability of corals to adapt or acclimatize to increasing sea temperature is largely unknown (Berkelmans and van Oppen 2006) and remains a research topic of paramount importance. In 2005, the most devastating Caribbean-wide coral bleaching event to date occurred that based on modeling, was highly unlikely to have occurred without anthropogenic forcing (Donner and others 2007).

Ocean Acidification

The ocean absorbs about one-third of the carbon dioxide added to the atmosphere by human activities each year (Sabine and others 2004); and the pH of ocean surface waters has decreased by about 0.1 units since the beginning of the industrial revolution (Feely and others 2004). A doubling of the concentration of atmospheric carbon dioxide, which could occur in as little as 50 years, could cause major changes in the marine environment, specifically impacting organisms that build skeletal material out of calcium carbonate (Table 1). Because of the greater solubility of CO_2 in cooler waters, reefs at the latitudinal margins of coral reef development (e.g., Florida Keys and Hawaiian Islands) may show the most rapid and dramatic response to changing pH. On the other hand, McNeil and others (2004) suggested that net coral reef calcification rates will increase with future ocean warming and exceed pre-industrial rates by the year 2100.

Although additional research is needed to resolve this issue, increasing seawater acidification has been shown in controlled studies to significantly reduce the ability of reef-building corals to produce their skeletons, affecting growth of individual corals and making reefs more vulnerable to erosion (Langdon and Atkinson 2005; Yates and Halley 2006). Some estimates indicate that at atmospheric CO_2 levels close to 2-3 times the pre-industrial levels coral reefs may erode faster than they can be rebuilt potentially making them less resilient to other environmental stresses (e.g., disease, bleaching, storms) (Hoegh-Guldberg and others 2007a). This could compromise the long-term viability of these ecosystems, perhaps impacting the thousands of species that depend on reef habitats (McLeod and others 2008b).

Sea Level Rise

During the last 100 years, global average sea level has risen an estimated 1–2 mm per year and is expected to accelerate due to thermal expansion of the oceans and melting ice-sheets and glaciers (Cabanes and others 2001; Albritton and Filho 2001; Rignot and Kanagaratnam 2006; Chen and others 2006; Shepherd and Wingham 2007; Bell and others 2007; IPCC 2007a). Rates of sea level rise at a local scale vary from -2 to 10 mm per year along U.S. coastlines (Nicholls and Leatherman 1996; Zervas 2001; Scavia and others 2002). The consequences of sea level rise include inundation of coastal areas, erosion of vulnerable shorelines, landward shifts in species distributions, and saltwater intrusion into estuaries and aquifers (Klein and Nicholls 1999) (Table 1). However, coastal development may interfere with landward plant migrations and cause submergence of wetlands and waterlogged soils, which in turn result in plant physiological stress or die-off. Depletion or loss of marshes, mangroves, and dune plants would affect nutrient flux, energy flow, and essential habitat for a multitude of species (Table 1).

Variability in Ocean-Atmosphere Interactions and Ocean Circulation

Natural climatic variability resulting from ocean-atmosphere interactions such as the El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and North Atlantic Oscillation/Northern Hemisphere Annular Mode result in changes in open ocean productivity, shifts in the distribution of organisms, and modifications in food webs that foreshadow potential consequences of accelerated climate change (e.g., Mantua and others 1997; McGowan and others 1998). These recurring patterns of ocean-atmosphere

Table 1 Climate change stressors, affected community or function, biotic response or effects, and location

Climate change stressor	Affected community/function	Biotic response/effects	Location	References
Ocean warming	Physiological processes	Enzyme reactions, reproductive timing, etc.	Near surface	Fields and others (1993), Roessig and others (2004), Harley and others (2006)
	Zooplankton, fish, and intertidal invertebrates	Poleward range shifts	California N. Atlantic	Walther and others (2002)
	Marine community structure	Altered larval dispersal, competitive interactions, and trophic interactions and webs	Widespread	Barry and others (1995), Roessig and others (2004), Precht and Aronson (2004), O'Connor and others (2007)
	Reef corals	Coral bleaching because of high sea surface temperatures	Tropics and subtropics	Wilkinson (1998, 2000, 2002), Fitt and others (2001), Donner and others (2005, 2007)
	Coral reef communities	Increasing frequency and severity of coral reef mass bleaching events	Tropics and subtropics	Smith and Buddemeier (1992), Wilkinson (1998, 2000), Hoegh-Guldberg (1999), Hughes and others (2003), Douglas (2003), Done and Jones (2006)
Ocean acidification	Invertebrates and fishes	Reduced metabolic rates, growth, and survivorship	Widespread	Michaelidis and others (2005), Shirayama and Thornton (2005), Pane and Barry (2007)
	Sea urchins, cold-water corals, coralline algae, and temperate plankton	Reduced calcification	Widespread	Hoegh-Guldberg (1999), Kleypas and others (1999, 2006), Hughes and others (2003), Feely and others (2004), Kleypas and Langdon (2006)
	Reef-building corals and coralline algae	Reduced calcification	Tropics	Kleypas and others (1999, 2006), Feely and others (2004), Orr and others (2005), Kleypas and Langdon (2006)
	Calcification rate	17–35% decline by 2100	Widespread	Hoegh-Guldberg (1999), Kleypas and others (1999), Hughes and others (2003), Orr and others (2005)
Sea level rise	Intertidal plant communities, e.g., mangroves and *Spartina* salt marshes	Inland distribution shifts	Widespread	Scavia and others (2002), Harley and others (2006)
	Intertidal and dune plant communities: nutrient production, stabilization of substrata, and provision of refuges and nurseries	Depletion or loss because of coastline development that interferes with plant migrations	Widespread	Scavia and others (2002), Galbraith and others (2002), Harley and others (2006)
	Projected 35–70% loss of barrier islands and sandy beaches (next 100 years)	Reduced nesting grounds for key species such as sea turtles and birds	Widespread	Scavia and others (2002)
Ocean circulation	Marine communities	Potential changes in connectivity (nutrient flux and larval dispersal)	Widespread	Bakun (1990), McPhaden and Zhang (2002), Snyder and others (2003), McGregor and others (2007)

Table 1 continued

Climate change stressor	Affected community/function	Biotic response/effects	Location	References
Storm intensity	Shallow coastal ecosystems	Physical damage	Tropics and subtropics	IPCC (2007a)
	Mangroves, marshes, and coral reefs	Physical damage	Southern U.S.	Davis and others (1994), Tilmant and others (1994), McCoy and others (1996), Lovelace and McPherson (1998), Baldwin and others (2001)
	Shallow coastal ecosystems	Increased turbidity, breakdown of mangrove peat soils, and elevated concentrations of ammonia, dissolved phosphate, and dissolved organic carbon	Southern U.S.	Davis and others (1994), Tilmant and others (1994), Lovelace and McPherson (1998)
Freshwater influx	Estuarine phytoplankton	Increased stratification, increased flushing, and reduced productivity	Areas with increased precipitation	Moore and others (1997), Scavia and others (2002)

variability have very different behaviors in time; ENSO events persist for 6–18 months and have major impacts in the tropics whereas the PDO occurs over a much longer time frame of 20–30 years and has primary effects in the northern Pacific (Mantua and others 1997). Regardless of the temporal scale and region of impact, these natural modes of climate variability have existed historically, independent of anthropogenically driven climate change. These climate phenomena may act in tandem with or in opposition to human-induced alterations, with consequences that are difficult to predict (Philip and van Oldenborgh 2006; Table 1). While there is no clear indication that ocean circulation patterns have changed (Bindoff and others 2007), modifications could have large effects within and among ecosystems through nutrient and pollutant fluxes, larval dispersal, and other factors. Considering that there is evidence for warming of Southern Ocean mode waters and Upper Circumpolar Deep Waters from 1960–2000, changes in oceanic current and upwelling patterns are likely in the future (Bindoff and others 2007). The direction that these changes will take, however, is not evident.

Storm Intensity

Whether or not storm frequency has changed over time is not clear because of large natural variability from such climate drivers as the ENSO (IPCC 2007a). However, since the mid-1970s there has been a trend toward longer storm duration and greater storm intensity (IPCC 2007a). Intensification of storms likely will cause increasing physical damage to coastal ecosystems, especially mangrove, marsh, seagrass, and coral reef habitats (Table 1), which may be exacerbated by rising sea levels in many areas. Even 30–60 days after storms, some areas still experienced deleterious environmental impacts (Table 1). In some instances, algal blooms further increased turbidity while driving down dissolved-oxygen concentrations (i.e., caused eutrophication), resulting in mortalities in fish and invertebrate populations (Tilmant and others 1994; Lovelace and McPherson 1998). Increased erosion from storms may also result in the smothering of coral reefs and seagrass beds.

Freshwater Influx

Observations indicate that changes in the amount, intensity, frequency, and type of precipitation are occurring worldwide (IPCC 2007a). Consistent with observed changes in precipitation and water transport in the atmosphere, large-scale trends in oceanic salinity have become evident for the period 1955–1998 (Bindoff and others 2007). These trends are manifested as lowered salinities at subpolar latitudes and increased salinities in shallower parts of the tropical and subtropical oceans.

In addition to altering salinity in major oceanic water masses, changes in precipitation patterns can have significant impacts in estuarine and other nearshore environments. For instance, in regions where climate change results in elevated rainfall, increased runoff may cause greater stratification of water layers within estuaries, less water column mixing and thus lower rates of nutrient exchange among water layers, and significantly reduced productivity because phytoplankton populations may be flushed from the system faster than they can grow and reproduce (Table 1). On the other hand, estuaries that are located in regions with lower rainfall may also show decreased productivity because of lower nutrient influx. Thus, the relationship between precipitation and marine ecosystem health is complex and difficult to predict.

Another source of fresh water is melting of polar ice (IPCC 2007a). In the Atlantic Ocean, accelerated melting of Arctic ice and the Greenland ice sheet are predicted to continue producing more freshwater inputs that may alter oceanic circulation patterns (Dickson and others 2002; Curry and others 2003; Curry and Mauritzen 2005; Peterson and others 2006; Greene and Pershing 2007; Boessenkool and others 2007).

Climate Change Interactions with "Traditional" Stressors of Concern

Land-Based Sources of Pollution

Marine water-quality degradation and pollution stem primarily from land-based sources, with major contributions to coastal watersheds and water-quality deterioration falling into two broad categories: point-source pollution and non-point-source pollution. Point-source pollution from factories, sewage treatment plants, and farms often flows into nearby waters. In contrast, marine non-point-source pollution originates from coastal urban runoff where the bulk of the land is paved or covered with buildings. These impervious surfaces prevent soils from capturing runoff, resulting in the input of untreated pollutants (e.g., fuels, oils, plastics, metals, insecticides, antibiotics) to coastal waters. Increased terrestrial runoff due to more intense storm events associated with climate change may increase land-based water pollution from both of these sources. In some areas, increased groundwater outflows may also contribute to coastal pollution.

Deterioration and pollution of coastal watersheds can have far-reaching effects on marine ecosystems, for example, the Gulf of Mexico "dead zone" that occurs each summer (Table 2). This mass of hypoxic water has its origins in the increased nitrate flux coincident with the exponential growth of fertilizer use that has occurred since the 1950s in the Mississippi River basin. Pollution has been one of the major drivers of decreases in the health of marine ecosystems such as coral reefs and seagrass and kelp beds (Table 2). Because pollution has usually been more local in scope, adopting integrated ocean and coastal management has enabled MPA and watershed managers to work cooperatively toward managing pollution (Cicin-Sain and Belfiore 2005).

The addition of climate change stressors such as increased oceanic temperature, decreased pH, and greater fluctuations in freshwater influxes and salinity may exacerbate potentially deleterious effects of pollution (Coe and Rogers 1997; Carpenter and others 1998; Khamer and others 2000; Burton and Pitt 2001; Sobel and Dahlgren 2004; Orr and others 2005; Breitburg and Riedel 2005; O'Connor and others 2007; IPCC 2007a). In regions where climate change causes precipitation and freshwater influxes to increase, the scale of water quality degradation may expand. Coral bleaching from the combined stresses of climate change and local pollution (e.g., high temperature and sedimentation) has already been observed (Jackson and others 2001; Hughes and others 2003; Pandolfi and others 2003). Identifying those stressors with the greatest effect is not trivial, and research in coral genomics may provide diagnostic tools for identifying stressors in coral reefs and other marine communities (e.g., Edge and others 2005, 2008).

Overfishing and Destructive Fishing Practices

Commercial fishing has ecosystem effects on three fronts: overfishing, often of multiple fishery species; physical impacts on habitats caused by fishing gear such as trawls, seines, and dredges and fishing practices that use dynamite or cyanide; and incidental take of non-targeted species (bycatch) (Table 2). Fishery populations that are overstressed and overfished exhibit greater sensitivity to climate change and other anthropogenically derived stressors than healthy populations (Hughes and others 2005). Overfishing can reduce mean life span as well as lifetime reproductive success and larval quality, making fished species more susceptible to both short- and long-term perturbations (such as changes in prevailing current patterns) that affect recruitment success (Pauly and others 1998, 2003; Jackson and others 2001; Dayton and others 2002; Sobel and Dahlgren 2004; Estes 2005; Law and Stokes 2005; Steneck and Sala 2005; O'Connor and others 2007). Changing climatic regimes can also influence species' distributions, which are set in part by physiological tolerances to temperature, dissolved oxygen, pH, and salinity. Because rates of climate change appear to exceed the capacity of many commercially fished species to adapt to changing local conditions, species may shift their ranges in accordance with physiological thresholds and may ultimately be forced

Table 2 Traditional stressors, affected community or function, biotic response or effects, and location

Traditional stressor	Affected community/function	Biotic response/effects	Location	References
Land-based sources of pollution	Benthic and pelagic communities in the "dead zone"	Changes in species diversity, community structure, and benthic-pelagic trophic links	1–125 km offshore of Louisiana and Texas	Rabalais and others (2002)
	Coral reefs and seagrass and kelp beds	Decreased ecosystem health	Widespread	Jackson and others (2001), Hughes and others (2003), Pandolfi and others (2003)
	Coral reefs	30–60% decrease in coral diversity	Indonesia	Edinger and others (1998)
	20% of coral reefs	Toxic algal blooms, macroalgal inhibition of larval recruitment	Southeast Asia	Burke and others (2002)
	One-third of coral reefs	Blocked light, smothering, impede coral growth, kill corals	Caribbean	Burke and Maidens (2004)
Overfishing and destructive fishing practices	Living benthic and geologic structures	Reduced habitat complexity and likely changes in associated communities	Widespread	Engel and Kvitek (1998), Thrush and Dayton (2002), Dayton and others (2002), Hixon and Tissot (2007)
	Commercial fishery stocks	At least 26% of fisheries overexploited	U.S. waters	Pauly and others (1998), NRC (1999), Jackson and others (2001), POC (2003), NMFS (2005), Lotze and others (2006)
	Invertebrates, fishes, sea turtles, marine mammals, birds, and early life stages of commercially targeted species	Mortality as incidental bycatch	Widespread	Condrey and Fuller (1992), Norse (1993), Sobel and Dahlgren (2004), Hiddink and others (2006)
	Coral reef community	Widespread damage	Southeast Asia	McManus (1997)
	Reef fish community	60% of coral reefs	Caribbean	Burke and Maidens (2004)
Nonindigenous/invasive species	Marine and estuarine communities	Shifts in relative abundance and distribution of native species and changes in species richness and community structure	Widespread	Sousa (1984), Moyle (1986), Mills and others (1993), Baltz and Moyle (1993), Carlton (1996, 2000), Marchetti and others (2004)
Diseases	Structure and function of marine ecosystems	Abundance and diversity of vertebrates (e.g., mammals, turtles, fish), invertebrates (e.g., corals, crustaceans, echinoderms, oysters), and plants (e.g., seagrasses, kelps)	Widespread	Harvell and others (1999, 2002)

to extend past the boundaries of their “known” native ranges, becoming seemingly invasive elements (Murawski 1993; Walther and others 2002; Roessig and others 2004; Perry and others 2005; Harley and others 2006).

Commercial exploitation of even a single keystone species, such as a top consumer, can destabilize ecosystems by decreasing redundancy and making them more susceptible to climate change stressors (Hughes and others 2005). Examples of such ecosystem destabilization through overfishing abound, including the formerly cod-dominated system of the western North Atlantic (Steneck 1997; Steneck and others 2004), and the fish grazing community on Caribbean coral reefs (e.g., Frank and others 2005; Mumby and others 2006, 2007).

Interestingly, the theoretical framework that links no-take marine reserves with improved coral condition has been a matter of some debate (e.g., Jackson and others 2001; Grigg and others 2005; Pandolfi and others 2005; Aronson and Precht 2006; Jackson 2008). This stems from the nature of cascading effects triggered by reserves, which may involve increases in herbivorous reef fishes in areas where they are fished; increased herbivory reduces macroalgae that can overgrow corals and inhibit coral recruitment. However, reserves also protect predators, so declines in herbivorous fish might occur unless there is an escape in size from predation and the rate of herbivory actually increases (Mumby and others 2006). Data from field studies provide conflicting results. Mumby and others (2006) showed that increased densities of large herbivorous fish in a marine reserve reduced algal growth after mass bleaching caused extensive coral mortality, but such increases in herbivore densities do not always occur after protection is provided (Mosquera and others 2000; Graham and others 2003; Micheli and others 2004; Robertson and others 2005). Further, Burkepile and Hay (2008) have documented important differences in grazing behavior among three Caribbean parrotfishes, highlighting the importance of herbivore community structure to grazing effects. Finally, there is widespread belief that the 1983–1984 mass mortality of *Diadema antillarum*—a major grazing sea urchin on Caribbean reefs—was a significant proximal cause of coral reef decline throughout the Caribbean. However, as reported in Aronson and Precht (2006) half the decline in live coral cover throughout the Caribbean reported by Gardner and others (2003) occurred before this die-off, and immediately after the die-off coral cover remained unchanged. Subsequent declines in cover were associated with mass coral bleaching events (1987, 1997–1998) and possibly with continued losses to diseases. It is important to highlight this complexity because it emphasizes how much is unknown about basic ecological processes on coral reefs and consequently how much needs to be learned about whether no-take marine reserves work effectively to enhance ecosystem resilience when disease and bleaching remain significant sources of coral mortality (Aronson and Precht 2006; Bruno and Selig 2007).

Nonindigenous/Invasive Species

Invasive species threaten all marine and estuarine communities (Table 2). Currently, an estimated 2% of extinctions in marine ecosystems are related to invasive species while 6% are the result of other factors including climate change, pollution, and disease (Dulvy and others 2003). Principal mechanisms of introduction vary and include both accidental and intentional release (Ruiz and others 2000; Carlton 2000; Hare and Whitfield 2003).

Some native species, particularly rare and endangered ones with small population sizes and gene pools, are unlikely to be able to adapt quickly enough or shift their ranges rapidly enough to compensate for the changing climatic regimes proposed by current climate change models (IPCC 2007a). These native species will likely have their competitive abilities compromised and be more susceptible to displacement by invasive species, and therefore should be considered for stronger protective measures by MPA managers. Increased seawater temperatures resulting from climate change may also enable introduced species to spawn earlier and for longer periods, thus increasing their population growth rates relative to natives while simultaneously expanding their range (Carlton 2000; McCarty 2001; Stachowicz and others 2002; Marchetti and others 2004). Furthermore, the same characteristics that make species successful invaders may also make them pre-adapted to respond to, and capitalize on, climate change. As one example, Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are now widely distributed and abundant off the southeastern coast of the United States and in the Bahamas less than 10 years after being first observed off Florida (Whitfield and others 2007; Snyder and Burgess 2007; Freshwater and others 2009). One of the few factors limiting their spread is intolerance to minimum water temperatures during winter (Kimball and others 2004); ocean warming could facilitate depth and range expansion in these species.

Diseases

Pathogen outbreaks or epizootics spread rapidly due to the lack of dispersal barriers in some parts of the ocean and the potential for long-term survival of pathogens outside the host (Table 2). Many pathogens of marine taxa such as coral viruses, bacteria, and fungi respond positively to temperature increases within their physiological thresholds (Porter and others 2001; Kim and Harvell 2004; Munn 2006; Mydlarz and others 2006; Boyett and others 2007). However, it is noteworthy that white-band disease was the primary cause (though not the only cause) of reduced coral cover on

Caribbean reefs from the late 1970s through the early 1990s (Aronson and Precht 2006). That outbreak did not correspond to a period of particularly elevated temperature [R. Aronson, personal communication; but see Lesser and others (2007)].

Exposure to disease compromises the ability of species to resist other anthropogenic stressors and vice versa (Harvell and others 1999, 2002). For example, in 1998, the most geographically extensive and severe coral bleaching ever recorded was associated with the high anomalies in sea surface temperatures associated with an ENSO event (Hoegh-Guldberg 1999; Wilkinson and others 1999; Mydlarz and others 2006). In some species of reef-building corals and gorgonians, this bleaching event was thought to be accelerated by opportunistic infections (Harvell and others 1999, 2001). Several pathogens—such as bacteria, viruses, and fungi that infect such diverse hosts as seals, abalone, and starfish—show possible onset with warmer temperatures (reviewed in Harvell and others 2002) and some coral species may become more susceptible to disease after bleaching events (Whelan and others 2007). The mechanisms for pathogenesis, however, are largely unknown. Given that exposure to multiple stressors may compromise the ability of marine species to resist infection, the most effective means of reducing disease incidence under climate change may be to minimize impacts of stressors such as pollution and overfishing.

Options for Marine Protected Area Management in the Context of Climate Change

Options for management of MPAs in response to climate change can be organized at two levels: actions at existing sites and establishment of new sites, particularly if they are arranged as networks (Table 3). Within MPAs, managers can increase efforts to ameliorate existing anthropogenic stressors with a goal of reducing the overall load of multiple stressors (Breitburg and Riedel 2005). For example, the concept of protecting or enhancing coral reef resilience has been proposed to help ameliorate negative consequences of coral bleaching (Hughes and others 2003, 2005; West and Salm 2003; Marshall and Schuttenberg 2006a; Salm and others 2006). Under this approach, resilience is an ecosystem property that can be managed, and is defined as the ability of an ecosystem to resist or absorb disturbance while maintaining key functions and processes (Gunderson 2000; Nyström and others 2000; Hughes and others 2003; McLeod and others 2008b). Managing for resilience includes addressing causes of disturbance and decline at a local scale such as overfishing and pollution, identifying and protecting potentially resilient areas, and designing networks of MPAs to address threats at broader scales. Networks of MPAs should be designed to take advantage of properties of systems of sites. These properties include connectivity, protection of ecologically critical areas, and replication and representation of multiple habitat types (Salm and others 2006; McLeod and others 2008b).

It is important to emphasize that variable and complex effects of climate on oceanographic processes and production (Soto 2002; Mann and Lazier, 2006) present MPA managers with major uncertainties about climate change impacts and effective management approaches. Nevertheless, it is imperative to integrate climate change into MPA management plans using the best available scientific information.

Table 3 Management options for MPA managers in the context of climate change (see McLeod and others 2008b)

✔ Manage human stressors such as fishing and inputs of nutrients, sediments, and pollutants within MPAs.
✔ Improve water quality by raising awareness of adverse effects of land-based activities on marine environments, implementing integrated coastal and watershed management, and developing options for advanced wastewater treatment.
✔ Manage functional species groups necessary to maintaining the health of reefs and other ecosystems.
✔ Identify and protect areas that appear to be resistant to climate change effects or to recover from climate-induced disturbances.
✔ Identify and protect ecologically significant ("critical") areas such as nursery grounds, spawning grounds, and areas of high species diversity.
✔ Identify ecological connections among ecosystems and use them to inform the design of MPAs and management decisions such as protecting resistant areas to ensure sources of recruitment for recovery of populations in damaged areas.
✔ Design MPAs with dynamic boundaries and buffers to protect breeding and foraging habits of highly migratory and pelagic species.
✔ Establish dynamic MPAs defined by large-scale oceanographic features such as oceanic fronts where changes in types and abundances of organisms often occur.
✔ Maximize habitat heterogeneity within MPAs and consider protecting larger areas to preserve biodiversity, ecological connections among habitats, and ecological functions.
✔ Include entire ecological units (e.g., coral reefs with their associated mangroves and seagrasses) in MPA design to help maintain ecosystem function and resilience.
✔ Ensure that the full breadth of habitat types is protected (e.g., fringing reef, fore reef, back reef, patch reef).
✔ Replicate habitat types in multiple areas to spread risks associated with climate change.

Ameliorate Existing "Traditional" Stressors

Managers may be able to increase resilience to climate change within MPAs by reducing impacts of local- and regional-scale stressors, such as fishing, input of nutrients, sedimentation and pollutants, and degraded water quality. While this concept is logical and has considerable appeal, evidence in support of this approach is limited. Behrens and Lafferty (2004) found that kelp forest ecosystems in no-take marine reserves were more resilient to ocean warming than in reference areas as a result of changes in trophic structure of communities in and around reserves. In reference areas where predators such as spiny lobster were fished, herbivorous sea urchin prey increased in abundance and consumed giant kelp and other algae. In reserves where fishing was prohibited, lobster populations were larger, urchin populations were diminished, and kelp forests persisted over a period of 20 years, including four ENSO cycles (Behrens and Lafferty 2004). Although MPAs have been shown to be effective at mitigating stresses at local scales, they may be less effective at addressing global climate change threats such as mass bleaching events (see Bruno and Selig 2007) unless they are designed specifically to address resilience.

Managing water quality has been identified as a key strategy for maintaining ecological resilience (Salm and others 2006; Marshall and Schuttenberg 2006a). In the Florida Keys National Marine Sanctuary and the Great Barrier Reef Marine Park water quality protection is recognized as an essential component of management (US-DOC 1996; Grigg and others 2005). Strong circumstantial evidence links poor water quality to increased macroalgal abundances, increased bioerosion, and higher susceptibility to some diseases in corals and octocorals (Fabricius and De'ath 2004). Addressing sources of pollution, especially nutrient enrichment that can lead to increased algal growth and reduced coral settlement, is critical to ecosystem structure and function. In addition to limiting point-source pollution within an MPA, sources from beyond MPA boundaries should be controlled as much as possible through collaborations with appropriate authorities in adjacent areas (see Crowder and others 2006). For example, MPA managers should work with land and watershed managers to develop and implement strategies to reduce land-based pollution, decrease nutrient and sediment run-off, eliminate the use of persistent pesticides, and increase filtration of effluent through wetlands to improve quality of coastal waters. Actions such as these should be coupled with research to investigate their efficacy.

Another mechanism that may help maintain resilience of coral reef ecosystems is the management of functional groups, specifically herbivores (Hughes and others 2003; Bellwood and others 2004; McLeod and others 2008b). Bellwood and others (2004) identified three functional groups of herbivores that assist in maintaining coral reef resilience: bioeroders, grazers, and scrapers. These groups work together to break down dead coral to allow substrate for recruitment, graze macroalgae, and reduce the development of algal turfs to provide substrata suitable for coral settlement. Attention must also be paid to the roles of individual species within these groups (Burkepile and Hay 2008). Bellwood and others (2006) identified the need to protect both the species that prevent phase shifts from coral- to algal-dominated reefs and species that help reefs recover from algal dominance. While parrotfishes and surgeonfishes appear to play a critical role in preventing phase shifts to macroalgae [but see Ledlie and others (2007)], they may have limited ability to reverse such a shift. In one study, phase-shift reversal from macroalgal- to a coral- and epilithic algal-dominated state surprisingly was caused by a single batfish species (*Platax pinnatus*) rather than parrotfishes and other herbivores (Bellwood and others 2006).

Although protecting functional groups may be a component of MPA management to enhance resilience, understanding which groups should be protected requires a detailed knowledge of species and interactions that is not often available. Coral reefs appear to require key herbivores in sufficient numbers to reduce macroalgae and enhance coral settlement, whereas kelp forests may require key predators on herbivores to reduce herbivory and promote kelp recruitment and growth. Manipulating functional groups should be field tested at different locations to verify their appropriateness. As a precaution, managers should strive to maintain the maximum number of species, particularly in the absence of detailed ecological data.

Protect Potentially Resilient Areas

Marine ecosystems face potential loss of habitat structure as climate change progresses (e.g., coral reefs, seagrass beds, kelp forests, and deep coral communities) (see Hoegh-Guldberg 1999; Steneck and others 2002; Roberts and others 2006; Orth and others 2006). It is likely that climate change contributes to mass coral bleaching events (Reaser and others 2000), which became global in 1998 (Wilkinson 1998, 2000) and have affected large regions in subsequent years (Wilkinson 2002, 2004; Whelan and others 2007). The amount of live coral has declined dramatically in the Caribbean region over the past 30 years as a result of bleaching, diseases, and hurricanes (Gardner and others 2003, 2005). In the Florida Keys, some fore-reef environments that formerly supported dense growths of coral are now depauperate, and highest coral cover is in patch reef environments (Porter and others 2002; Lirman and Fong 2007). Irrespective of the mechanism—resistance, resilience, or exposure to relatively low levels of past environmental stress—these patch reefs are good candidates for additional protective measures because they may have high potential to survive climate stress.

Done (2001; see also Marshall and Schuttenberg 2006b) presented a decision tree for identifying areas that would be suitable for MPAs under a global warming scenario. Two types of favorable outcomes included reefs that survived bleaching (i.e., were resilient) and reefs that were not exposed to elevated sea surface temperatures (e.g., may be located within refugia such as areas exposed to upwelling or cooler currents). This type of decision tree has already been adapted to guide site selection for mangroves (McLeod and Salm 2006), and could be extended further for other habitat types such as seagrass beds and kelp forests.

In addition, thermally stressed corals may exhibit less bleaching and higher survival if they are shaded during periods of elevated temperatures (West and Salm 2003; Hoegh-Guldberg and others 2007b). On a small scale, MPA managers may be able to select sites that are naturally shaded by high islands, emergent rocks or corals overhead. For example, in the Rock Islands of Palau, corals in more shaded parts of the reef survived a bleaching event better than those in more exposed parts of the reef (West and Salm, 2003). MPA managers may also consider shading areas during bleaching events to reduce UV radiation impacts and overall stress (Hoegh-Guldberg and others 2007b). On a larger scale, managers should protect mangrove shorelines and support restoration of areas where mangroves have been damaged or destroyed because tannins and dissolved organic compounds from decaying mangrove vegetation contribute to absorbing light and reducing stress on adjacent coral reefs (Hallock 2005). Extensive discussions of coral bleaching and management responses are provided in Marshall and Schuttenberg (2006a, b), Johnson and Marshall (2007), and McLeod and others (2008b).

Develop MPA Networks

The concept of networks of MPAs has gained appeal for a number of reasons, and network design to address impacts of climate change was recently reviewed by McLeod and others (2008b). Emergent properties of systems such as representation, replication, and connectivity (Ballantine 1997; NRC 2001; Roberts and others 2003a; West and Salm 2003; Salm and others 2006; McLeod and others 2008b) are attractive to MPA managers who have realized that relatively small, isolated protected areas may not adequately protect ecosystem structure and function. Also, networks likely lower the risk of catastrophic habitat loss (Palumbi 2002; Allison and others 2003), which may provide a form of "insurance" for management of biogenically structured, slow-growing habitats such as coral reefs. Finally, networks may provide functional wilderness areas sufficiently extensive to resist fundamental changes to ecosystems (Kaufman and others 2004). While MPA networks have been recognized as a valuable tool to conserve marine resources in the face of climate change, there have been a number of challenges to their implementation (Pandolfi and others 2005; Mora and others 2006). A set of recommendations has been developed to aid MPA network design and implementation, which include MPA size and spacing, risk spreading, protection of critical areas, connectivity, ecosystem function, and ecosystem-based management (McLeod and others 2008b).

Guidelines for the minimum size of MPAs and no-take marine reserves, and spacing between adjacent MPAs, vary depending on their goals (Hastings and Botsford 2003). For example, Friedlander and others (2003) suggested that no-take zones should measure ca. 10 km^2 to ensure viable populations of a range of species in the Seaflower Biosphere Reserve, Colombia. Palumbi (2003) concluded that marine reserves tens of km apart may exchange larvae in a single generation. Shanks and others (2003) similarly concluded that marine reserves spaced 20 km apart would allow larvae to be carried to adjacent reserves. The Science Advisory Team to California's Marine Life Protection Act Initiative recommended spacing highly protected MPAs, such as marine reserves, within 50–100 km in order to accommodate larval dispersal distances of a wide range of species of interest. Halpern and others (2006) corroborated these findings using an uncertainty-modeling approach.

It has been suggested that no-take zones measuring a minimum of 20 km in diameter may accommodate short-distance dispersers in addition to including a significant portion of local benthic fish populations, thus generating fisheries benefits (Shanks and others 2003; Fernandes and others 2005; Mora and others 2006; McLeod and others 2008b). A single network design is unlikely to satisfy the potential dispersal ranges for all species; Roberts and others (2003b) recommended an approach using various sizes and spacing of MPAs in a network to accommodate the diversity of dispersal ranges, which likely will be all the more necessary in the context of further variabilities caused by climate change. Recommendations to protect highly migratory and pelagic species include designing MPAs to protect predictable breeding and foraging habits, ensuring these have dynamic boundaries and extensive buffers, and establishing dynamic MPAs that are defined by the extent and location of large-scale oceanographic features such as oceanic fronts where changes in types and abundances of marine organisms often occur (Hyrenbach and others 2000).

Risk spreading to minimize the likelihood of loss of habitat types (Salm and others 2001; West and Salm 2003; McLeod and others 2008b) involves protection of multiple samples of each type (Hockey and Branch 1994; Ballantine 1997; Roberts and others 2001, 2003b; Friedlander and others 2003; Salm and others 2006; Wells 2006). Examples of marine habitat types include coral reefs with varying degrees of exposure to wave energy (e.g., offshore, midshelf, and inshore reefs) and a range of types of mangrove forests (riverine, basin, and fringe forests in areas of varying salinity, tidal fluctuation, and sea level) (Salm and others 2006).

There are several recommendations about proportions or numbers of habitat types to protect. For example, it has been recommended that more than 30% of appropriate habitats should be included in no-take marine reserves (Bohnsack 2000). In 2004, the Great Barrier Reef Marine Park Authority increased the area of no-take marine reserves from less than 5% to approximately 33% of the area of the Marine Park, ensuring that at least 20% of each bioregion (area of every region of biodiversity) was zoned as no-take (Day and others 2002; Fernandes and others 2005). Also, Airamé and others (2003) recommended a network of three to five no-take zones in each biogeographic region of the Channel Islands National Marine Sanctuary, comprising approximately 30–50% of the area, in order to conserve biodiversity and contribute to sustainable fisheries in the region. An additional consideration is placement of reserves, which could be designed to minimize the risk of loss to catastrophic disturbances such as mass bleaching events in order to maximize achieving conservation targets (Game and others 2008).

Biologically or ecologically significant "critical areas" should be protected; critical areas include nursery habitats, spawning aggregations or areas, areas of high species diversity, heterogeneous habitat clusters, and areas that are not exposed to extremes of climate change (Allison and others 1998; Sale and others 2005; Sadovy 2006; McLeod and others 2008b). For example, areas of coral reefs that appear to be resilient to climate change should be provided with a high level of protection to help ensure a secure source of recruitment to damaged areas within an MPA network (Salm and Coles 2001). Responses to past bleaching events and other disturbances may provide insights into resilience; some coral colonies may have genetic characteristics that confer resistance to bleaching or may avoid bleaching because of environmental factors such as currents and shading that provide protection from temperature and/or irradiance anomalies. Highly protected critical areas should be as large as possible to maximize their effectiveness as sources of recruits (Palumbi and others 1997; Bellwood and Hughes 2001; Salm and others 2006).

Connectivity via larval dispersal and the movement of adults and juveniles has been investigated and reviewed extensively (e.g., Roberts 1997; Crowder and others 2000; Stewart and others 2003; Roberts and others 2003b; Cowen and others 2006; Salm and others 2006; Steneck 2006; McLeod and others 2008b). In addition to designing MPA networks for connectivity among different sites containing a particular habitat type, connectivity among habitat types such as mangroves, coral reefs, and seagrass beds (Ogden and Gladfelter 1983; Roberts 1996; Nagelkerken and others 2000; Mumby and others 2004; McLeod and others 2008b).

Although maintaining connectivity within and between MPAs may help maintain marine biodiversity, ecosystem function, and resilience, many challenges exist. For example, the same currents and pathways that enable larval recruitment can expose an ecosystem to invasive species, pathogens, parasites, and pollutants, which can undermine the resilience of a system (McClanahan and others 2002). Numerous challenges also exist in estimating larval dispersal patterns. Although there have been detailed studies addressing dispersal *potential* of marine species based on their larval biology (e.g., Shanks and others 2003; Kinlan and Gaines 2003), little is known about where in the oceans larvae go and how far they travel. Larval duration in the plankton also varies from minutes to years, and the more time propagules spend in the water column, the farther they tend to be dispersed (Shanks and others 2003; Steneck 2006). Evidence from hydrodynamic models and genetic structure data indicates that in addition to large variation of larval dispersal distances among species, the average scale of dispersal can vary widely—even within a given species—at different locations in space and time (e.g., Cowen and others 2003; Sotka and others 2004; Engie and Klinger 2007). Some information suggests long-distance dispersal is common, but other emerging information suggests that larval dispersal may be limited (Jones and others 1999, 2005; Swearer and others 1999; Warner and others 2000; Thorrold and others 2001; Palumbi 2003; Paris and Cowen 2004). Additional research will be required to better understand where and how far larvae travel in various marine ecosystems.

For both terrestrial and marine systems, species diversity often increases with habitat diversity, and species richness increases with habitat complexity; the greater the variety of habitats protected, the greater the biodiversity conserved (Friedlander and others 2003; Carr and others 2003). High species diversity may increase ecosystem resilience by ensuring sufficient redundancy to maintain ecological processes and protect against environmental disturbance (McNaughton 1977; McClanahan and others 2002). This is particularly the case in the context of additive or synergistic stressors. Maximizing habitat heterogeneity is critical for maintaining ecological health, thus MPAs should include large areas and depth gradients (Done 2001; Hansen and others 2003; Roberts and others 2003a). By protecting a representative range of habitat types and communities, MPAs have a higher potential to protect a region's biodiversity, biological connections between habitats, and ecological functions (Day and others 2002).

Table 4 Integrate climate change into MPA planning, management, and evaluation: The Great Barrier Reef as an example

The Great Barrier Reef Marine Park Authority (GBRMPA) is exemplary with regard to the degree to which it has inawcorporated climate change into its management program. GBRMPA has implemented a comprehensive Climate Change Response Program (http://www.gbrmpa.gov.au/, accessed 23 May 2008) that establishes guidelines for other MPA managers to consider. A thorough assessment of vulnerabilities to climate change (Johnson and Marshall 2007) set the stage for management recommendations. "A Reef Manager's Guide to Coral Bleaching" (Marshall and Schuttenberg 2006a) provided information on the causes and consequences of coral bleaching and management strategies to help local and regional reef managers reduce this threat to coral reef ecosystems. GBRMPA has expanded its area of no-take management of human uses from a total proportion of less than 5 to 33%, using a representative areas approach (Day and others 2002; Fernandes and others 2005). It remains to be seen whether this expansion of no-take zoning within the Great Barrier Reef Marine Park will influence susceptibility of coral reefs to mass bleaching events (see Bruno and Selig 2007).

Integrate Responses to Impacts of Climate Change in MPA Management

Scientists and managers involved with coral reef MPAs have collaborated on a guide about coral bleaching that provides a number of recommendations to MPA managers (Marshall and Schuttenberg 2006a). In contrast, impacts of ocean acidification (Caldeira and Wickett 2003) do not have clearly articulated management strategies, although efforts are currently being made to develop these strategies (McLeod and others 2008a). Further research is needed on impacts of high concentrations of CO_2 in the oceans, possible acclimation or evolution of organisms in response to changes in ocean chemistry, and how management might respond (TRS 2005). Possible responses to other climate change stressors such as sea level rise, ocean circulation, storm intensity, and freshwater influx also require further research, and may not have management options as well explored and tested as those for traditional stressors such as pollution, commercial fishing, invasive species, and diseases.

Interactions of climate change stressors with traditional stressors compress the spatial extent of impacts and management responses from global and regional scales to more local manifestations.

Nevertheless, we suspect that many management plans for coral reef and other MPAs do not explicitly address actions or options in the context of climate change, and we hope that recommendations provided here and elsewhere (Table 4) will help fill this gap. Managers and scientists need to work together closely with stakeholders to consider regional scenarios of impacts of climate change and ecosystem responses, and determine how best to implement science-based management responses.

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