

## What role for marine protected areas in a future of climatic change?

By

Neil A. Davis<sup>1</sup>

Centre for Applied Conservation Research,  
University of British Columbia

### Abstract

Climate change threatens the ability of marine protected areas to deliver intended biodiversity and resource conservation outcomes. In light of this, should governments and stakeholders pursue their creation? This paper reviews the implications of climate change for marine ecosystems and suggests that marine protected areas can serve several important conservation functions in spite of climatic change. The paper also outlines recommendations for marine protected area design and management that will mitigate detrimental effects of climate change on the efficacy of marine protected areas. Recommendations are based on three central themes that should guide marine protected area design and management: acknowledging uncertainty, adopting a precautionary approach, and implementing adaptive management.

*“Decisions about the siting and design of reserves and assumptions about how much management will be needed in the future must reflect the increased demands, both economic and biological, of global warming.”*  
(Peters and Darling 1985: 707)

### Introduction

Marine ecosystems are extremely valuable, providing an irreplaceable array of essential ecosystem goods and services worth over \$20 trillion, or 63% of the global total (Costanza et al. 1997). They are also subject to anthropogenic stressors such as overfishing and habitat degradation that have resulted in large-scale changes to their composition and function (Dayton et al. 1995; Pauly et al. 1998; Jackson et al. 2001; Myers and Worm 2003; Pandolfi et al. 2003). Marine protected areas (MPAs) have been promoted as a key tool that can mitigate these threats by conserving marine biodiversity and facilitating more sustainable fisheries management. The implementation of MPAs

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<sup>1</sup> Neil A. Davis, Centre for Applied Conservation Research, c/o Paul Wood, University of British Columbia, 2424 Main Mall, Vancouver, Canada, V6T 1Z4, Email: [nadavis77@gmail.com](mailto:nadavis77@gmail.com), Tel: +01 604 731-1811, Fax: +01 604 822-9106

around the world is growing quickly; indeed, the 2002 World Summit on Sustainable Development called for a global network of MPAs by 2012 (Sherman 2006).

Empirical research has documented numerous outcomes of spatial protection for marine areas, including higher organism density, biomass, species diversity, and numbers of large organisms than in adjacent areas (Russ and Alcala 1996a; Murawski et al. 2000; Roberts et al. 2001; Halpern 2003). They can also function as refugia from the genetic or selection changes imposed by fisheries and provide a buffer against the consequences of management errors and stochastic events (Allison et al. 1998; Murray et al. 1999; Pauly et al. 2002; Lubchenco et al. 2003). With respect to fisheries management, these functions can decrease the chance of stock collapse, accelerate population recovery rates, decrease variability in annual catches, provide fishery independent data, and prevent habitat destruction associated with destructive fishing practices (Murray et al. 1999). These conservation benefits can be accompanied by the spillover of fish into adjacent areas and the export of eggs and larvae (Bohnsack 1993; Russ and Alcala 1996b; Roberts et al. 2001; Gell and Roberts 2003). Ecological modeling suggests that MPAs can even be useful for highly mobile species such as cod in reducing the risk of fishing overexploitation (Guenette and Pitcher 1999).

The ability of MPAs to deliver these outcomes may be threatened by anthropogenically-driven global climate change. Atmospheric concentrations of carbon dioxide (CO<sub>2</sub>) have risen 31% above average pre-industrial levels within this millennium. Sea levels have risen an average of 1-2 mm per year in the 20<sup>th</sup> century due primarily to the thermal expansion of seawater and freshwater runoff from glacial melt (IPCC 2001). CO<sub>2</sub> levels are expected to rise another 50-250% by 2100, with sea levels rising as much as 1 m (IPCC 2001). Global mean surface temperatures will likely rise by 1.4-5.8°C in the next 100 years, a rate without precedent in the last 10 000 years that will cause further ocean warming (IPCC 2001). Climate change has already triggered significant change in the earth's physical systems and biogeochemical cycles, with more dramatic change expected in the near future. These changes will in turn dramatically alter the distribution and abundance of species and reconfigure the composition and function of marine ecosystems (Harley et al. 2006; Lovejoy 2006). Thus, the features represented in marine areas set aside for protection may shift or disappear over time. This raises important questions about spatially static protective measures like MPAs, which are the basis for this paper: are MPAs a rational long-term marine conservation tool given that climate change will alter marine ecosystems? If so, how should our understanding of climate change affect the planning and management of existing and future MPAs? Examining these questions is paramount for determining the most viable means of marine conservation for the future. Questions about protected areas in the context of climate change have only begun to be

seriously addressed, and even then only on land, despite the recommendation of Peters and Darling over 20 years ago (Peters and Darling 1985; Halpin 1997; Suffling and Scott 2002).

To examine these questions, this paper reviews relevant academic literature to determine if and how MPAs can be effective long-term conservation tools. First, I describe salient features of marine environments in comparison to terrestrial environments to highlight how and why climate change will affect oceans in unique ways. This comparison will also make clear how MPAs have a different set of challenges than terrestrial protected areas which preclude the direct transference of terrestrial protection strategies to the marine environment (Allison et al. 1998). Next, I summarise the potential effects of climate change on abiotic ocean processes and resultant possible effects on marine biotic communities, focusing on coastal marine ecosystems. The paper then examines whether MPAs have a long-term conservation role to play and considers strategies for making MPAs more effective in the face of climate change. To inform the latter stages of the paper, I draw from literature on biodiversity and resilience, management and planning principles for complex systems, and applicable elements of reserve theory that may be important in the face of climate change. The scope of this paper is limited primarily to the scientific and technical aspects of MPAs and climate change, but it is imperative to recognise that the political, economic, and social dimensions of MPA planning and management are equally or more important to their efficacy over the long term.

## **The marine environment**

The properties of the marine environment are different from those of terrestrial environments in fundamental ways that have implications for the effects of climate change on oceans and our management actions in response to it. The heat capacity of water moderates temperature changes in oceans, making changes slower and of less magnitude than on land, meaning that species inhabit environments that are relatively thermally stable, particularly in tropical waters. Water is 60 times more viscous and 850 times denser than air, which provides buoyancy, permitting a large proportion of marine biota to live most of their lives in the water column, away from the interface with the geological substrate (Norse 1993 as cited in Soto 2001). The world's oceans are also much larger than the global landbase and life is distributed throughout the entire water column, meaning that oceans account for 99% of the biosphere, though most marine life is concentrated close to the sea-air interface (Norse and Crowder 2005).

Ocean water circulates as air masses circulate on land, although due to its viscosity and density, it does so more slowly. However, unlike land, many marine organisms and nutrients exist in the medium which circulates, and there are fewer barriers to movement through the marine

environment (Soto 2001). Thus, species can be wide ranging and the pelagic larval stages typical of most marine fishes and invertebrates can be passively dispersed over long distances. This suggests that marine metapopulation dynamics operate over much longer distances than terrestrial ecosystems, ecologically linking larger areas (Lipcius et al. 2005).

The types and sources of primary production are also very different between land and sea. Marine primary production is dominated by microscopic phytoplankton that reproduce rapidly at a high turnover rate, limiting the standing stock to an average of 1% of annual production (Ricker 1968). There is no accumulation of biomass over years or decades as there is in plants and trees on land - primary producer biomass is processed quickly by consumers or reducers (Day and Roff 2000). The rapidity of primary production combined with the fluidity of water that can concentrate nutrients and transport species make biological responses to environmental changes tightly coupled. Short generation times link population and community cycles more closely to physical processes. This creates an interesting juxtaposition of quickly responding marine biotic communities within a slowly changing, insulating ocean - a contrast to longer lived, slower responding terrestrial communities that exist in a physical environment characterised by comparatively rapid changes of greater magnitude (Day and Roff 2000). Accordingly, marine communities are expected to respond more rapidly to climate change than terrestrial environments (Soto 2001).

In addition to the natural features of marine environments, there are also important features of our relationship to them. Humans are awkward visitors to marine environments. Ocean research is expensive, difficult, potentially dangerous, and incapable of meaningfully investigating all aspects of oceans, given their vast breadth and depth. Nothing happening below the surface is directly observable which means that a concerted effort is required to collect information (Norse and Crowder 2005). It also means that the dynamics and health of this alien environment are easily put 'out of sight and out of mind', particularly given that the majority of humans have little direct interaction with oceans (Day and Roff 2000). Partly as a result of these factors, less research is conducted on marine environments than terrestrial ones, further limiting our understanding of their dynamics (Norse and Crowder 2005).

## **Effects of climate change on oceans**

### **Physical and chemical processes**

Ocean conditions vary naturally across a range of temporal and spatial scales. Seasonal changes in sea surface temperature may be local or regional, the El Niño Southern Oscillation varies interannually, and the North Atlantic and Pacific Decadal Oscillations cycle over decades, affecting

large ocean areas. The distribution of species and communities reflects this variation, and changes in biotic communities in response to natural shifts in ocean conditions are well documented. Human-caused climate change, stemming primarily from increased levels of CO<sub>2</sub> and resultant increases in atmospheric temperatures, introduces a new driver of variation in ocean conditions that will alter ocean temperatures and ocean chemistry with cascading effects on ocean processes and biotic communities. There are several different methods of exploring potential impacts of climate change on marine environments (Soto 2001). First, historical analogies can be developed using sources of information such as palaeoecological data. Second, research can draw from recent datasets, which provide less than 100 years of data for most variables. Though a brief period climatically, it is long enough to demonstrate changes in temperature and responses in biotic communities. Third, modeling can develop predictions based on current trajectories and understanding of natural systems processes and causal mechanisms. They typically include a range of proxies that draw from either of the data types outlined above or theoretical deduction. Proxies are selected based on availability and the model's objective(s), level of complexity, and resolution (Rahmstorf 2002). Though limited in their ability to inform our understanding of changes for which we have no analogous experience, all of these methods are present in the summary of effects outlined here.

Ocean warming and sea level rise, the two most commonly cited effects of climate change on oceans, will be accompanied by a host of other physical changes. Atmospheric circulation patterns will affect patterns of precipitation which may alter ocean salinity, turbidity, and inputs of terrestrially-derived nutrients washed into the ocean by precipitation-driven runoff (Harley et al. 2006). Bakun (1990) forecasts increased winds as a result of comparatively greater heating over land than water as atmospheric temperatures rise. In wind-driven coastal upwelling systems such as the California coast, this could increase upwelling. Snyder et al.'s (2003) regional climate model predicted that upwelling in this system would increase with rising CO<sub>2</sub> concentrations and an increased temperature gradient between land and sea. This contributed to the alongshore winds which drive upwelling. However, these dynamics may be somewhat offset by rising sea surface temperatures and increased freshwater inflows (from glacial melt) resulting from warmer atmospheric temperatures, both of which increase the stability of the water column by increasing the buoyancy of surface water (Roessig et al. 2004). A more stable water column can repress upwelling (Roemmich and McGowan 1995).

Climate change will likely affect patterns of ocean circulation. Currents are driven by winds, thermohaline circulation (THC), or tidal influences (Roessig et al. 2004). THC, the slow, large-scale movement of deep ocean water masses, is the result of water density gradients (Hansen et al. 2004). Thus, changes in temperature and salinity mentioned above may have implications for the

persistence of THC patterns, particularly in the north Atlantic. Relatively faster warming at the poles is melting ice in northern latitudes, which increases freshwater inputs, decreases salinity, and increases surface water buoyancy. This may stem the sinking of typically denser, colder ocean water in the north Atlantic that then travels south to displace deep water which in turn rises and travels north (Hansen et al. 2004). The warmer southern water which travels north transports enormous quantities of heat that keep much of western and northern Europe warmer than they would be otherwise (Rahmstorf 2002). The possibility of weakening THC in the north Atlantic remains unclear, though its relationship to other large circulation patterns make the implications of its future function global in scope (Vellinga and Wood 2002). In the Pacific, a global climate model forced by a future scenario of increasing greenhouse gas concentrations forecasts more frequent occurrences of El Niño conditions and a strengthening of the equatorial thermocline (Timmerman et al. 1999). El Niño brings warmer water that is lower in nutrients to the west coast of the Americas, and has feedback effects on global climate systems.

Harley et al. (2006) suggest that climate-induced changes to the chemical composition of oceans may have greater impacts on the performance and survival of many species than temperature changes. Rising levels of atmospheric CO<sub>2</sub> have led to higher ocean uptake of CO<sub>2</sub> and acidification of ocean water (Feely et al. 2004). Projected atmospheric concentrations of CO<sub>2</sub> acidification are expected to rise from current levels of approximately 380 ppm (Sabine et al. 2004) to between 540-970 ppm, which may cause a drop in surface water pH of .4 by the end of the century - a magnitude of change in the oceanic CO<sub>2</sub> system probably unique within the past 20 million years (Feely et al. 2004). The upward trend in CO<sub>2</sub> concentrations will continue to decrease the degree of saturation of the alkaline minerals aragonite and calcite in the oceans- minerals that are essential for the multitude of marine organisms that form calcium carbonate (CaCO<sub>3</sub>)-based skeletal structures. This decrease will be greater at higher latitudes (Feely et al. 2004).

### **Ecological responses and implications**

Summaries of the ecological responses to changes in the abiotic ocean environment are arranged by climatic variable, with consideration of proximate effects primarily at the individual and population levels (Harley et al. 2006). The summary is not exhaustive - it focuses on key variables with the most relevance and importance for MPAs. It is worth noting that some of the most powerful effects may arise from the interactions and feedback between different stressors. The exponentially increasing complexity of these interactions makes accurate predictions practically impossible, though even exploring potential directions and magnitudes of change can be useful. Broader level outcomes resulting from multiple factors are considered last in the section on emergent effects.

### ***Rising water temperatures***

The effects of climate change-induced temperature increases on different species will likely be highly variable and conditional. Species responses in terms of performance and survival may also not be linear. Temperatures at the extreme ends of species tolerance ranges can decrease foraging, growth, and fecundity, and affect migratory behaviour, which in turn can influence population and community dynamics via their implications for performance, resource use patterns, and survival (Roessig et al. 2004). Perhaps the most well-known example of the effects of increased seawater temperatures is the widespread coral bleaching that has occurred throughout the tropics during anomalously warm periods (Hughes et al. 2003). Rising seawater temperatures also coincided with decreased reproductive output and a mismatch between the larval production of bivalves and peak food supply that increased competition (Philippart et al. 2003). These outcomes resulted in reduced recruitment and smaller adult populations (Philippart et al. 2003). Species distributions have also changed with rising temperatures, moving towards the poles to remain within their optimum temperature range (Parmesan and Yohe 2003). Perry et al. (2005) used historic fisheries and ocean temperature data to demonstrate that centres of abundance for two thirds of the North Sea demersal fishes included in the study have shifted northward over the past 25 years as ocean temperatures increased approximately 1°C in the same period. Those species whose distributions shifted had faster regeneration times, which may suggest that other species have simply been slower to respond. However, Schiel et al. (2004) warn that the theory that warm water species will replace colder water species as temperatures rise does not always hold true. In their study of elevated sea temperatures caused by thermal discharge of a power plant, communities were altered as key habitat-providing kelp species declined with higher temperatures, and other species abundances increased. The community changes did not correspond with a shift toward warmer water species, and was not adequately explained by ecological interactions, highlighting our limited understanding of complex ecosystems' responses to change (Schiel et al. 2004).

### ***Sea level rise***

The predicted effects of rising sea levels include a reduction in some areas of intertidal habitat due to steep coastline topography and the proliferation of anthropogenic structures such as seawalls and groynes (Galbraith et al. 2002). Projected rates of sea level rise may also outstrip the rate at which biogenic habitats such as marshes, seagrass beds, and coral reefs are capable of shifting or accreting (Knowlton 2001). Due to the dependency of these systems on sunlight, they may drown as sea levels rise above them and the overlying waters attenuate more sunlight. The death and decay of these habitat-forming species complexes would have dramatic effects on the diverse species that live primarily or exclusively in association with them; coral reef-associated species may number between 1-9 million (Knowlton 2001).

***Changes in ocean circulation patterns***

Increased mean wind speeds and increased frequency of extreme wind events will have strong impacts on shallow subtidal and intertidal communities (Harley et al. 2006). This may exacerbate the pressures on biogenic habitats such as marshes, seagrass beds, and coral reefs mentioned above, as well as kelp forest ecosystems, all of which can be damaged by wind-driven storm waves. These multispecies complexes perform a range of functions related to biodiversity and production - they provide habitat and refuge, act as nurseries for young fish, and retain larvae and detritus (Boesch and Turner 1984; Carr 1989; Pakhomov 2001). Increased intensity and frequency of wind and waves could reduce the recovery of damaged coastal ecosystems between disturbance events and also result in a shift in dominant species towards those that are faster growing or more resistant to damage (Harley et al. 2006).

Marine ecosystems are often dominated by organisms with planktonic life history stages, which make the composition of those ecosystems sensitive to oceanographic patterns that disperse and concentrate larvae (Harley et al. 2006; Day and Roff 2000). Those same patterns also play a role in concentrating, enriching, and retaining nutrients in different areas, which has implications for the production, species composition, and species diversity at a given site as well as the distribution and abundance of species among sites (Bakun 1996). Gaylord and Gaines (2000) observe that clusters of range boundaries of coastal marine species occur where ocean currents meet and suggest that the flow patterns of the currents themselves (in addition to the current's water properties) may play a role in determining species distribution patterns. Thus, currents can constrain species distributions even when suitable habitats exist elsewhere (Gaylord and Gaines 2000). If circulation changes shift current patterns, species distributions could also shift- due to distribution into previously 'out of reach' but suitable habitats, or because of the species associated with the water conditions particular to a given current. Conversely, if water temperatures rise beyond a species' tolerances, but they are not dispersed to more suitable habitats by currents or advection patterns, local extinctions may occur. Changing current and circulation patterns may also serve to facilitate the spread of invasive species (Harley et al. 2006).

***CO<sub>2</sub> concentrations and pH change***

Unlike terrestrial systems, increasing CO<sub>2</sub> concentrations will not increase production through increased photosynthesis because most marine primary producers are carbon saturated (Harley et al. 2006). However the acidification of the oceans due to increased CO<sub>2</sub> uptake and associated decrease in the availability of CaCO<sub>3</sub>-forming minerals will limit the rate of biogenic calcification- the rate at which calcifying organisms form their skeletal structures (Feely et al. 2004). These include primary producers, coccolithophorid zooplankters, corals, coralline algae, crustaceans,

and molluscs (Harley et al. 2006). The population and community-level impacts of potential CO<sub>2</sub> changes are largely unknown (Harley et al. 2006). However, the possibility that coral reefs at the northern and southern edges of the global coral range could lead to a shift (rather than a shrink) in coral's distribution- as sea temperatures outside their current range warm and become favourable- may be hampered by the comparatively larger impacts of increased CO<sub>2</sub> concentrations on waters at higher latitudes (Kleypas et al. 1999). These increased CO<sub>2</sub> concentrations mean less availability of the CaCO<sub>3</sub>-forming minerals essential for the growth of reef-building corals.

### ***Emergent effects***

Harley et al. (2006) identify four fundamental groups of emergent effects of climate change on marine biota and biological processes, all of which are interconnected: shifts in species distributions; changes in species composition, diversity, and community structure; changes in primary and secondary production; and changes in population dynamics and evolution.

Shifts in species distributions may be vertical or biogeographical. Species distributions in intertidal and nearshore benthic habitats are strongly vertically stratified, and changes in temperature or light conditions with rising water levels may cause some species to shift into the vertical zones of other species (Harley et al. 2006). These shifts may cause competitive exclusion of certain species if they are, for example, caught between competitive stress from below and temperature or exposure-induced stress from above (Mathieson et al. 1998; Harley et al. 2006). Biogeographical shifts can occur in a number of ways. Some species exhibit behavioural thermoregulation, actively seeking temperatures that are within their optimal range, though these preferences may be tempered by other environmental factors such as food availability (Roessig et al. 2004). Community level interactions between species may change at range boundaries, also shifting species distributions as a result of synergistic effects of multiple stress factors. For example, warmer waters are generally more conducive to the spread of pathogens (Harvell et al. 2002). For species at the warmer boundary of their range, the compounding stresses of rising water temperatures and the incursion of pathogens may suffice to decimate the local population. These changes also highlight a way in which community composition may change. Schiel et al. (2004) documented significant changes in the diversity and composition of nearshore communities in response to higher temperatures. Species respond to environmental changes individually at their own speed and direction, and thus, biological communities do not necessarily move as units. Communities may disassemble, with new ones reforming (Lovejoy 2006).

Current and circulation patterns play a key role in shaping primary production. Changes in these patterns will alter the locations of fronts, where production is high, and the intensity of upwelling at shelf and coastal locations, which bring cold, nutrient-rich water to the surface and drive

productivity. An increased frequency of El Niño events, which discourage upwelling, would have significant negative impacts on anchovy production on the South American coast. The anchovy, which is the target of one of the largest-volume fisheries in the world, is associated with the colder, nutrient rich upwelling regimes off the South American coast (Alheit and Niquen 2004). Climate change may also cause shifts in the timing of seasonal stratification of seawater, with warming potentially causing stratification earlier in the spring and mixing later in the fall. This in turn may mean that different organisms whose life cycles correspond (or adapt more quickly) with the altered timing of highest productivity become more dominant (Soto 2001). Organisms with faster generation times are expected to have quicker responses to climatic changes (Berteaux et al. 2004). Changing currents and circulation patterns will also have implications for the dispersal of genes among populations, with potential impacts on the genetic diversity of species and their abilities to adapt to changes in their environments (Harley et al. 2006).

## **The role for marine protected areas**

The rationality of MPAs as a long-term conservation measure in the face of climate change will depend on the purpose that governing agencies and societies define for them. When their purpose is clearly outlined, their efficacy in achieving that purpose amid changing environmental conditions can be meaningfully examined. MPAs have a range of potential functions that include conserving biodiversity, facilitating tourism, protecting habitats, providing refuge for fished species, enhancing production of target species, providing a management framework for sustainable multiple use, acting as sites of scientific research, and demonstrating the extent of human impacts on marine ecosystems (Allison et al. 1998). The term MPA also covers an array of spatially explicit management measures that vary in their degree of protection. Thus, the concept of an MPA is somewhat malleable, and their goals and purposes have often been unclear (Agardy et al. 2003; Willis 2003). Further, priorities have often remained unstated for the many MPAs that have multiple objectives. Limited resources usually preclude detailed attention to all of them, some objectives may compete (e.g., biodiversity conservation and target species enhancement), or climate change may force choices about what to protect.

Some of the MPA functions outlined are less directly focused on biological objectives and serve a more managerial or educational role. Climate change may have less direct implications for the efficacy of MPAs that make these functions their primary objectives. However, the majority of MPAs state biodiversity conservation and/or sustainable fisheries management objectives among their priorities (Ray 2004). For these reasons, I focus on MPAs whose primary objectives are biological in nature, and I accept that the conservation of resources and biodiversity is a broadly agreed-upon, desirable objective.

The preceding summary of potential effects of climate change on oceans makes it clear that any given portion of the world's oceans is likely to experience numerous types of change in the future. As protective measures particular to portions of the ocean, the content of what MPAs "protect" is therefore also likely to change, potentially in ways that are deemed undesirable- hence the rationale for this examination of their capacity as conservation tools. Despite these possibilities and the inability of MPAs to protect against these boundary-less threats, they remain a useful and important long-term conservation tool because (1) they provide unique protection for marine ecosystems that may serve to increase the resilience of those ecosystems to perturbations caused by climate change, (2) they can function as control sites that can help discern causal agents of future change (Soto 2001), and (3) the creation of marine protected areas can raise the profile of marine ecosystems (Cocklin et al. 1998).

MPAs are just one of many marine conservation strategies that address the variety of human stressors on oceans. Other strategies include pollution prevention initiatives, coastal development restrictions, harvest bans on certain species, and restrictions on fishing gear, effort, and season, all of which have been used around the world, in some cases for decades or centuries. MPAs are effective in controlling different kinds of local impacts, though the focus has been on their potential to serve as refugia from fishing pressure, and several authors have indicated that this is where their greatest conservation value lies (Roberts and Polunin 1993; Allison et al. 1998; Agardy 2000). Their potential in this regard is important in light of the strong evidence that fishing constitutes the greatest current threat to marine ecosystems (Pauly et al. 1998; Jackson et al. 2001; Myers and Worm 2003; Pandolfi et al. 2003; Crowder and Norse 2005). If mitigating fishing pressure is where MPAs are most effective, and fishing is the most important current human impact on the world's oceans, it is appropriate to focus on the long-term capacity of MPAs with respect to these factors. Critically assessing whether or not MPAs are a useful long-term conservation tool should also entail weighing their capabilities against other conservation options, again with a focus on these factors.

MPAs are unique in that they can offer permanent spatial protection that prohibits some or all human activities. This preserves the abundance, species richness, species age structures, and habitats of communities to an extent that other measures do not. Put differently, the natural variability, or biodiversity, of the community at the site is more comprehensively protected. Though measures such as fishing effort limitations or gear restrictions may reduce and minimise effects on communities, fishing still selects for species and size, generally first taking bigger, older individuals thereby altering age structures and reducing the system biodiversity (Hilborn and Walters 1995). Decreasing diversity within a system can lead to less resilience. Resilience is a term defined in

several ways, but thought of here as a measure of a system's creative ability to sustain itself- to absorb perturbations and maintain function (Holling 1986). Although a full discussion of the concept and empirical support for resilience is beyond the scope of this paper, key functions of resilience and its relationship to biodiversity as they pertain to MPAs and climate change are included here. The relationship between biodiversity and resilience stems from the ecological functions that species perform. Each species is capable of performing a limited number of ecological functions, and as species are added to an ecosystem, more ecological functions accumulate, generating functional diversity (Peterson et al. 1998). With continued species additions, species functions may begin to overlap, creating functional redundancy which can increase ecological stability; the ecosystem develops the capacity to sustain disturbances to some species without a total loss or impairment of ecosystem functioning (Peterson et al. 1998). Although there are different theoretical models for the relationships between biodiversity and ecological stability (e.g., rivet, idiosyncratic, keystone), these underlying principles are similar. Diverse systems may also be faster to re-establish ecological functions when they *are* impaired or lost.

Rigorous experimental testing of the relationship between biodiversity and resilience *in situ* is challenging, perhaps most so for large, pelagic systems with few spatially stationary elements. Testing would require similar ecosystems with varying levels of biodiversity, the measured application of disturbances, and the monitoring of system responses, all the while controlling for the myriad other factors affecting ecosystems, and preferably at the large scales that interests society (Raffaelli 2006). However, there is other evidence that suggests altering the natural variability of marine ecosystems impairs the structure and function of those systems, that the losses of functions can have negative impacts on ecosystem goods and services of interest to humans, and that more diverse systems with all functional groups present recover faster from disturbance, including thermal disturbance (Bythell et al. 2000; McClanahan 2000; Allison et al. 2004; Dulvy et al. 2004; Worm et al. 2006). A well-known marine example derives from Caribbean coral reefs, where overfishing of herbivorous fishes lead to a population explosion in another herbivore, the black-spined sea urchin. Herbivory, which keeps algal growth on corals in check, continued. However, diversity and functional redundancy in the ecosystem had been reduced. When a pathogen killed over 90% of the sea urchins throughout the Caribbean, the ecological function of herbivory was drastically impaired, enabling a shift in the ecosystem away from a coral reef-dominated state to an ecosystem dominated by macroalgae which supports less fish (Grimsditch and Salm 2006). Thus, the loss of diversity reduced the resiliency of the coral reef ecosystem and left it less able to sustain function in the face of subsequent disturbance, which resulted in a shift away from that ecosystem type.

What role do MPAs play with respect to climate change, biodiversity, and resilience? While functional redundancy within marine ecosystems appears to vary naturally, fully protected MPAs have been found to host higher species diversity and higher levels of functional diversity than surrounding areas (Clark and Warwick 1998; Micheli and Halpern 2005). Though MPAs do not prevent the spread of warmer waters resulting from climate change, they can play a role in reducing the number of other stressors present in a marine environment. MPAs can thus facilitate the maintenance of higher degrees of ecosystem resilience in those locations, putting those ecosystems in a better position to absorb climatic perturbations. A role for them in this respect is clear in the following climate-related example outlined by Hughes et al. (2003): anthropogenic impacts on coral reefs including overfishing of herbivorous fishes, excess nutrient inputs, persistent physical disturbance that increases coral mortality, and increased levels of disease all impair the ability of corals to recover from acute disturbance events such as coral bleaching that result from high water temperatures. Water temperatures at the extremes of coral tolerances are expected to become more common as atmospheric and sea temperatures rise with global warming. Reducing the magnitude of other human impacts promotes higher levels of reef resilience to climate change-related disturbances.

There are several signs that the relationship between climate change and fishing is key for marine ecosystem health. Fishing and climate change may act synergistically to reduce fish populations to such a small population size that they cannot recover (Scavia et al. 2002). Climate or fishing accounted for the primary forcing mechanism in 27 of the 29 Large Marine Ecosystems assessed for forces driving change in biomass yields (Sherman 2006). Based on a review of the effects of climate and additional stressors on marine environments, Harley et al. (2006) suggest that marine ecological responses to climate change will depend primarily on fishing pressure. These indicators underscore the role for MPAs given their capacities to act as fishing refugia.

Soto (2001) suggests that MPAs may also have an important role to play as control sites that can help to separate out causal factors like coastal development or fishing from the effects of climate change on marine ecosystems, thus facilitating scientific understanding of the effects of climate change on marine environments. This purpose may blend well with the functions that MPAs can serve as sites of scientific research. Additionally, the creation of MPAs has heightened interest in marine ecosystems, leading to increased tourist visits in areas and sentiments among adjacent communities that local MPAs have raised environmental awareness (Dixon et al. 1993; Cocklin et al. 1998). Insofar as this interest and awareness facilitates an understanding of the links between marine ecosystem health and global climate change, the existence and proliferation of MPAs may have the potential to contribute to a societal willingness for behavioural changes that reduce greenhouse gas emissions.

## Effective marine protected areas for the future

The preceding section demonstrates that MPAs can be useful long term conservation measures. However, the evidence provided does not *mitigate* the challenges that climate change poses to the efficacy of MPAs; it primarily demonstrates how they can be useful *in spite of* climate change. This section will explore how MPA planning and management can be approached in order to better prepare and cope with climate changes- that is, how climate change challenges for MPAs can be mitigated. I outline three related tenets that can function as central guiding themes for MPA planning and management. The first two, uncertainty and the precautionary approach, detail an appropriate 'mindset' for approaching MPA choices, and the third, adaptive management, provides a model for the management of MPAs through time as conditions change. The section closes with a series of specific recommendations about how MPA planning and management can be changed for increased long-term efficacy in achieving biodiversity conservation. Recommendations are aimed primarily at national and state government agencies responsible for conservation or resource management, though other MPA practitioners will also find them applicable. These levels of government are most commonly those with the jurisdiction, the mandate, and the capacity to implement MPAs.

The complexity of the atmospheric, oceanographic, and ecological systems relevant to MPAs prevents our ability to understand them perfectly and predict their future states with certainty. There is also uncertainty in our understanding of what human activities are conducted in marine environments systems and how they affect marine systems (Lauck et al. 2004). Uncertainty is particularly prevalent in managing and conserving marine systems because of several characteristics mentioned earlier: marine communities are not directly observable; data collection is difficult, expensive, and therefore sparse; and most species' life histories involve a larval stage that is prone to variable dispersal over potentially large distances (Botsford and Parma 2005). Chaos theory suggests that this unpredictability is an inherent property of complex systems, and that pursuing more detailed understanding of these systems cannot resolve this (Hilborn et al. 1995). The enormous number of interacting components in these systems and the feedback mechanisms between them mean that even slight errors or imprecisions in our calculations of their initial conditions can quickly compound and lead to very different futures than those anticipated (Cartwright 1991). The uncertainty that pervades all of our knowledge regarding these natural systems, and the decisions we make with respect to them poses a major challenge to MPA planning and management. It makes clear that we cannot assume that, with enough information, we can anticipate what will happen and determine how to act to promote or discourage projected changes, such as those stemming from climate change (Cartwright 1991). Instead, uncertainty must be explicitly acknowledged and taken into account during scientific analyses and

management decisions (FAO 1995). Predictions can be developed as a range of probabilistic outcomes based on repeated iterations of models. Cartwright (1991) recommends that even the model's initial conditions should be varied, as we cannot assume that we have perfect knowledge of the present state. Planning can then explore plans for dealing with different futures, and dealing with the unexpected.

There are three standard responses to the risks posed by uncertainties (Peterman 2004). First, we may make optimistic assumptions about the impacts of human activities on marine ecosystems and act aggressively, harvesting or polluting with little concern for conservation. Second, we may suggest that our incapability of fully understanding our impacts on the ecosystem means that we should do nothing- frequently used as an argument for maintaining the status quo. Third, we can make a more pessimistic assumption about human impacts on the ecosystem and act cautiously, building in buffers that allow for our assessment of the system state and prediction of its response to disturbance to be wrong to some degree. Given the importance of marine ecosystem goods and services, and our poor record of marine conservation to date, a precautionary approach is a sensible response to the risk that uncertainty poses. The implementation of MPAs can be understood as a precautionary measure, or hedge, against the risks of uncertainty (Lauck et al. 2004). But further, a precautionary approach suggests that the design of the MPAs themselves also incorporate precaution, such that a buffer is built in to better ensure that they achieve conservation objectives.

The last tenet that should guide MPA planning is adaptive management, a management model which acknowledges uncertainty and 'learns by doing' (Ludwig et al. 1993). There is an explicit role for monitoring and making adjustments based on results of previous decisions, and future modifications to the management approach are anticipated (Botsford and Parma 2005). This is in contrast to other management approaches which do not systematically question the knowledge of the marine system upon which decisions are based, nor consciously approach decisions as iterative experiments (Parma 1998). Adaptive management is well suited for situations where learning by observing past instances of similar problems is not possible because problems are new, as is the case with climate change (Hilborn et al. 1995). The uncertainty of (1) how global climate will change, (2) how this will affect marine systems, and (3) what this means for MPAs, combined with the certainty that change *will* occur, demands that planning and management of MPAs 'plan for surprise' and adapt if they are to remain effective amid changing environmental conditions (Holling 1986). Though adaptive management has drawbacks such as the difficulty of detecting ecosystem change and the political risks of constant management alterations, it is the management model best suited for planning for surprise and adjusting to the ecological changes caused by climate change (Suffling and Scott 2002).

Parks Canada's review (Suffling and Scott 2002) of the implications of climate change for national parks is reflective of the rationale outlined here. In a review of policy directions for protected areas in the face of climate change, Parks Canada identified four options:

- 1) *static management*: manage and protect current ecological communities within current parks, using current goals.
- 2) *passive management*: accept ecological responses to climate change and allow processes to take place unhindered.
- 3) *adaptive management*: maximise the capacity of species and ecological communities to adapt to climate change through active management interventions.
- 4) *hybrid*: some combination of the above options.

Options one and two were ruled out as (1) unfeasible given the probability of change and (2) unpalatable given the likely opposition to the loss of symbolic species or places, respectively. The authors recommended pursuing adaptive management as the best means of achieving the goal of preserving ecological integrity. Kay and Schneider (1992) define ecological integrity as “the ability of an ecosystem to self-organise over a broad range of organisational levels and spatial-temporal scales”. This concept of ecological integrity is closely related to that of resilience- a key reason for the use of MPAs and a property of marine ecosystems that MPAs should attempt to maintain. This paper supports Suffling and Scott's (2002) suggestion that adaptive management is the most appropriate approach for managing MPAs to ensure that the resilience of protected ecosystems is maintained.

## **Recommendations**

In light of the likely effects of climatic change on marine ecosystems, nine recommendations are outlined here that operationalise the guiding themes for planning and management detailed above:

- 1) Create more, sufficiently large MPAs to hedge against stochastic events, management errors, and human impacts (Soto 2001). Fewer, larger MPAs are generally preferable to many smaller MPAs, and in the absence of specific factors suggesting the contrary, this is an appropriate guideline to follow (Frid et al. 2006). Criteria for determining sufficient size have yet to be defined in MPA design theory, but will vary according to the targets of protection and ecosystem attributes. One model developed for the Gulf of California calculated that reserves needed to be at least 50 km<sup>2</sup> in order to retain significant proportions of fish and algal larvae (Sala et al. 2002).

- 2) Build insurance factors into the design of MPAs so that there is more of each desirable ecosystem feature than deemed necessary under current conditions- this is especially applicable for quantifiable features (e.g., the total area of x habitat desired within the park) (Allison et al. 2003). Replicate the protection of conservation targets where feasible to diversify and mitigate risk (Salm et al. 2005). Consider sites that may be less affected by certain effects of climate change such as increased storm frequency.
- 3) Integrate planning and management of MPAs within a broader coastal zone management framework (Cicin-Sain and Belfiore 2005). This may help in planning for and limiting the boundary-less stressors that affect MPAs from surrounding waters.
- 4) Consider how MPAs may be networked for functional linkages when planning, and coordinate MPA planning between different agencies to facilitate this. Functionally linked networks across latitudes could allow for species distributions to shift and remain partially protected. Connectivity in this respect is more difficult to define for MPAs than terrestrial protected areas. Dispersal patterns of larvae are an important link between MPAs that can replenish disparate populations, and are essential to consider in network design (Botsford and Parma 2005). Thus, hydrography, distance between sites, and 'downstream' or 'upstream' dispersal dynamics with respect to other reserves and management areas may be critical (Frid et al. 2006). Conversely, while MPAs should be close enough to be functionally linked, planners should also consider adequate spacing to reduce the risk that one catastrophe might impact multiple MPAs (Roberts et al. 2003). This may be particularly relevant given predictions of increased frequencies of extreme events.
- 5) Plan for representativeness of 'enduring features' that play roles in shaping community types in MPA networks. This may be a more effective strategy for maintaining representativeness of future biological communities than planning based solely on the current distribution of biotic communities, which is likely to change (Day and Roff 2000).
- 6) Recognise that the implementation of MPA networks is a long-term, sequential process. This acknowledges the uncertainty surrounding future MPA opportunities with respect to (1) where and when conservation opportunities will arise, (2) budgets for conservation initiatives, and (3) the degradation, loss, or shift of conservation values (e.g., biodiversity) at different sites due to effects of different stressors, including climate change, over intervening periods (Meir et al. 2004). This is a more adaptive approach that fosters a move away from a static blueprint for an optimal MPA network based on a snapshot in time, and enables the design of each component

of a MPA network to reflect any situational changes and enhanced understandings that have evolved since previous choices.

- 7) Identify communities that have demonstrated resilience to past warming events. This is particularly relevant for coral reef MPAs, where reef responses to recent extreme temperature events have demonstrated variable resistance to and recovery from coral bleaching (Salm et al. 2005).
- 8) Consider flexible MPA boundaries, especially for MPAs zoned for multi-use, where highly protected core areas could be expanded without requiring more potentially politically difficult changes to the total area of the MPA (Peters and Darling 1985).
- 9) Make planning incremental as chaotic systems can be better understood at the local, incremental level (Cartwright 1991). This approach is closely linked to the iterative focus of recommendation 6.

## Conclusions

Myriad challenges exist for understanding the effects of climate change on oceans and planning for, or evaluating the value of, MPAs accordingly. Humans are attempting to understand how systems change in response to environmental conditions for which there is no real analogue (Harley et al. 2006). There is also the potential for non-linear, non-independent, unpredictable, and dramatic changes- properties characteristic of complex systems such as atmospheric, oceanographic, and ecological systems (Southwick 1976; Schneider and Kay 1992). Climate-related examples of these changes already exist for marine biota's responses to environmental change (Reynaud et al. 2003; Hsieh et al. 2005). Even where the causes of certain changes can be determined, removing or mitigating the cause will not necessarily return the system to its former state, as changes are not always reversible (Knowlton 2001). Changes may also favour some life history strategies over others, such as generalist or opportunist species that are readily able to adjust their diets and habitats, which may make these species less in need of conservation attention than others (Harley et al. 2006).

MPAs are one component of a marine conservation strategy that will need to include many other measures in order to adequately conserve marine ecosystems. Managers and planners will need to think strategically about MPA conservation priorities and adaptively direct effort where it is feasible and can make the largest or most essential differences to the conservation values that society has deemed most important. They will also have to think carefully about what the different uses of

MPAs mean when taken together; if MPAs are valued as control sites to determine causes of ecological change, what does this mean for an adaptive management approach that will adjust management to promote resilience and ecological integrity? Can MPAs still be thought of as benchmarks in this case? Given the intensive information and management requirements of adaptive management, are fewer MPAs that are better monitored a preferable strategy to many MPAs with less monitoring? Thompson et al. (2002) also point out that other stressors should not be overlooked, as those with the most potential to further degrade some marine environments in the foreseeable future are already familiar to us: pollution, coastal development, fishing practices, introduced species, and others.

## Literature Cited

Agardy, T. 2000. Information needs for marine protected areas: Scientific and societal. *Bulletin of Marine Science* **66** (3): 875-888.

Agardy, T., P. Bridgewater, M. P. Crosby, J. Day, P. K. Dayton, R. Kenchington, D. Laffoley, P. McConney, P. A. Murray, J. E. Parks, and L. Peau. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation-Marine and Freshwater Ecosystems* **13** (4): 353-367.

Alheit, J., and M. Niquen. 2004. Regime shifts in the Humboldt current ecosystem. *Progress in Oceanography* **60** (2-4): 201-222.

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs* **74** (1): 117-134.

Allison, G. W., S. D. Gaines, J. Lubchenco, and H. P. Possingham. 2003. Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecological Applications* **13** (1): S8-S24.

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8** (1): S79-S92.

Bakun, A. 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, San Diego.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* **247**(4939): 198-201.

Berteaux, D., D. Reale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change: Can arctic life count on evolution? *Integrative and Comparative Biology* **44** (2): 140-151.

Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes—the role of food and refuge. *Estuaries* **7** (4A): 460-468.

Bohnsack, J. A. 1993. Marine reserves—they enhance fisheries, reduce conflicts, and protect resources. *Oceanus* **36** (3): 63-71.

Botsford, L. W., and A. M. Parma. 2005. Uncertainty in Marine Management. Pages 375-392 in E. A. Norse and L. B. Crowder, editors. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, DC.

Bythell, J. C., Z. M. Hillis-Starr, and C. S. Rogers. 2000. Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology-Progress Series* **204**: 93-100.

Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* **126** (1): 59-76.

- Cartwright, T. J. 1991. Planning and chaos theory. *Journal of the American Planning Association* **57** (1): 43-55.
- Cicin-Sain, B., and S. Belfiore. 2005. Linking marine protected areas to integrated coastal and ocean management: A review of theory and practice. *Ocean & Coastal Management* **48** (11-12): 847-868.
- Clarke, K. R., and R. M. Warwick. 1998. Quantifying structural redundancy in ecological communities. *Oecologia* **113** (2): 278-289.
- Cocklin, C., M. Craw, and I. McAuley. 1998. Marine reserves in New Zealand: Use rights, public attitudes, and social impacts. *Coastal Management* **26** (3): 213-231.
- Costanza, R., R. d'Arge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387** (6630): 253-260.
- Crowder, L. B., and E. A. Norse. 2005. The Greatest Threat: Fisheries. Pages 183-184 in E. A. Norse and L. B. Crowder, editors. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, DC.
- Day, J. C., and J. C. Roff. 2000. *Planning for Representative Marine Protected Areas: A Framework for Canada's Oceans*. World Wildlife Fund Canada, Toronto.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation-Marine and Freshwater Ecosystems* **5** (3): 205-232.
- Dixon, J. A., L. F. Scura, and T. Vanthof. 1993. Meeting ecological and economic goals - marine parks in the Caribbean. *Ambio* **22** (2-3): 117-125.
- Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**(5): 410-416.
- FAO (Food and Agricultural Organization of the United Nations). 1995. Precautionary approach to fisheries. Part 1. Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fisheries Technical Paper No. 350/1. FAO, Rome.
- Frid, C. L. J., O. A. L. Paramor, and C. L. Scott. 2006. Ecosystem-based management of fisheries: Is science limiting? *ICES Journal of Marine Science* **63** (9): 1567-1572.
- Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page. 2002. Global climate change and sea level rise: Potential losses of intertidal habitat for shorebirds. *Waterbirds* **25** (2): 173-183.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* **155** (6): 769-789.
- Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: The fishery effects of marine reserves. *Trends in Ecology & Evolution* **18** (9): 448-455.
- Grimsditch, G. D., and R. V. Salm. 2006. *Coral Reef Resilience and Resistance to Bleaching*. IUCN, Gland.

- Guenette, S., and T. J. Pitcher. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fisheries Research* **39** (3): 295-303.
- Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* **13** (1): S117-S137.
- Halpin, P. N. 1997. Global climate change and natural-area protection: Management responses and research directions. *Ecological Applications* **7** (3): 828-843.
- Hansen, B., S. Osterhus, D. Quadfasel, and W. Turrell. 2004. Already the day after tomorrow? *Science* **305** (5686): 953-954.
- Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* **9** (2): 228-241.
- Hilborn, R., and C. J. Walters. 1995. *Quantitative Fisheries Stock Assessment*. Chapman and Hall, New York.
- Hilborn, R., C. J. Walters, and D. Ludwig. 1995. Sustainable exploitation of renewable resources. *Annual Review of Ecology and Systematics* **26** : 45-67.
- Holling, C. S. 1986. The resilience of terrestrial ecosystems: Local surprise and global change. in Clark and Munn, editors. *Sustainable Development of the Ecosphere*. Cambridge University Press, Cambridge.
- Hsieh, C. H., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the north Pacific Ocean. *Nature* **435** (7040): 336-340.
- Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301** (5635): 929-933.
- Intergovernmental Panel on Climate Change (IPCC). 2001. *Climate Change 2001: Synthesis Report*. IPCC, Geneva.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293** (5530): 629-638.
- Kay, J., and E. Schneider. 1992. Thermodynamics and Measures of Ecological Integrity. in D. McKenzie and V. McDonald, editors. *Ecological Indicators*. Elsevier Applied Science, New York.
- Kelleher, G. 1999. *Guidelines for Marine Protected Areas*. IUCN, Gland, Switzerland and Cambridge, UK.
- Kleypas, J. A., R. W. Buddemeier, D. Archer, J. P. Gattuso, C. Langdon, and B. N. Opdyke. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284** (5411): 118-120.

- Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* **98** (10): 5419-5425.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. *Implementing the precautionary principle in fisheries management through marine reserves*. *Ecological Applications* **8** (1): S72-S78.
- Lipcius, R. N., L. B. Crowder, and L. E. Morgan. 2005. Metapopulation Structure and Marine Reserves. Pages 328-346 in E. A. Norse and L. B. Crowder, editors. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, DC.
- Lovejoy, T. E. 2006. Protected areas: A prism for a changing world. *Trends in Ecology & Evolution* **21** (6): 329-333.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* **13** (1): S3-S7.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation - lessons from history. *Science* **260** (5104): 17-20.
- Mathieson, A. C., C. J. Dawes, and E. J. Hehre. 1998. Floristic and zonation studies of seaweeds from Mount Desert Island, Maine: An historical comparison. *Rhodora* **100** (904): 333-379.
- McClanahan, T. R. 2000. Recovery of a coral reef keystone predator, *Balistapus undulatus*, in east African marine parks. *Biological Conservation* **94** (2): 191-198.
- Meir, E., S. Andelman, and H. P. Possingham. 2004. Does conservation planning matter in a dynamic and uncertain world? *Ecology Letters* **7** (8): 615-622.
- Micheli, F., and B. S. Halpern. 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* **8** (4): 391-400.
- Murawski, S. A., R. Brown, H. L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large-scale closed areas as a fishery management tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science* **66** (3): 775-798.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A. McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: Sustaining fishery populations and marine ecosystems. *Fisheries* **24** (11): 11-25.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423** (6937): 280-283.
- Norse, E. A., and L. B. Crowder. 2005. Why Marine Conservation Biology? Pages 1-19 in E. A. Norse and L. B. Crowder, editors. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, DC.
- Pakhomov, E. A., S. Kaehler, and C. D. McQuaid. 2002. Zooplankton community structure in the kelp beds of the sub-antarctic Prince Edward archipelago: Are they a refuge for larval stages? *Polar Biology* **25** (10): 778-788.

- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301** (5635): 955-958.
- Parma, A., and NCEAS Working Group on Population Management. 1998. What can adaptive management do for our fish, forests, food, and biodiversity? *Integrative Biology* **1** (1): 16-26.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421** (6918): 37-42.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* **279** (5352): 860-863.
- Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* **418** (6898): 689-695.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* **308** (5730): 1912-1915.
- Peterman, R. M. 2004. An overview of the precautionary approach in fisheries and some suggested extensions. Pages 233-240 in P. Gallagher and L. Wood, editors. *Proceedings of the World Summit on Salmon*, June 2003. Vancouver, BC.
- Peters, R. L., and J. D. S. Darling. 1985. The greenhouse-effect and nature reserves. *Bioscience* **35** (11): 707-717.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* **1** (1): 6-18.
- Philippart, C. J. M., H. M. van Aken, J. J. Beukema, O. G. Bos, G. C. Cadee, and R. Dekker. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography* **48** (6): 2171-2185.
- Raffaelli, D. G. 2006. Biodiversity and ecosystem functioning: Issues of scale and trophic complexity. *Marine Ecology-Progress Series* **311**: 285-294.
- Rahmstorf, S. 2002. Ocean circulation and climate during the past 120,000 years. *Nature* **419** (6903): 207-214.
- Ray, G. C. 2004. Reconsidering 'dangerous targets' for marine protected areas. *Aquatic Conservation-Marine and Freshwater Ecosystems* **14** (2): 211-215.
- Reynaud, S., N. Leclercq, S. Romaine-Lioud, C. Ferrier-Pages, J. Jaubert, and J. P. Gattuso. 2003. Interacting effects of CO<sub>2</sub> partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biology* **9** (11): 1660-1668.
- Roberts, C. M. 2000. Selecting marine reserve locations: Optimality versus opportunism. *Bulletin of Marine Science* **66** (3): 581-592.
- Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* **13** (1): S199-S214.

- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. *Science* **294** (5548): 1920-1923.
- Roberts, C. M., and N. V. C. Polunin. 1993. Marine reserves - simple solutions to managing complex fisheries. *Ambio* **22** (6): 363-368.
- Roemmich, D., and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the california current. *Science* **267** (5202): 1324-1326.
- Roessig, J. M., C. M. Woodley, J. J. Cech, and L. J. Hansen. 2004. Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* **14** (2): 251-275.
- Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? evidence from Apo Island, central Philippines. *Marine Ecology-Progress Series* **132** (1-3): 1-9.
- Russ, G. R., and A. C. Alcala. 1996. Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* **6** (3): 947-961.
- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. *Science* **298** (5600): 1991-1993.
- Salm, R. V., A. Green, L. Z. Hale, P. Kramer, E. McLeod, G. Miles, A. Smith, S. E. Smith, and S. Wear. 2005. *Building Resilience into MPAs: Impact from Sites to Global Policies*. IMPA Congress, Geelong, Au.
- Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, V. Burkett, D. R. Cayan, M. Fogarty, M. A. Harwell, R. W. Howarth, C. Mason, D. J. Reed, T. C. Royer, A. H. Sallenger, and J. G. Titus. 2002. Climate change impacts on US coastal and marine ecosystems. *Estuaries* **25** (2): 149-164.
- Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* **85** (7): 1833-1839.
- Schneider, E. D., and J. J. Kay. 1992. Life as a manifestation of the second law of thermodynamics. Preprint from: *Advances in Mathematics and Computers in Medicine*.
- Sherman, K. 2006. The Large Marine Ecosystem network approach to WSSD targets. *Ocean & Coastal Management* **49** (9-10): 640-648.
- Snyder, M. A., L. C. Sloan, N. S. Diffenbaugh, and J. L. Bell. 2003. Future climate change and upwelling in the california current. *Geophysical Research Letters* **30** (15): 1823.
- Soto, C. G. 2001. The potential impacts of global climate change on marine protected areas. *Reviews in Fish Biology and Fisheries* **11** (3): 181-195.
- Southwick, C. H. 1976. Principles of the Ecosystem. in C. H. Southwick, editor. *Ecology and the Quality of our Environment*. 2nd edition. Van Nostrand, New York.
- Suffling, R., and D. Scott. 2002. Assessment of climate change effects on Canada's national park system. *Environmental Monitoring and Assessment* **74** (2): 117-139.

- Thompson, R. C., T. P. Crowe, and S. J. Hawkins. 2002. Rocky intertidal communities: Past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* **29** (2): 168-191.
- Timmermann, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Nino frequency in a climate model forced by future greenhouse warming. *Nature* **398** (6729): 694-697.
- Vellinga, M., and R. A. Wood. 2002. Global climatic impacts of a collapse of the atlantic thermohaline circulation. *Climatic Change* **54** (3): 251-267.
- Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: Putting descartes before des horse? *Environmental Conservation* **30** (2): 97-103.
- Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* **314** (5800): 787-790.