

BUYING TIME:

A User's Manual for Building Resistance and Resilience to Climate Change in Natural Systems



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Designing Reserves to Sustain Temperate Marine Ecosystems in the Face of Global Climate Change

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TEMPERATE MARINE ECOSYSTEMS include a wide array of habitats: estuaries, marshes, seagrass and kelp beds, rocky coastlines, sandy, muddy, and cobble shores, the deep sea and the open ocean. To cover the details of conservation and climate change in each habitat type would turn this chapter into a lengthy book. Instead, I will highlight those aspects of the marine realm in general that set it apart from terrestrial ecosystems and discuss their implications for both reserve design and responses to climate change. Because of their relative accessibility, coastal habitats have received the most attention from marine conservation biologists and the public alike, and information presented in this chapter reflects this bias. Still, we should remember that we are only just beginning to understand the rich diversity of life in the deep and open seas, and the ways in which apparently distinct marine ecosystems interact with each other. While designing conservation strategies with only partial information about the ecosystems in questions is difficult, we ignore unfamiliar habitats in our conservation planning at our peril.

Temperate seas are rich in life, and have played a central role in human history. Both coastal and open seas are critical sources of food for humans, and traditionally supplied other resources as well. People turn to oceans and coasts for recreation, employment, and spiritual fulfillment. Population, development, and economic activity are often concentrated in coastal areas, both providing incentive to keep coasts attractive and healthy, and threatening their health and beauty. Despite this, marine ecosystems and organisms are often poorly understood. The first part of this chapter, then, addresses key differences between marine and terrestrial ecosystems.

Although the science of marine reserves is relatively young, reserves have demonstrated success as a conservation tool. The establishment of a reserve will, on average, double the density, triple the biomass, and increase the size and diversity of organisms present by 20-30% (Halpern, 2003). To ensure the long-term success of reserves, we need address their strengths and weaknesses in responding to climate change, which is now an inevitability. West and Salm (2003) have suggested designing reserves to enhance the ability of communities within reserves to be "resistant and resilient" in the face of climate change. What aspects of marine ecosystems and reserves will best serve this

purpose? What aspects are most vulnerable to climate change? Parts two and three of this chapter examine current and predicted threats to and changes in marine ecosystems, both as a result of climate change and other factors.

There are already several excellent guides on marine reserve design (e.g. Kelleher 1999; Salm et al 2000). Parts four and five of this chapter provide a brief review of what's known about reserve design and success, discuss it in the context of global climate change, and suggest approaches to reserve design that might be particularly relevant in the face of global climate change. The Strategies for implementation section, pg. 163, offers suggestions for reserve planners wishing to incorporate these suggestions into their own planning. Finally, the Existing adaption programs section, pg. 164, reviews existing approaches to adaptation in temperate marine reserve planning and suggests a few areas where more information would be particularly helpful.

Unique Aspects of the Marine Environment/marine Conservation

Like terrestrial ecosystems, marine ecosystems are diverse mosaics of interacting physical and biological elements. In many other regards, however, marine ecosystems are quite distinct, and any approach to marine conservation must be based on a solid understanding of the unique physical, biological, and sociopolitical aspects of the marine environment. Several key differences are reviewed below; further reading on differences between marine and terrestrial habitats and their implications can be found in e.g. Carr et al. (2003), Day and Roff (2000), or Strathmann (1990). The overriding point is to realize that ecological knowledge gained from terrestrial systems may not be directly applicable to marine systems.

PHYSICAL DIFFERENCES

THREE-DIMENSIONALITY

Compared to air, water is relatively dense, viscous, nutrient-rich, and wet. Thus buoyancy is relatively easy, desiccation isn't a problem, and there is less need for elaborate support structures. As a result, the marine world is strikingly three-dimensional. While terrestrial life exists by and large within 100 m of the Earth's surface, marine communities exist from the ocean's edges to its abyssal planes thousands of meters below the surface. Many organisms spend all or significant parts of their lives in the water column. Thus, in addition to covering about 70% of Earth's surface, the oceans make up about 99% of Earth's biosphere.

TEMPERATURE

The thermal regimes of intertidal and open ocean habitats are distinct both from each other and from those in most terrestrial habitats. Intertidal organisms experience extremes of temperature and desiccation, in some cases experiencing temperature swings of 20 °C between immersion and emersion. Differences in the timing of low tides (midday vs. early morning) can override latitude in determining degree of thermal stress (Helmuth et al., 2002); cyclic changes in the timing of low tides due to lunar oscillations can have significant effects on intertidal zonation (Denny and Paine, 1998). Some inter-

tidal organisms are living close to their thermal tolerance limit (e.g. Stillman and Somero, 1996), in which case even small changes in temperature could lead to dramatic changes in community structure (Bertness et al., 1999). Conversely, because of water's high heat capacity, open ocean and subtidal organisms are generally spared any rapid temperature shifts akin to the day-night or seasonal shifts in terrestrial ecosystems (Harley et al. in press). The buffering capacity of oceans may cause ocean temperatures to rise more gradually than air temperatures as climate change progresses.

PHYSICAL CONNECTIVITY

Waves and currents cause nutrients, sediment, and pollution to mix and travel much more freely in the marine environment than in most terrestrial environments. Thus marine communities may depend on nutrients coming from remote sources, and likewise may be negatively affected by pollutants from distant locales. Nutrient pollution from the Mississippi River has rendered thousands of square kilometers of the Gulf of Mexico uninhabitable creating an area referred to as "the dead zone" (National Science and Technology Council, 2000). On a more positive note, connectivity means that marine populations are less sensitive to habitat fragmentation than terrestrial systems.

ECOLOGICAL DIFFERENCES

THE BENTHOS AND THE PLANKTON

On a very basic level, the marine realm can be divided into two categories: the benthos and the plankton. Benthic organisms are those that live in or on the sea floor. While the most diverse benthic communities are in the photic zone, there is also substantial diversity in the deep sea, beyond the reach of sunlight. Vibrant hydrothermal vent communities thrive in an ecosystem based on chemosynthesis rather than photosynthesis. The availability of water-borne food allows marine ecosystems to support an array of filter feeders, animals that take bacteria, algae, other animals, and debris from the water passing overhead (or overfoot, in the case of barnacles). There are no terrestrial equivalents to filter-feeders (unless one considers spiders).

The oceans also contain an ecosystem for which there is no terrestrial equivalent: the pelagic realm. The most obvious inhabitants of the pelagic world are nektonic organism, strong swimmers like whales and fish who can move independently of oceanographic currents. Less visible but equally important are planktonic organisms, those with weak or absent motility who exert relatively little control over their large-scale movement.

LIFE HISTORIES

Most marine animals have complex life histories wherein adult and larval stages are physically, ecologically, and physiologically distinct. Adults are often relatively sessile, while larvae may travel for tens or thousands of kilometers through the water column. Thus larval supply, dispersal, and recruitment are critical in determining the persistence of adult populations, or the ability of populations to recover from disturbances. Understanding these phenomena will also be critical in designing reserves that can succeed in the long term, particularly as climate change alters current patterns and other elements

of marine ecosystems that determine where and when larvae recruit to adult populations. Despite their importance, our understanding of many aspects of larval transport and recruitment, particularly as they affect reserves, is still fairly rough. Many models treat larval dispersal as a spatially symmetrical process, ignoring the existence of unidirectional transport by currents, and model settlement as evenly distributed in space, despite the common existence of regions of high and low settlement (Gaines et al., 2003). The concept of source and sink populations suggests that certain populations may depend mostly or entirely on larvae supplied by distant populations to persist. Protection of adult populations and habitat may thus be insufficient for population persistence.

In addition to having planktonic larvae, many marine invertebrates release gametes directly into the water column, where sperm may become limiting. Since individuals of many sessile or sedentary species cannot or do not move long distances in search of mates, declining population density may lead to significant decreases in fertilization success. This phenomenon is suspected to play a role in the decline of at least one commercially important species, the white abalone (Hobday et al., 2000).

The fecundity of marine animals—producing thousands of eggs per season is quite common—led many to think that marine populations could not be overfished. However, mortality rates for larvae and juveniles are also extremely high, and current rates of population decline show that high fecundity is no panacea.

POPULATION CONNECTIVITY

Because of the abundance of life in the water column and the movement of water over vast distances by currents, marine populations are thought to be much more interconnected than terrestrial ones. Numerous studies of population genetics bear this out, at least for species with planktonic larvae (reviewed in Grosberg and Cunningham, 2001). Adult rafting may add to the connectivity of distant populations. As would be expected, marine species tend to have greater genetic polymorphism and less spatial or geographic structure than terrestrial ones (Carr et al., 2003). This may ignore the existence of cryptic species, however.

The depth of the ocean, the scale of movement of marine organisms, and, for planktonic organisms, their small size makes tracking movement difficult. Thus our knowledge of the extent of movement by marine organisms is fairly limited. One approach to determining movement of planktonic organisms is to assume that they track oceanographic current patterns, and recent models indicate that currents patterns rather than other environmental variables may be responsible for some marine biogeographic boundaries (e.g. Gaylord and Gaines, 2000). Nonetheless, it is clear that even weak swimmers are able to affect their horizontal distribution by altering their vertical position (reviewed in Forward and Tankersley, 2001; Hill, 1998). This has been particularly well demonstrated for larvae of estuarine crab species (e.g. Garrison, 1999), and recent evidence suggests that fish larvae also have mechanisms that allow them to recruit back to natal populations (Warner et al., 2000). Analysis of genetic structure can provide some clues as to the extent of

genetic intermixing of populations across a wide geographic range, although it doesn't give information about who moves where. More recently, investigators have used chemical signals preserved in calcium carbonate structures (e.g. bones, statoliths) to infer geographic movement of fish and invertebrate larvae (Thorrold et al., 2002).

FOOD WEB STRUCTURE AND COMPLEXITY

In general, marine food webs are more complex than terrestrial food webs. While terrestrial ecosystems exhibit relatively little lateral transfer of energy or materials, the diverse array of planktonic organisms and planktivores in marine systems allows for significant lateral transfer. Unlike terrestrial carnivores, which actively seek out their prey, many planktivores generally depend on currents to bring their meals to them. In addition, the turnover rate of marine autotrophs is rapid relative to terrestrial ones; phytoplankton divide approximately daily, depending on location, and the majority of macroalgae are annual or short-lived.

NATURAL VARIABILITY AND RATE OF RESPONSE TO CHANGE

Marine ecosystems, by and large, exhibit a more rapid response to environmental changes in climate than do terrestrial systems, probably because of the relatively short lifespan of many key marine organisms (Carr et al., 2003). Such rapid ecosystem changes have been observed in response to cyclic environmental shifts such as the El Niño Southern Oscillation (e.g. Lubchenco et al., 1993) and the Pacific Decadal Oscillation (Hollowed et al., 2001). Many marine species, particularly those lacking planktonic dispersal, also exhibit large interannual variability in population size (Eckert 2003), making it more difficult to identify long-term trends in response to changes in climate.

The rate of response to change, in particular to temperature shifts, may also be related to the relatively large proportion of thermoconformers in marine as compared to terrestrial ecosystems. The vast majority of marine animals are cold-blooded; although many have some techniques for altering their body temperature, they track environmental temperatures more closely than warm-blooded animals.

SOCIOPOLITICAL DIFFERENCES

VISIBILITY AND FAMILIARITY

Aside from intertidal areas, the marine world is largely invisible to humans, except with respect to commercial fishery productivity. Also, the structure of marine communities is conceptually foreign to most people. Because there are no terrestrial equivalents to many marine life histories and community structures, it is difficult for people to appreciate what matters. Also, much of the devastation of marine life occurs beyond the reach of the human eye: destructive bottom trawling is invisible to most, but has a profound effect not just on the previous communities of those areas of the seabed, but on populations of commercially important species. It is this invisibility that allows people to see destructive programs like carbon sequestration in the deep sea as relatively benign. Because we have not explored the deep sea in any great detail, there is a false impression that it is a barren wasteland.

OWNERSHIP AND USE

Currently, less than 1% of oceans are included in reserves, compared to approximately 6% of the terrestrial world (Carr et al., 2003). Marine resources in most regions have been managed as common-pool resources where open access is the rule. While some coastal cultures have ownership rights for marine resources, in the global market the oceans and their resources are by and large expected to be available to anyone. This has lead to a "tragedy of the commons," wherein there is more incentive for over-extraction than for protection. Unlike terrestrial food industries, in which both plants and animals are harvested extensively and are mostly domestically raised, marine harvest is primarily wild-caught animals. Given the environmental problems associated with marine aquaculture, however, whether or not switching to farmed marine fish would ease the pressure on wild populations is unclear. Perhaps related to this general lack of ownership, marine ecosystems are rarely the result of positive human intervention; in other words, there are few marine equivalents to setting fires to maintain open grasslands, irrigating land to create rice paddies, or the like. While the idea of active intervention to shape terrestrial ecosystems reflects attitudes common in human societies, our approach to marine ecosystems and perhaps conservation as well seems more guided by a desire for an absence of human activity.

Current Stresses on Temperate Marine Ecosystems, Other Than Climate Change

Marine ecosystems face myriad stresses, of which climate change is only one. To adequately address climate change, we must do so in the context of other known stressors. An adaptation strategy for climate change that increases the risk from other stressors would serve little use.

PROBLEMS ASSOCIATED WITH COMMERCIAL FISHERIES

OVERHARVEST AND TROPHIC CASCADES

It is estimated that 90% of the world's large fish, both open ocean and groundfish species, have been lost; once an industrial fishery opens, it takes only 10-15 years to achieve this level of reduction (Myers and Worm, 2003). Although overexploitation of marine stocks is not a new phenomenon, the advent of industrial fishing technology has allowed unprecedented rates and levels of depletion (reviewed in Pitcher, 2001).

It is not simply the loss of fish that matters; the loss of apex predators or keystone species can have profound and long-lasting ecological effects (reviewed in Coleman and Williams, 2002). A classic example is the overharvest of sea urchin predators (or potentially of the predators of urchins' predators) leading to increases in urchin populations and thus decreases in kelp abundance (Estes and Palmisano 1974). Loss of kelp forests can lead to declines in many fish species relying on kelp forests as nursery grounds, and to increases in other populations (Lubchenco et al., 1993). The loss of large pelagic fish may lead to increases in gelatinous zooplankton such as ctenophores and jellyfish (Mills, 1995).

FISHERIES-ASSOCIATED HABITAT DESTRUCTION

Many fisheries use mobile gear that drags along the sea floor, such as trawls and dredges. Such practices lead to long-term decreases in numbers of individuals, species diversity, and biomass, as well as changes in the physical and chemical nature of the habitat (Veale et al., 2000; Kaiser et al., 2000). Areas that have been subjected to long-standing dredging or trawling tend to be dominated by small-bodied organisms that are less likely to get captured by bottom trawls, although whether overall changes in community structure are due to selective species removal or decreased habitat complexity is unclear (National Research Council, 2002).

A different sort of habitat destruction occurs when driftnets are accidentally lost or purposefully discarded when they wear out or are damaged. They then drift through the ocean, entangling animals from fish to mammals.

DISEASES ASSOCIATED WITH AQUACULTURE FACILITIES

When animals are transported around the globe for aquaculture, unwanted organisms inevitably accompany them (Bower et al., 1994). In addition, aquaculture facilities are often overcrowded and stressful, providing a perfect incubator for diseases (e.g. Wagner et al., 2002; Avnimelech and Ritvo, 2003). Diseases are transmitted between farmed and wild animals through escapees and outfall.

NON-NATIVE SPECIES

Most invasions by non-native species occur accidentally as a result of shipping (Ruiz et al., 2000), although even estuaries with no international shipping may have numerous non-native species (Wasson et al., 2001). Invasions also occur due to purposeful introduction of non-natives for aquaculture, primarily fish, bivalves, and crustaceans; these purposeful introductions are often accompanied by the accidental introduction of predators, parasites, or other hangers-on accompanying the species of interest. A well-characterized example of this is the introduction of several predatory oyster drills along with Pacific oyster to the northwest coast of North America. Non-native species have also been introduced by scientific researchers: witness "Freeman's blight," a species of tunicate introduced to New England by a visiting researcher at the Marine Biological Laboratories, and now a major pest up and down the coast. Private and commercial aquaria are the likely sources of the "killer alga" Caulerpa taxifolia in both California and the Mediterranean. C. taxifolia is an aggressive competitor, which outcompetes native seagrasses and algae, thereby radically altering community structure. In most cases, some effort is made to contain the non-native species, but rarely are such efforts entirely successful. Indeed, attempts at biocontrol of both invasive and native pests are yet another source of exotic species (reviewed in Secord, 2003).

Non-native species can have numerous impacts on their new ecosystems, including altering physical structure, changing decomposition rates, out-competing natives for resources or shifting competitive hierarchies, and, of course, eating native species (reviewed in

Grosholz, 2002). Invasive snails have been implicated in the decline and local extinction of native mud snails in California as a result of more efficient feeding and production of offspring (Byers, 2000), and invasive mussels have changed an unstructured mud flat into a mussel reef (Crooks, 1998). The latter invasion completely transformed both the physical and biological structure, resulting in a community assemblage completely distinct from that in the surrounding unaltered mud flats. Invasive species play key roles in structuring rocky intertidal zonation as well (e.g. Leonard et al., 1999). In addition to species- and community-level effects, introduced species can alter trophic transfer within entire ecosystems. A non-native clam in San Francisco Bay (perhaps the most invaded estuary in the world) is such an efficient filter feeder that it has shut down the usual spring phytoplankton bloom, shifting primary production from planktonic to benthic ecosystems (Alpine and Cloern, 1992). For a review of both some effects of and problems associated with assessing the ecological impact of invaders, see Parker et al. (1999) and Grosholz (2002).

PHYSICAL DISTURBANCE

COASTAL DEVELOPMENT

Human populations have always been concentrated in coastal areas, and it is no different today. As the human population continues its exponential growth and lifestyles in many cases become increasingly resource-intensive, coastal marine communities around the world are showing signs of strain. Around 60% of the world's population lives within 100 kilometers of the coast (Vitousek et al., 1997), although this area encompasses only 20% of Earth's landmass. Thirty percent of all land within 100 kilometers of the coast has been at least moderately altered by human use (World Resources Institute, 2000). For many important types of coastal ecosystems, such as seagrass beds, there simply aren't sufficient data to know the extent of loss, although in some highly developed areas loss approaches 90% (Burke et al., 2001). Destruction of wetlands reduces nursery grounds for commercially important species such as oysters and salmon, decreases filtration of input from terrestrial sources, and increases coastal erosion and flooding. Levees starve beaches and wetlands.

TOURISM

While people who spend time in particular habitats are more likely to be invested in preserving those habitats, even the most environmentally-conscious visitors are not without effect. For instance, a coralline alga-dominated intertidal community in New Zealand showed a 50% decline in meiofaunal biomass after only five days of trampling (Brown and Taylor, 1999). Negative affects of trampling have also been documented on rocky shores in Europe (e.g. Fletcher and Frid, 1996) and North America (e.g. Brosnan and Crumrine, 1994), as well as in salt marshes (Chandrasekara and Frid, 1996), although a study in South Africa found no long-term effects of trampling (Bally and Griffiths, 1989). Although snorkeling and scuba diving are not as common in temperate marine systems as they are in tropical systems, they do occur, and can cause noticeable effects.

Tourism has numerous effects on the physical environment as well. Increased use of a coastal area generally increases nutrient input, particularly when high-level sewage

treatment is not available. In some cases, beaches are created artificially to encourage tourism, and beachfront areas are altered to become more "attractive" to tourists. Sunscreens, bug repellants, and other topically applied chemicals may wash off into the seawater, accumulating to noticeable levels in highly-used areas.

NOISE AND LIGHT POLLUTION

Although probably less important than many other anthropogenic influences, both increases in noise and light can have negative effects on many marine animals. The presence of strong light from shore has been implicated in the migration of sea turtle hatchlings away from rather than towards the ocean (Witherington and Martin, 1996), and light pollution may also cause disturbed vertical or horizontal migration by squid and zooplankters.

For whales that depend on sonar for migration and communication, noise pollution, particularly sonar, may cause a number of effects, including death, deafness, stranding, and altered behavior (National Research Council, 2003). Excess noise may also make it hard for juvenile fish to find their natal reef (Graydon, 2003). Although the use of sound as a location cue has not been documented for temperate marine organisms other than cetaceans, it may have an effect.

CHEMICAL POLLUTION

Ideally, marine reserves can be located so as to reduce the possibility of chemical pollution. If a pollutant is fairly non-dispersive and has a known source, it is possible to design reserves to avoid the source, or to contain the pollutant in case of an unanticipated spill. In contrast, highly dispersive pollutants are difficult to contain, and pollutants coming from multiple small or mobile sources are difficult to avoid.

OIL SPILLS

One of the best-studied oil spills was the 1989 Exxon Valdez Spill in Prince William Sound, Alaska, USA. Monitoring of long-term affects of this spill shows not only that spills have long-lasting effects, but that recovery rates vary tremendously among habitats. Although most kelp forest taxa recovered within two years, over 80% of subtidal eelgrass taxa had not recovered even six years after the spill, despite a relatively rapid recovery of the eelgrass itself (Dean and Jewitt, 2001). Similarly, Driskell et al. (2001) found that even seven years after the spill, rocky intertidal community structure had still not returned to normal. Two studies of recovery in soft-sediment communities found only incomplete recovery ten years after the spill.

Invertebrate taxa also vary strongly in their sensitivity to oil spills. A fine-sand amphipod community took over ten years to recover from the Amoco Cadiz oil spill off the coast of Brittany, France (Dauvin, 1998), while polychaetes in the same region seemed to be relatively unaffected (Gesteira and Dauvin, 2000). Such differential sensitivity would likely lead to shifts in population structure following oil spills, as was indeed seen in waters off Cape Cod, Massachusetts, USA following a 1969 oil spill (Sanders, 1977).

The decreased mixing of marine waters predicted to accompany global warming in many regions may alter the effects of oil spills, increasing residence time on the surface and slowing biological degradation. While higher temperatures, which could increase biodegradation rates, may counteract this effect, the overall effect of increased temperatures on ecological effects of oil spills is unclear. For enzymatic repair processes, increased temperature may speed recovery, up to a point (e.g. Hoffman et al., 2003); conversely, increased temperature may be a stressor, and combine synergistically with other stressors (e.g. coral bleaching, Fitt and Warner, 1995).

POINT SOURCE POLLUTION

Point source pollution is pollution coming from an identifiable source such as a factory outfall or a stream running through a heavily used agricultural area. While point sources often produce large quantities of pollutants, they are relatively easy to pinpoint and in many countries are regulated at regional or national levels. Traditional point sources have been industrial, dumping large quantities of heavy metals and polycyclic aromatic hydrocarbons (PAHs) into marine waters. More recently, coastal aquaculture facilities have become a more wide-spread problem, draining excess antibiotics and fertilizer into nearby waters. Another fairly recent type of point-source pollution is desalination plants. As fresh water becomes an increasingly valuable commodity, it is likely that more and more desalination plants will be built to serve the needs of coastal cities. The environmental effects of the hypersaline outflow from such facilities are as yet poorly understood.

NON-POINT SOURCE POLLUTION

In heavily populated areas, non-point sources can be as or more important than point sources in polluting marine ecosystems. Antifouling paint and oil and gas leaks from private boats can be problematic, as can the combined pesticides and fertilizers used by individuals on their lawns and gardens. Reducing non-point source pollution is difficult, and requires a concerted community education effort, as well as regulations governing the sale and use of toxic chemicals.

NUTRIENT POLLUTION

Excess nutrients entering the water due to fertilizer runoff, untreated human and animal waste, or sewage outfalls leads to eutrophication, oxygen depletion and the creation of "dead zones" as has been documented in a number of locations worldwide. The Gulf of Mexico is perhaps the most famous, with fertilizer from the Mississippi Basin leading to the annual formation of an anoxic area encompassing thousands of square kilometers (Malakoff, 1998). Nutrient over-enrichment can also cause harmful algal blooms, which injure or kill marine animals including fish, birds, and mammals (Conley et al., 2002; Anderson, 1997). Increased water temperatures and the resultant stratification that may accompany climate change make the occurrence of anoxic zones more likely, and may worsen existing zones. Ironically, it has also been suggested that increases in nutrients from agricultural runoff and sewage have allowed the recovery of fisheries that had been

starved of nutrients. This has been studied off the coast of Egypt, where the Aswan Dam virtually stopped the input of terrestrial nutrients from the Nile (Nixon, 2003).

SEDIMENTATION

Both increases and decreases in terrestrial sediment input have been documented as problems in marine ecosystems. The construction of bulkheads and seawalls actually increases shoreline erosion and results in "starved" beaches, where a decline in the amount of incoming sediment causes an increase in substrate coarseness as well as increasing erosion rates. Damming major rivers also radically reduces sediment as well as water input into coastal areas. Conversely, poor land use practices and the clearing of soil-stabilizing vegetation in river catchments have lead to increases in sedimentation in other areas. Increased sedimentation can be particularly problematic for seagrass beds.

THERMAL POLLUTION

The use of seawater to cool power plants may cause significant alterations in local thermal regimes. In Florida (USA), some manatees now congregate around thermal effluent rather than natural heat sources such as thermal vents and artesian springs (Packard et al., 1989). Warm water outflow has also caused alteration in benthic communities in California (USA) near the Diablo Canyon nuclear power plant (Tissot et al., 1991). These later studies are particularly interesting in that community-level changes did not reflect predictions based on individual-level thermal sensitivities.

Observed and Predicted Effects of Climate Change on Temperate Marine Ecosystems

The all-pervasive nature of climate change—its effects are likely to be felt globally and throughout the depths of the ocean—demands that its effects be considered in reserve design and planning. Changes in climate are not a new phenomenon. Paleoecological records provide insight into effects of past cycles of global warming and cooling, and cyclical changes in climate regime in certain regions have allowed us to look at short-term (year-long to decades-long) changes in ecosystems. This information, combined with experimental work on individual organisms and communities and mathematical models, provides the basis for most predictions about future effects of global climate change. In making such extrapolations, however, there are several caveats. The causes of global climate change are not the same as the causes of regional regime shifts, and we should not assume that the effects will be the same either. Also, small-scale experiments or observations don't capture the complex interactions characteristics of marine ecosystems. Trophic cascades such as those described by Estes and Palmisano (1974) are one example of unanticipated chains of events; there are likely many other such unrecognized connections that will determine the ultimate effects of climate change.

PHYSICAL CHANGES

Seascapes generally classified based on factors such as temperature regime, hours of sunlight, extent of ice cover, etc. While some of these factors (hours of sunlight) will not

be significantly affected by climate change, others will, creating new combination of physical variables and thus new seascapes.

TEMPERATURE CHANGES

While the global mean temperature will rise as a result of climate change, it is possible that in certain areas, average sea temperature may drop as a result of changing current and upwelling regimes. Also, it is unclear for many organisms what aspects of temperature change matter most: maximum, minimum, or mean temperature, or rate of change and thermal history, measured daily, seasonally, or annually.

RISING SEA LEVEL

As global temperatures increase, sea level is expected to rise both as a result of thermal expansion of sea water, and as a result of melting glaciers and ice caps. In some areas, temperature-related sea level increase is exacerbated by decreased rates of soil-building in wetlands due to decreased sediment input either because of drought or shoreline modification. Some salt marshes won't be able to keep up with sea level rise (Moorhead & Brinson 1995). Even if they can, landward shoreline armoring may interrupt their natural advance upshore. Some coastal areas are sinking because of decreases in sediment input without any reduction in erosion. Areas such as the Rhône, Po, and Ebro deltas in the Mediterranean that are subsiding are further threatened by sediment starvation.

Changes in sea level may also affect the type of coastal system present in any given region. Recent research suggests that sea level rise over the 18,500 years has changed the Southern California Bight from a productive, diverse rocky coastline to a less productive, less diverse sandy coastline (Graham et al., 2003).

Changes in sea level have also been implicated in paleontological patterns of diversification and extinction in a number of marine taxa (e.g. House, 1989). In general, shallow seas are the most productive marine areas; increasing sea level increases the extent of shallow seas, and may increase overall marine productivity. Falling sea level, which reduces the area available for shallow-seas organisms, is associated with several mass extinction events.

INCREASING ULTRAVIOLET RADIATION

In marine organisms, UV causes death and deformity, alters behavior, sex ratio, and development, and can change community composition (reviewed in Hansen and Hoffman, 2001; Häder et al., 1998). Despite the common misconception that ultraviolet (UV) does not penetrate deeply enough into marine waters to play a significant role in marine ecosystems, both UVA and UVB cause measurable effects to down to several meters depth (e.g. Karentz and Lutze, 1990). In the clearest tropical waters, levels of UVA detectable by deep-sea shrimp can penetrate to 500-600 m (Frank and Widder, 1996).

UV levels in marine ecosystems are changing due to stratospheric ozone depletion, alterations in solar luminosity, and changes in water clarity due to a number of influences.

There is still only a rudimentary understanding of how elements of global change such as altered precipitation will affect UV levels in marine ecosystems, although the changes in sedimentation rates and primary productivity discussed above will certainly influence the depth to which UV penetrates. While progress is being made in reducing the production of ozone-depleting chemicals, the same cannot be said for other factors influencing UV levels in marine environments. Additionally, changes in vertical water circulation will affect the length of time planktonic organisms spend in the high-UV surface waters.

ALTERED NUMBERS/INTENSITY OF STORM EVENTS

Although increased severity and frequency of storm events has been predicted to result from global climate change (Houghton et al., 2001), data at this point are inconclusive. Wave heights have increased globally over the past 30 years, and higher sea levels will increase the height of storm waves and surges, increasing the frequency of extreme events. Storms may also have increased precipitation intensity; this would increase both erosion and salinity stress for coastal marine ecosystems.

Interannual climate fluctuations such as the El Niño/Southern Oscillation (ENSO) or the Interdecadal Pacific Oscillation, which strongly influence number and intensity of storms, may themselves be affected by global climate change (Timmermann et al., 1999). Although it is clear that such periodic climate oscillations have varied in frequency and intensity in the past, the causes of such variation is uncertain (Tudhope et al., 2001; Urban et al., 2000)

WATER CHEMISTRY

The decreased freshwater input and increased evaporation expected to accompany global warming trends may lead to increased salinity in small or shallow semi-enclosed bodies of water such as tide-pools and estuaries. The implications of such changes are unclear, as many tide-pool and estuarine organisms are adapted to alterations in salinity. This does not mean, however, that they will be able to compensate for any future changes.

Increased CO₂ concentrations may lead to a gradual decrease in the ocean's pH and calcium carbonate concentration. Studies have shown that calcification rates of many marine organisms, including corals, coralline algae, and coccolithophorids, are decreased by increases in CO₂ (reviewed in Gattuso and Buddemeier, 2000).

Additionally, there will likely be alterations in seasonal levels of freshwater input: more rain rather than snow in winter may lead to more runoff in winter and less in summer. For animals such as herring that respond to drops in salinity as a spawning cue, altered timing and amount of freshwater influx could have profound effects.

UPWELLING AND CURRENTS

Numerous changes in water movement are expected to occur as a result of increased temperature. These include increased stratification and stability of the water column due

to surface water warming, and consequently reduced upwelling, both near-shore and open-ocean (summarized in Soto, 2002; Field et al., 2001). Decreased upwelling in turn decreases nutrient input to surface waters, leading to a decline in primary productivity. Effects of decreased phytoplankton reverberate through the food web, leading to reduction in density of zooplankton and likely secondary consumers as well. Such changes have been documented off the coast of Southern California following an abrupt and sustained increase in water temperature in the 1970s (reviewed in Field et al., 1999).

Conversely, climate change may alter wind patterns in ways that increase offshore winds and thus upwelling (Bakun, 1990). Accurately predicting local changes in upwelling regimes, then, requires understanding the relative strength of changes in offshore winds vs. surface warming.

There may also be altered current regimes, such as reduction in area and a coastward migration of shelf-tidal fronts, a reduction in strength of the Gulf Stream, and an increase in strength of the Labrador Current (Soto, 2002). Such large-scale changes in currents would result in changes in larval transport, affecting both how many larvae recruit to adult populations, and where the larvae end up.

ALTERED RATES OF SEDIMENT INPUT

Changes in amount and timing of rainfall will affect input of sediment as well as of fresh water. Winter rainstorms have the potential to wash greater amounts of sediment into rivers, since in many regions there is less vegetation to hold soil in place in winter than in summer. Increases in sedimentation will also occur in regions experiencing decreasing sea ice cover, as land is exposed to the erosional forces of waves for longer parts of the year.

On the other hand, sediment input may decrease for a number of reasons. Increasing coastal development is leading to increasing hardening of coastlines. Seawalls, bulkheads, and riprap all decrease the amount of sediment reaching adjacent coastal areas, resulting in sediment-starved beaches. Reduced sediment input resulting from the damming of rivers will be exacerbated by the drier conditions expected in much of the world. Changes in grain size and character of sediment-starved beaches can lead to dramatic changes in community composition and structure.

Climate change may increase the problem of human alteration of shorelines. Coastal homeowners wary of increased numbers or intensity of storms and rising sea level may build more and bigger bulkheads, further starving shorelines in developed areas. This negative feedback cycle can already be seen in highly erosional coastlines like the Wadden Sea.

BIOLOGICAL CHANGES

EFFECTS ON INDIVIDUALS

Temperature can affect individual organisms both behaviorally and physiologically, with effects ranging from mild to lethal. Not surprising, then, is the range of adaptations and sensitivities organisms display to both absolute temperature and to changes in tem-

perature (Hochachka and Somero, 2002). Animal species inhabiting the high intertidal, for instance, can generally survive significantly higher temperatures than their low intertidal congeners, and susceptibility to thermal stress can occur on multiple levels (reviewed in Somero, 2002).

Temperature also affects growth rate and development, potentially affecting generation times or juvenile size. In over 90% of aquatic ectotherms studied, increased rearing temperature resulted in decreased organismal size (Atkinson, 1995). While average individual size does decrease with latitude in many invertebrate species, it is unclear whether changes in ocean temperature directly affect individual size.

POPULATION-LEVEL EFFECTS

For many species, temperature serves as a cue for reproduction (Olive, 1995). If species synchronize their reproduction with such environmental factors as food availability using cues sensitive to global climate change, such as temperature, climate change may disrupt this synchrony and thus alter developmental success (Olive, 1995). Bhaud et al. (1995) describe the disruptive effects of even short-term temperature fluctuations on the reproduction of some marine polychaetes.

Temperature can also affect reproduction by altering sex ratios. Temperature-dependent determination of sex occurs in all sea turtles (Davenport, 1997) as well as some copepods (Voordouw and Anholt, 2002) and fish (Pavlidis et al., 2000; Goto et al., 1999; Conover, 1984). Changing climate cycles will potentially skew sex ratios to the extent that population growth is threatened.

EFFECTS ON COMMUNITIES

Within any community, it is likely that different members of the community will respond differently to various elements of global climate change depending on their sensitivity to and tolerance for various aspects of environmental change. Changes in temperature, sedimentation rate, ultraviolet radiation, and disturbance regime can shift competitive interactions, favoring some species over others. Species with high genetic diversity and short generation times may be able to undergo evolutionary adaptation, while genetically depauperate species are less likely to do so. Mobile species may track preferred temperatures, while less mobile species must either adapt or disappear locally. For instance, northward range expansions following warming trends have been documented for sardine populations off the coast of California (Lluch-Belda et al., 1992). On a rocky shoreline in central California, where annual mean ocean temperature has increased 1 °C over the past 60 years, researchers have documented an increase in southern animal species and a decrease in northern animal species (Sagarin et al., 1999). Likewise, a study of kelp forest fish in Southern California found that since the 1970s there had been a 50% drop in cold-water, northern species, and a 150% increase in warm-water, southern species (Holbrook et al., 1997).

Predicting changes in communities in response to climate change may not be as simple as understanding species thermal biology, however. Fox and Morin (2001), for instance,

found that protist populations with density-dependent regulation were relatively immune to effects of temperature change, while Davis et al. (1998) found that interspecific interactions made effects of temperature changes difficult to predict for three species of fruit fly. For intertidal barnacles, interspecific interactions shifted from competitive to facilitative as environmental conditions became harsher (Bertness et al., 1999).

Global warming could also alter the strength of interaction between keystone predators and their prey, potentially causing strong shifts in intertidal communities by affecting feeding by a keystone species (Sanford, 1999). On the coast of Oregon, decreasing temperature slowed the feeding of two key rocky intertidal predators by around 30% (Sanford, 2002). Thus the timing and number of upwelling events determined the reproductive output of some intertidal prey species.

BIOGEOGRAPHIC EFFECTS

The role of temperature and desiccation in determining zonation patterns in rocky intertidal habitats is well established. In general, biotic interactions such as competition and predation set a species' lower boundary, and physical stress sets the upper boundary. Species thus exist at tidal heights where predators are scarce or absent, but abiotic conditions fall within survivable ranges. A study in Washington State found that intertidal bands of mussels and barnacles were broader on exposed than sheltered coastlines; in less wave-exposed locations, temperature stress lowered the upper limit for these species, but predation by a sea star, which sets their lower limit, remained unchanged (C. Harley, pers. comm.). If climate change lowers the upper limit of barnacles and mussels in all locations, it will likely lead to an overall decrease in the populations of these animals, since expanding downward will not be an option where predatory sea stars are present. A similar interaction between thermal stress and predation was found to exclude one species of alga from south-facing slopes, where high temperatures during emersion pushed their upper limit down into the zone of high predation (Harley, 2003). The lesson for climate change is that this alga may go locally extinct because its upper limit will shift down while its lower limit remains stationary.

On a larger scale, species ranges may shift poleward in response to global warming. Such a shift may be dictated by a species' need to stay within a particular water temperature range, or, in the case of intertidal organisms, to stay within an acceptable range of air temperatures (Lubchenco et al., 1993). Such range shifts appear to be occurring in some marine environments (Sagarin et al., 1999).

NON-NATIVE SPECIES

Climate change is likely to affect the relative success of biological invaders. Stachowicz et al. (2002), for instance, found that warmer temperatures favored non-native over native ascidians. In some cases, marine animals have been imported to new environments with the understanding that colder temperatures in the new location would limit the exotic's ability to reproduce (e.g. Pacific oysters). As temperatures increase and limits to reproduction decline, such species will spread more readily throughout their new home. Alter-

ations in currents may bring larvae from populations of introduced species to new locations, and disruption of native, natural ecosystems by climate change may render them more vulnerable to successful invasion by non-natives. If stocks of native marine organisms become too unstable or depleted, there may be an increase in aquaculture of non-natives species, and a consequent increased risk of invasion/dominance by these species.

DISEASES

Climate change has been linked with increases in marine disease outbreaks (Harvell et al., 1999; Hofmann et al., 1999) and range extensions in marine parasites (Ford, 1996). Warming trends associated with ENSO cycles correlate with shellfish diseases on the US Atlantic and Gulf coasts (McLean and Tsyban, 2001). Increased outbreaks may be due to increased pathogen transmission or decreased host resistance. Decreased resistance may result from behavioral or physiological changes in marine populations, and may also be affected by interactive effects with pollutants. Many new diseases are caused by host shifts rather than the appearance of previously unknown organisms (Harvell et al., 1999); as mentioned previously, increased in aquaculture may also increase the global transmission of diseases. Indeed, transfer of infected stocks may have been responsible for some of the most devastating disease outbreaks in farmed bivalves (discussed in Harvell et al., 1999)

Considerations and Suggestions for Marine Reserve Design With a Focus on Possible Adaptation Options

A number of criteria have been proposed for evaluating potential marine reserve sites, including ecological, social, and economic considerations (see Roberts et al., 2003 for ecological criteria, and refs therein for other approaches). Although it is clear that the biophysical characteristics of temperate marine ecosystems will change, uncertainty about the nature and rate of change is compounded by our lack of knowledge about how complex ecological interactions will respond to change. The UNFCCC suggests the possibility of natural ecosystem adaptation to climate change, if we limit the rate of change sufficiently. Also key to successful adaptation is looking at interactions between climate change and other anthropogenic stressors on marine systems: which factors will be exacerbated by climate change and which will be ameliorated?

SPATIAL CONSIDERATIONS

CREATE NETWORKS OF RESERVES

It has been suggested that fewer large reserve might be better for protecting biodiversity while numerous smaller reserves might be more effective for fisheries enhancement; given the range of dispersal distances of marine larvae, however, many biologists now believe that networks of marine reserves will be more effective than single large reserves (e.g. Hastings and Botsford, 2003). Networks allow a greater diversity of habitats to be covered over a greater geographical range for the same amount of total area protected. Increasing the geographical range included in a network will become increasingly important if the anticipated latitudinal species migrations occur in response to climate change. Although there are few empirical data on size and spacing of reserves within

networks, these issues have been the focus of recent theoretical work. Based on a review of published dispersal distances, Shanks et al. (2003) suggested that reserves of 4-6 km2 would be sufficient to retain short-distance dispersers. Roberts et al. (2001) noted that even reserves as small as 5 km² have been shown to be effective in increasing densities of commercially valuable species. Spacing between reserves and location of reserves within the network area is less clear. Long-distance dispersers may travel between 20 and 4400 km, and remain in the plankton for almost 300 days (Shanks et al., 2003). Their exact route is unknown. As discussed previously, the common assumption has been that planktonic marine larvae by and large follow ocean currents, but at least some larvae have behavioral mechanisms to aid in local retention.

DESIGN RESERVES TO PROVIDE TEMPERATURE REFUGIA

One "natural adaptation" to climate change is for species ranges to shift to higher latitudes. Such latitudinal changes have been demonstrated for numerous terrestrial species (Parmesan and Yohe, 2003), and for marine species on the west coast of North America during a recent warming trend there (reviewed in Field et al., 1999). To the extent that this migration allows the preservation of species that would otherwise go extinct, marine reserves should attempt to provide robust corridors for such poleward movement. Designing latitudinally extensive networks serves this purpose. Many species may not be able to migrate fast enough to keep pace with climate change, however (Malcolm and Markham, 2000).

It may also be possible for some populations to shift their habitat into deeper, cooler water as global warming progresses. As mentioned previously, however, downward range expansions may be prohibited for some species by the presence of competitive dominants or predators, and photosynthetic organisms are limited by the depth of the photic zone. Also, in a study of rocky intertidal community response to warming, Sagarin et al. (1999) found no overall downward shift in tidal range, although there was evidence of a latitudinal shift.

While shifting habitats to greater depth and higher latitudes is one way of finding cooler temperatures, most regions have identifiable "hot spots" and "cold spots" (see, e.g., Helmuth et al. 2002) due to factors such as upwelling, shade, subhabitats, timing of tides, and freshwater input. Designing reserves to include "cold spots" may reduce thermal stress from climate change. Areas with a high degree of vertical mixing or rapid water movement, for instance, have lower average temperatures than stratified areas. Such areas may also be higher in nutrients and thus provide a more stable food supply for zooplankton and planktivores. Areas of shoreline with ample shading and cooler microhabitats (cracks, crevices, etc.) can also provide temperature refugia and increase survivorship (Moran and Emlet, 2001).

ESTABLISH RESERVES IN TRANSITIONAL ZONES

BETWEEN BIOGEOGRAPHIC REGIONS AS WELL AS IN CORE AREAS

Species are often assumed to be more successful and stable in the core region of their geographic distribution, and conditions are assumed to become increasingly stressful to-

wards the edges of the species' range. Thus, in the absence of climate change, it has been assumed that to preserve a species, it may be preferable to locate reserves away from range edges. As climate changes, however, the "best" area for a species may shift away from what had been the core of its range. Thus creating reserves throughout a species' range, or at least including locations near its poleward boundaries, is a safer approach.

Additionally, this "abundant center" concept of species distribution has recently been challenged. In nine of 12 temperate marine invertebrate species studied by Sagarin and Gaines (2002), areas of peak density occurred in sites near the edges of the species' range as well as in the center. These findings underline the importance of designing spatially heterogeneous networks of reserves.

ADD AN "INSURANCE FACTOR" TO RESERVE SIZE CALCULATIONS

To buffer against periodic severe disturbances such as hurricanes or oil spills, researchers have suggested adding an "insurance factor" when calculating the necessary size of a reserve (Allison et al., 2003). The insurance factor is simply extra area added to the reserve, and should assure that a reserve's function goals are met despite catastrophes. The amount of extra area needed as insurance can be calculated based on the anticipated frequency of and vulnerability to disturbances in the region covered by the reserve or reserve network. Such an approach could also be effective in buffering against possible effects of climate change, and would work well in conjunction with other bethedging approaches. This approach may be ineffective in protecting many spatially restricted habitats and ecosystems, however.

INCLUDE A DIVERSITY OF HABITATS AND BIOGEOGRAPHIC REGIONS

Traditional reserve planning has been focused on single-species conservation, and as such has focused on the selection of critical habitat areas for the species of interest. While such considerations should continue to be included in planning, particularly for reserves whose aim is increased yield of commercially valuable species, there is a growing recognition that to be successful in the long term, reserves must be designed more broadly. Rare or vulnerable habitats should be included in reserves even if they have no known connection to species of interest; such habitats may play ecological roles we are unaware of, and would be hard to restore/replace. Also, such habitats contribute to the overall habitat heterogeneity, another key element of reserve design. Habitat heterogeneity, or the presence of multiple habitat types, has at least two potential benefits. First, habitat diversity generally corresponds with overall biodiversity, since a heterogeneous habitat provides more microhabitats and opportunities for specialization. Second, preserving multiple habitat types within a reserve or a network of reserves may benefit species that live in different habitats during different stages of their life. From the climate change perspective, protecting multiple habitat types increases the odds that at least some of the protected habitats will be resistant or resilient to the effects of climate change.

Including a diversity of habitats in marine reserve networks is also important for species that use different habitats at different times of year or during different life stages.

On a somewhat larger scale, reserve design should also maximize biogeographic representation. Although there is as yet no universally accepted set of biogeographic classifications for marine ecosystems, several such classifications have been proposed. Roff et al. (2003) present a table of possible factors to consider in designating marine biogeographic regions, and discuss local variation in the relative importance of these factors.

DESIGN RESERVES BASED ON FEATURES OF THE ENVIRONMENT UNLIKELY TO CHANGE While which organisms will inhabit any stretch of shoreline decades in the future may be unpredictable, there are some elements of existing ecosystems whose persistence is more likely. Day and Roff (2000) termed these "enduring and recurrent features." Physiographic features such as topography will persist regardless of climate change, and can influence the biological communities that develop in any given area. Areas of high relief, for instance, are usually associated with greater species diversity and richness than areas of low relief. This may be in part because high relief provides a greater diversity of habitat, and in part because high relief also creates upwelling, which increases the supply of nutrients and oxygen, and thus productivity. Currents, waves and mixing related to fetch and tidal forces are also unlikely to change; as mentioned above, areas with strong currents and stronger wave action may experience less warming than calmer waters.

Certain oceanographic features are also enduring or recurrent. Convergence and divergence zones occurring in the open ocean, for instance, have fairly predictable locations in temperate waters of the southern hemisphere, although their location is not predictable in northern temperate waters. Oceanographic features may be more affected by climate change than physiographic features, however. For instance, upwelling is a fairly regular occurrence on the Pacific coast of the Americas, but increased frequency or strength of ENSOs might decrease the amount of upwelling significantly. The potential decrease of climate-driven upwelling underscores the importance of including topography-driven upwelling zones in reserves. Local topography and current patterns may also determine areas of higher or lower larval settlement (Shanks and Wright, 1987).

DESIGN RESERVES AROUND AREAS THAT SHOW

RESISTANCE AND RESILIENCE TO CLIMATE CHANGE

Researchers and planners concerned with coral reef conservation have begun to identify locations that are resistant to bleaching, and factors that allow for more rapid recovery from bleaching (resilience) (West and Salm, 2003). If temperate events equivalent to bleaching in terms of sensitivity to climate change can be identified, they may assist in developing a similar approach for temperate marine ecosystems. For instance, if particular species are found to be most sensitive to the effects of climate change, areas where those species continue to thrive may be areas with natural resistance to climate change, either because of cooler conditions or some other combination of factors. Similarly, habitats or locations that recover quickly from more short-term changes in climate such as the Pacific Decadal Oscillation may be best able to cope with longer-term climate change. By identifying local areas with increased resistance or resilience, reserve planners can enhance the capacity of particular communities to persist (West and Salm, 2003).

SOCIOPOLITICAL CONSIDERATIONS

USE ADAPTIVE MANAGEMENT STRATEGIES

Because we have relatively little hard data on how well marine reserves work, and because the factors influencing reserve success may change over time, many scientists and practitioners are recommending the use of adaptive management strategies (e.g. Salafsky et al., 2002; Botsford et al., 2003; Parma et al., 1998). This approach requires practitioners to monitor the success of reserves and the on-going effects of design and management choices, and to adjust management practices in response to this information. This will allow the evolution of the most appropriate management practices for each reserve or network of reserves, and begin to provide much-needed information to aide in the design of future reserves. Such an adaptive, iterative approach is particularly important in creating reserves that will be most robust or resilient relative to climate change: there is so much uncertainty in our knowledge of the physical and ecological effects of climate change that future flexibility is essential.

Adaptive management is also important, as it allows reserve managers to respond to changes not only in the ecology of reserves, but in the sociopolitical context of reserves. It is likely that climate change will affect the relationship of local communities to the marine environment; such changes could significantly affect the effectiveness of reserves. For instance, the size needed for reserve effectiveness depends on fishing pressure outside the reserve; if climate change alters fishing pressure, the effectiveness of the reserve would likewise change.

ESTABLISH A TEMPORALLY RESPONSIVE APPROACH THAT ALLOWS

YOU TO TRACK COMMUNITIES/SPECIES OF INTEREST AS CLIMATE CHANGES

Setting up a successful reserve in the first place is challenging; the idea of adjusting the boundaries of and restrictions in reserves over time may seem like it simply prolongs the struggle. However, the potential usefulness of such temporally-responsive reserve management is such that the idea is worth at least considering. In conversations with stakeholders and other planners, bring up the idea that to fulfill the management goals identified by the group, reserve boundaries may have to change in the future, just as many ranchers rotate their animals among different fields. If members of the community understand the importance and potential benefits of reserves they may be willing to do what it takes to ensure reserve success in the long term. Also, the periodic reassessments of reserve locations and activities required by this approach provide an opportunity to reengage community members and strengthen their commitment to the reserve.

INVOLVE STAKEHOLDERS FROM THE BEGINNING

While most discussions of reserve design focus on where to site reserves and what activities to allow, there is increasing awareness that committed and invested community stakeholders can be as essential to the long-term success of a reserve as appropriate selection of location and ecological characteristics (Salm and Clark, 2000; Kelleher, 1999). Given the degree of uncertainty involved in planning reserves in the face of climate change, the commitment of local communities to the ongoing success and effective

management of reserves gains even greater importance. If people living and working near reserves feel responsible for the reserve, they are less likely to engage in destructive activities, more likely to police themselves and other community members, and more likely to support changes in reserve location or restrictions as necessitated by climate change or other factors.

To maximize community investment in a reserve, community involvement and empowerment must be part of even early planning. If people feel that they have been excluded at any stage of planning, reserve managers may start to look like adversaries rather than colleagues. Also important is taking the time to understand how local communities relate to marine resources, which community members use or control various aspects of the marine environment. This requires sensitivity to both culture and gender issues.

IDENTIFY CLEAR GOALS AND CRITERIA FOR MEASURING SUCCESS

In the past, reserve and conservation efforts have often focused on "species of interest," either culturally or commercially important or endangered species. It has been suggested (e.g. Simberloff, 1997; Franklin, 1993) that a single-species focus leads to a myopic approach in which overall ecosystem stability and function may be sacrificed; additionally, cryptic or unknown species will remain unprotected. An ecosystem approach, in contrast, may be more likely to support the species of interest.

LIFE HISTORY CONSIDERATIONS

Because marine populations are much more open than terrestrial ones, and marine organisms often have complex life cycles with two or more ecologically distinct life history phases, the appropriate size and location of reserves is tricky to determine. The degree of larval and juvenile dispersal can radically affect both the ideal size of a reserve and its ability to fulfill different goals (i.e. preserving biodiversity vs. enhancing fisheries; Botsford et al., 2003), and adult, larval, and juvenile stages must be considered for reserves to succeed. For species with distinct feeding and spawning grounds, both types of habitat must be preserved. Unfortunately, the full life history is understood for relatively few species, and may be quite different even for closely related species (Grantham et al., 2003; Strathmann, 1987). While larvae of some species recruit locally, in other cases adult populations may depend largely on larvae arriving from upcurrent locations. A decline in a particular adult population may reflect local problems for those adults, problems in the larval habitat, or problems with an upcurrent adult population that is a significant source of recruits.

Because knowledge of larval dispersal is spotty but dispersal distance seems critical to reserve sustainability (Botsford et al., 2003), the best approach may be to design reserve networks using a "bet-hedging" strategy. As mentioned earlier, Shanks et al. (2003) suggest making reserves large enough to sustain locally-recruiting populations (4-6 km in diameter), and spacing reserves such that larvae with longer dispersal distances can recruit to adjacent reserves (10-20 km spacing). Reserve placement also needs to reflect

both major ocean currents and smaller currents and eddies, since the extent to which larger- and smaller-scale currents matter for larval dispersal and recruitment is unclear. Different habitats seem to have different frequencies of dispersing vs. non-dispersing larvae; a recent study on the west coast of the United States found that over 60% of sandy intertidal species had non-planktonic larvae, as compared to less than 22% of species in rocky intertidal and sandy subtidal habitats (Grantham et al., 2003).

Despite the ability of planktonic larvae to travel hundreds of kilometers, it appears that larvae of at least some species have mechanisms to enhance larval retention. These may reflect a complex balance of larval behavior, currents, salinity, and even sound. By assessing the existence of such mechanisms for populations of interest, reserves can be designed to give the best chance of larval retention. For instance, some larval fish use sound to locate appropriate adult habitats (Leis and Carson-Ewart, 2003, and refs therein). In this case, restricting use of motorized craft or other sources of extraneous noise might help increase or maintain larval recruitment.

In designing reserves to benefit particular species, it is essential to first identify the most vulnerable life stages of that species. Often the stage that is most visible, well understood, or accessible receives the most attention, with no consideration of which life stage is most in need of protection, or whose protection would do the most to boost adult populations.

CONTROLLING NON-CLIMATOLOGICAL STRESSES

Coastal ecosystems are intricately linked with the land they adjoin. Reserves should be located away from major sources of terrestrial pollution such as agricultural runoff, sewage outfall, or industrial outfall. While point sources of pollution are relatively easy to identify, non-point sources may be harder to avoid. In general, locating reserves away from heavily populated areas or areas that receive a lot of human use will help to reduce the negative impacts of non-point pollution. Locating reserves away from human use areas also reduces the risk of coastline alterations leading to sediment starvation of beaches, or conversely excessive sediment input due to poor land use practices and erosion. Ideally, marine reserves can be linked with terrestrial reserves, so that the major sources of terrestrial input (sediment, nutrients, fresh water) are preserved along with the marine ecosystem they serve.

Limiting anthropogenic stresses in marine reserves becomes even more critical when considering mitigation of climate change effects. Anthropogenic stressors can act synergistically with increasing temperature and other elements of climate change; minimizing non-climate stressors thus mitigates the negative effects of climate change as well. For instance, the recent increase in number and extent of harmful algal blooms (HABs) is thought to result from both warming and increased nutrient pollution (Mudie et al., 2002). Limiting excess nutrient input in areas near reserves would decrease the likelihood of devastating HABs affecting the reserve.

Identifying and Selecting Strategies for Your Particular Location

Given the variability of biophysical and social systems in and affecting marine ecosystems, there can be no single "right" way to create a reserve. Each reserve must be designed to best meet the needs and attitudes of local ecosystems and inhabitants. WWF has identified this location-based approach as a key to reserve success, along with the existence of stakeholder involvement, community enforcement, a clear management plan, legal protection, monitoring, financial sustainability, and sufficient numbers of well-trained personnel.

SOCIOPOLITICAL ISSUES OF RESERVE DESIGN

It is essential to identify the stakeholders in your region, their background knowledge and economic options, and what restrictions on use they would be willing to accept. As mentioned above, stakeholder input and support is a significant predictor of reserve success. Locally based, sustainability-driven resource users may have a different degree of commitment than profit-driven users, and the percent of users who are local and permanent (ostensibly having a more long-term view) vs. transient (tourists, big business) will have a significant impact on what strategy works best. Ideally all users may be convinced that the long-term sustainability of their enterprise, be it commercial or sustenance-oriented, is intricately linked with the long-term health of the marine ecosystem. Achieving stakeholder buy-in allows for a greater reliance on voluntary compliance and self-monitoring rather enforcement, which is often both more expensive and less effective. Given the financial uncertainty inherent in conservation planning, the more self-sustaining reserves can be, the better.

BIOPHYSICAL ASPECTS OF RESERVE DESIGN

Given the limited time and money available to planners, along with our still uncertain understanding of ecosystem response to climate change, most reserve planning will occur without what would be considered the ideal amount of information. Nonetheless, taking the time to inventory certain key aspects of the marine ecosystems in your region is essential.

First, map habitat types in your region, including location and area covered. The map should cover both structural elements of habitat (sand, kelp forests, seagrass beds, boulders, etc.) and functional elements of habitat (e.g. spawning grounds for particular species, nursery grounds, etc.). Identify key biotic and abiotic variables controlling species distribution in your area, and how they'll be affected by climate change. For instance, what types of catastrophes does your region experience (how extreme, how frequent, how prolonged, rate of onset), and how will climate change likely change those? Is your region likely to experience sea temperature increases or decreases? Remember, there's a great degree of local variability in the effects of climate change: just because warming will be the norm, doesn't mean your area will warm up. What major current regimes in your area, if any, will likely be affected by climate change (e.g. ENSOs, NAO, PDO, NO)? Consider the tidal regime in your region. Areas in which low tides occur in

the middle of the day will have more temperature stress on intertidal organisms (Helmuth et al. 2002), and will thus need different planning strategies than less-stressed areas.

Strategies for Implementation

"Best practice" approaches for planning reserves that will provide the best chance of success in the face of global climate change are not wildly different from "best practice" approaches for reserve planning as they exist now. Certain elements of reserve planning may gain increased importance, however, and are emphasized below.

REGIONAL AND TRANSBOUNDARY COOPERATION

Transboundary agreements and treaties, already important because of the open nature of marine ecosystems, may be essential to meet new spatial refugia or larval transport needs, or to reduce stressors other than climate change to acceptable levels. Also, given uncertainty about how communities and ecosystems may rearrange themselves as climate change progresses, the possible inclusion of temporally-sensitive management options may become increasingly important.

MONITORING

The science and practice of marine reserves are fairly young. There are not yet any time-tested design tools or best management practices, although there is wide-spread recognition that they must rapidly be developed if marine reserves are to fulfill their promise as conservation tools. Systematic monitoring, evaluation, and information-sharing will enable us to understand the factors essential for reserve success, and the particular challenges faced in variety of situations. The adaptive management approach suggested previously requires on-going input of information so that effectiveness can be iteratively evaluated and reserve management appropriately adapted as the environment changes and as more information becomes available. This approach enhances the probability that a reserve will achieve its long-term goals.

Enlisting the help of volunteers can be a good way to encourage community involvement and investment in the reserve. It also familiarizes you with the nature of your reserve, its cycles and processes. Also, monitoring lets you know whether or not your reserve is working. If your reserve isn't working, you need to redesign the reserve, alter restrictions on use, or establish another reserve. Which option you choose will depend on your best assessment of why the reserve isn't working. Further, more data are needed to help us design effective reserves in the future and assess the extent to which reserves can solve our conservation problems.

What to monitor depends on reserve goals, size, and budget. Some basic variables of interest are number, size, density and biomass of species inside, adjacent to, and far from the reserve; ideally, data should be collected before as well as after establishing the reserve to provide a baseline. Replicate counts inside the reserve are essential to ensure adequate and accurate sampling. Monitoring often focuses on vertebrates (Halpern

2003), but should be focused on overall biodiversity. This would provide more information for understanding ecosystem function and stability.

Existing Adaptation Programs and Some Needed Information EXISTING PROGRAMS

There are few if any marine reserves that have been designed and monitored specifically with climate change adaptation in mind. Nonetheless, the need to incorporate potential effects of climate change in reserve design is gaining attention (e.g. Soto, 2002; MPA News, 2001), and suggestions for doing so are beginning to appear. Parks Canada, for instance, surveyed all national parks in Canada to identify sites and species most at risk from climate change, and predicting probable effects of climate change on each park (David Suzuki Foundation, 2000).

Australia has recently created the world's largest marine reserve, the Heard Island and McDonald Islands Marine Reserve in the Southern Ocean (Australian Antarctic Division, 2003). In addition to maintaining these subantarctic islands in a relatively pristine state, this reserve will be specifically monitored for possible effects of climate change in a region that has seen little direct anthropogenic impact.

INDICATOR SPECIES, COMMUNITIES, AND PROCESSES

As we head into an uncertain climate future, it would be useful to know which species, communities, or processes might serves as harbingers of changes to come. Identifying species most sensitive to climate change ("indicator species") would give us early warning signs of ecosystems on the brink of collapse, or early indications of successful conservation approaches. Identifying the most sensitive elements of ecosystems may also help us anticipate unexpected or indirect effects of climate change on ecosystems.

Species that live in variable environments (e.g. seasonal, intertidal) tend to have broader latitudinal ranges and occupy more biogeographic provinces than species from more stable environments. Species with broad geographic ranges also tend to be more long-lived on a geological scale than species with restricted ranges. Thus it might be expected that species naturally occurring in stable habitats or with geographically restricted ranges would be more susceptible to some aspects of climate change, and might make a good first guess as indicator species (Harley et al., in press).

Another broad-brush approach to predicting potential sensitivity of species to climate change centers on the prediction that mobile organisms, which can escape stressful situations behaviorally, should have a narrower tolerance range for a variety of stressors than sessile organisms, which must deal with whatever stressors come their way (Huey et al., 2002). Thus mobile organisms may prove more sensitive indicators of environmental change that sessile ones.

Since species do not live in a vacuum, it may also be useful to know which biological communities are most sensitive to climate change. Roberts et al. (2003) suggest that

communities that depend on biological rather than physical matrices, such as eelgrass beds or mangrove swamps, are often the least resistant or resilient. Such communities may require particular attention in reserve design and sustainability.

LONG-TERM, LARGE-SCALE DATA SETS

While numerous models exist to predict the future of climate change and its effects on ecosystems, there is a strong need for real-world data to complement these models. Studies documenting effects of short-term climate changes such as ENSOs are an excellent first step, as are studies of the effects of thermal effluents on marine communities; both approaches should be expanded to include more geographic regions. Because such phenomena are much more short-lived and smaller-scale than global climate change, however, we must also accumulate data on community structure over broad geographic and long temporal scales.

Conclusions

When it comes to marine reserves and climate change, our level of knowledge is inadequate, and will remain so for the foreseeable future (see the excellent discussion of uncertainty in climate change modeling in Hannah, this volume). We cannot wait for certainty before taking action, however; we must make the best decisions we can based on our current understanding of marine ecosystems and climate change, and incorporate bet-hedging and flexibility into our planning.

The suggestions in this chapter are not in any way meant to undercut the importance of global efforts to halt global climate change, or to imply that immediate global reduction of greenhouse gas emissions is not critical. Since global climate is not under local control, however, and since some level of global climate change is now inevitable, local and regional planners need to take what actions they can to mitigate the effects of climate change. Also, reserves are a critical element of conservation planning, and failure to consider climate change when designing reserves may decrease the effectiveness of reserves dramatically.

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