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Resilience to Climate Change in Coastal Marine Ecosystems

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recovery, resistance, diversity, interactions, adaptation

Abstract

Ecological resilience to climate change is a combination of resistance to increasingly frequent and severe disturbances, capacity for recovery and self-organization, and ability to adapt to new conditions. Here, we focus on three broad categories of ecological properties that underlie resilience: diversity, connectivity, and adaptive capacity. Diversity increases the variety of responses to disturbance and the likelihood that species can compensate for one another. Connectivity among species, populations, and ecosystems enhances capacity for recovery by providing sources of propagules, nutrients, and biological legacies. Adaptive capacity includes a combination of phenotypic plasticity, species range shifts, and microevolution. We discuss empirical evidence for how these ecological and evolutionary mechanisms contribute to the resilience of coastal marine ecosystems following climate change–related disturbances, and how resource managers can apply this information to sustain these systems and the ecosystem services they provide.

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INTRODUCTION

Climate Change and Coastal Ecosystems

Coastal marine ecosystems are among the most valuable and heavily used natural systems worldwide (Halpern et al. 2008, Millenn. Ecosyst. Assess. 2005). They provide many important ecosystem services, including shoreline protection and food from fisheries and aquaculture. As human populations in coastal areas continue to grow, so does our dependence on the functioning of these valuable systems. Among the multiple human impacts that threaten the functioning of coastal ecosystems, anthropogenic climate change acts on the most extensive spatial and temporal scales (Halpern et al. 2008) and poses some of the most severe threats (Doney et al. 2012, Hoegh-Guldberg & Bruno 2010).

Rising greenhouse gas concentrations have triggered a suite of changes in the ocean. The upper layers of the ocean have warmed by approximately 0.6°C over the past 100 years (Intergov. Panel Clim. Change 2007). Along with warming comes a set of additional abiotic changes in marine ecosystems, including sea level rise (Rahmstorf et al. 2007), more intense storms (Knutson et al. 2010), and changes in wind strength and upwelling patterns (Bakun & Weeks 2004). In addition, increases in the ocean's heat content are likely to have important impacts on the world's major current systems (Pisias et al. 2001). Aside from warming, increased concentrations of anthropogenic CO_2 in the atmosphere have led to ocean acidification: The pH of ocean surface layers has decreased by approximately 0.02 pH units per decade since the preindustrial period (Doney et al. 2009). These changes in ocean temperature and pH are significant when compared with the geochemical conditions prevalent in the world's oceans in the past (Pelejero et al. 2010, Petit et al. 1999). Moreover, the expected magnitude of pH change over the next few hundred years is greater than that of any other pH changes inferred from the fossil record over the past 200–300 million years (Caldeira & Wickett 2003). Together, these environmental changes impact all levels of biological organization and can disrupt ecosystem functioning.

The direct effects of climate changes, such as warming water temperatures, start at the cellular level (Hochachka & Somero 2002) and cascade up to the individual organism and population levels by altering metabolic rates, survival, and other life-history traits (O'Connor et al. 2007). Other population-level impacts arise from shifts in oceanographic processes that affect dispersal and recruitment. Community-level effects arise from changes in the relative abundances of interacting species and changes in per-capita interaction strength (Sanford 1999). Finally, these population- and community-level impacts may result in ecosystem-level changes (e.g., in species diversity and distributions, ecosystem productivity, and ecosystem service production) (Doney et al. 2012).

Ecosystems and their responses to changing conditions are often unpredictable, and are characterized by thresholds and nonlinear dynamics (Folke et al. 2004). Slowly accumulating changes in both biotic and abiotic variables can push coastal ecosystems toward critical thresholds, resulting in loss of ecosystem functioning and services (Hoegh-Guldberg & Bruno 2010). One example of such a threshold is an atmospheric CO_2 concentration of 450 ppm, beyond which coral growth rates will decline dramatically and reefs will be pushed into a negative carbonate balance and lost to erosion (Hoegh-Guldberg et al. 2007; but see also Pandolfi et al. 2011). As rates of mortality and erosion exceed rates of coral growth, coral reef structure will be lost and important ecosystem functions such as wave attenuation will decline. As a consequence, valuable ecosystem services, such as protection from erosion and flooding, are threatened (**Figure 1**). Given the cumulative effects of climate change and the valuable ecosystem functions at risk, there is a need for predictive conceptual frameworks and management that explicitly integrate across multiple scales of biological organization and function.

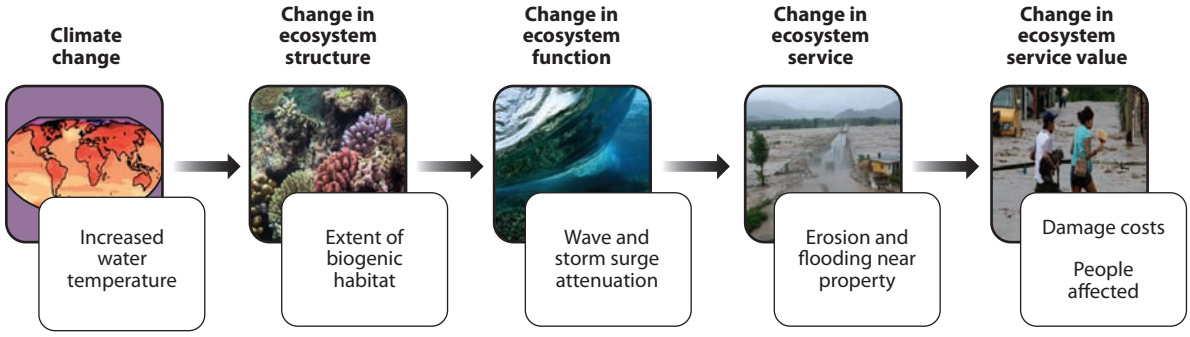

Figure 1

Climate change threatens the delivery of valuable ecosystem services and human well-being. Through impacts such as increased temperature and rising pH, ecosystems, including coral reefs, may be pushed toward critical thresholds. Crossing these thresholds may lead to major changes in ecosystem structure (such as coral cover) and function (such as wave attenuation), which will then impact the delivery and value of ecosystem services (such as protection from storms), with consequent impacts on human well-being. Adapted from Arkema & Samhouri (2012).

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Resilience Theory in the Context of Climate Change

Resilience theory originated in the ecological literature in the 1970s and has since informed marine reserve design, conservation planning, and related analyses of coupled human-ocean systems (e.g., Folke et al. 2004, Halpern et al. 2012, Hughes et al. 2005, Leslie & Kinzig 2009, Olsson et al. 2008, Steneck et al. 2011). Although resilience has been conceptualized in varied ways by anthropologists, ecologists, engineers, and other systems scientists, here we adopt the broad definition of Folke and others, which is particularly relevant to the effects of climate change over tens to hundreds of years: Resilience is the capacity of a system to maintain functioning, structure, and feedbacks in the face of disturbance (Folke et al. 2004).

The ecological resilience framework focuses on a system's response to shocks and long-term change as well as on emergent properties and feedbacks among system components (Folke et al. 2004, Leslie & Kinzig 2009). The changing climate will impose both short-term shocks, such as extreme weather events, and longer-term changes in environmental variables, such as ocean temperature and pH. Further, ecosystem services, like the protection from coastal storms provided to coastal human communities by marshes and other biogenic habitats, result from multiple ecological processes, including nutrient cycling and primary productivity. Thus, the focus of resilience science on a system's emergent properties rather than on the functioning of its individual parts is particularly relevant to understanding the effects of the changing climate on ecosystem service provisioning.

Resilience: the capacity of a system to maintain functioning, structure, and feedbacks in the face of disturbance (after Folke et al. 2004)

Self-organization: the development of structure and functioning on the basis of local interactions (after Levin 1999)

Three components of resilience emerge from the literature (**Figure 2**). The first is the amount of change a system can undergo and still retain the same controls on structure and functioning (i.e., resistance). In the context of climate change, this component refers to an ecosystem's ability to persist despite increasingly frequent and severe pulse disturbances, such as coastal storms and heat waves. The second component is a system's capacity for recovery and self-organization (versus vulnerability to organization by external factors) following disturbance. The final component is the degree to which a system can adapt to new conditions, such as higher air temperatures or lower ocean pH.

Although these resilience elements are helpful heuristic tools, they have rarely been investigated in real systems. Further, they remain too abstract for managers to incorporate them easily into the

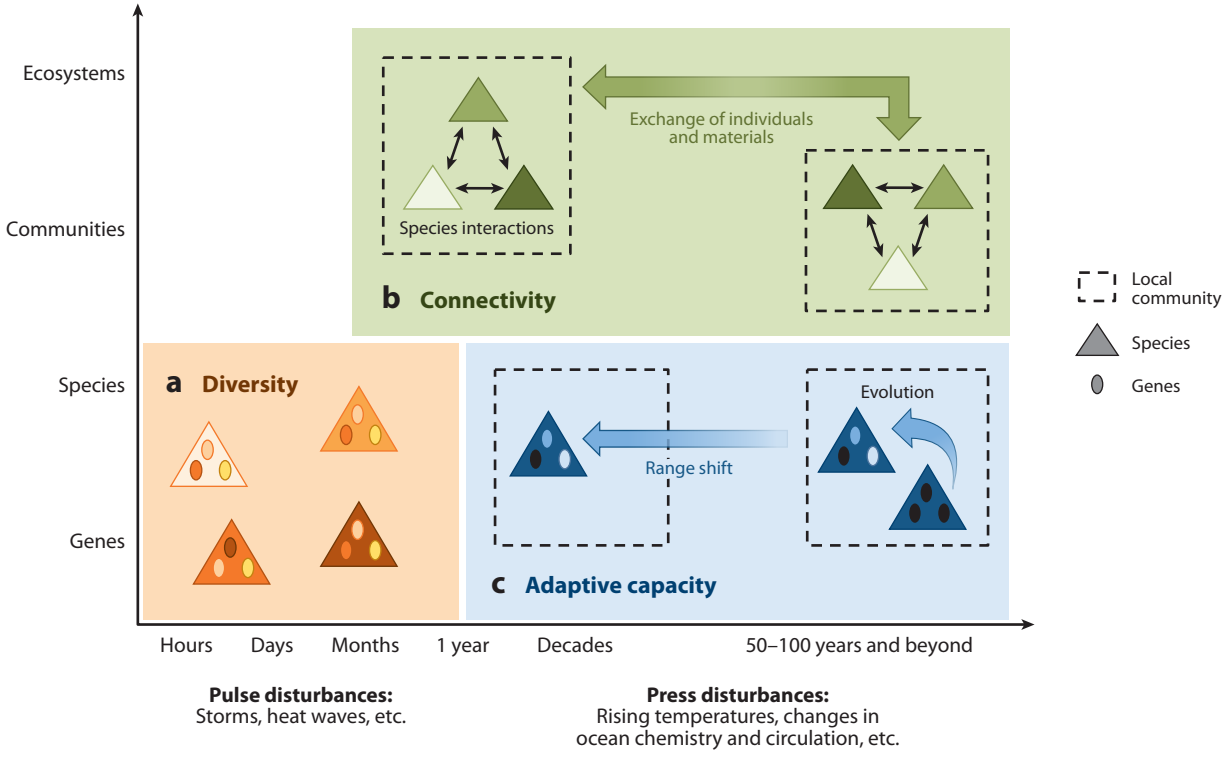

Figure 2

Ecological mechanisms that underlie resilience at multiple scales of biological organization and time. (*a*) Genetic and species diversity enhance resistance by increasing the range of responses to the environment and the likelihood that species can functionally compensate for one another following disturbance. (*b*) Connections among species, populations, and ecosystems contribute to self-organization, stabilize ecosystems in the face of fluctuating environmental conditions, and enhance recovery following severe disturbances. For example, reseeding of individuals from other sites can prevent local extinction following disturbance. (*c*) Adaptation to the changing climate will include a combination of phenotypic plasticity, species range shifts, and rapid evolution of traits better suited to new conditions. For example, to keep up with the changing climate, a species may either shift its range by dispersing to newly climatically suitable locations or evolve new adaptive traits in situ. High genetic diversity, population size, and dispersal rates enable adaptive strategies.

design and monitoring of management strategies. To bridge the gaps between resilience theory, our understanding of climate effects, and management, we propose three broad categories of ecological properties that underlie resilience: diversity, connectivity, and adaptive capacity. We discuss empirical evidence for these ecological properties, and how resource managers can use this information to manage and monitor coastal systems for resilience in the face of climate change and other, more local-scale perturbations.

ECOLOGICAL PROPERTIES AND PROCESSES THAT ENHANCE RESILIENCE TO CLIMATE CHANGE

Diversity: the variety of life, particularly from the genetic to the seascape scale

Diversity Increases Resistance and Recovery

Biological diversity from the genetic to the species to the seascape scale facilitates continued ecosystem functioning in a changing environment by increasing the range of biological responses

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and the odds that species can compensate for one another if some are lost (**Figure 2*a***). Further, because diverse communities tend to use resources more efficiently and be more productive (Duffy 2008), they often have an increased capacity for recovery following disturbance. Diversity operates in several distinct ways, as we detail below.

Connectivity: the connections that promote stability and recovery at multiple scales of biological organization; it includes interactions among species as well as demographic and material flows among populations, biological communities, and ecosystems

Adaptive capacity: the ability of populations, communities, and ecosystems to adapt to changing climate conditions through a combination of phenotypic plasticity, physiological responses, distributional shifts, and rapid evolution of traits better suited to new conditions

Response diversity: the diversity of responses to environmental change within and among species contributing to the same ecosystem function (adapted from Elmqvist et al. 2003)

Functional redundancy: the capacity of one species to functionally compensate for the loss of another, thereby preventing losses in ecosystem functioning if diversity declines owing to disturbance

Response diversity. Diversity within a species can enhance resistance to disturbance by increasing the range of responses populations exhibit in any given environmental context. For example, in Bristol Bay, Alaska, there are several hundred discrete spawning populations of sockeye salmon, which display diverse life-history characteristics. These subpopulations spawn at different times and places, thus compensating for one another as the broader environmental context shifts. In fact, over the past century, fish yields from Bristol Bay have remained relatively constant, despite documented regime shifts associated with the Pacific Decadal Oscillation (Hilborn et al. 2003). Similarly, the increasing genotypic diversity of clonal eelgrass enhances resistance to disturbances such as heat waves and geese grazing by increasing the range of responses to disturbance and increasing the chance of having a resistant genotype in any given area (Ehlers et al. 2008, Reusch et al. 2005). Because of the initial increased resistance to disturbance, the time to return to the predisturbance state decreases with increased genotypic diversity (Hughes 2004). Thus, increased genetic diversity can contribute to increased resistance to environmental changes by enabling ecosystems to continue functioning in the face of increasing disturbance.

Functional redundancy. Functional redundancy is the capacity of one species to functionally compensate for the loss of another. Greater species diversity increases the odds that species are capable of functionally compensating for one another following disturbance, resulting in no net change in productivity or other ecosystem processes (Hooper et al. 2005). Similarly, redundancy of similar functions replicated at multiple scales confers resistance because most disturbances influence ecosystem structure and/or functioning at specific scales (Thrush et al. 2009). In a comparison of subtidal kelp forests with high and low grazer diversity, respectively, Steneck et al. (2002) proposed that forests with higher grazer diversity are more resistant to deforestation triggered by El Niño events and overexploitation of top predators, because the remaining grazer species can compensate for others that are lost. Similarly, on the rocky shores of Panama, Menge & Lubchenco (1981) found that crustose coralline algae are much more resistant to algal overgrowth when grazer diversity is high. Although systems with low species diversity are likely to lose functional traits as diversity declines, the level of species diversity necessary for functional redundancy remains a critical question (Duffy 2008, Naeem 2002).

Complementarity effects. Diverse (i.e., species-rich) assemblages are better able to recover from disturbance because they are often more productive, use resources more efficiently, and facilitate recruitment of other species (Duffy 2008, Hooper et al. 2005). For example, after experimentally perturbing rocky shore algal communities, multiple investigators found that plots with high species diversity exhibited higher standing cover and lower variability in biomass, and recovered completely within the two- to three-year experimental period. Plots with low diversity did not recover within this period (Allison 2004, Stachowicz et al. 2008). Diversity in epifaunal communities enhances resistance to invasion (Stachowicz et al. 2002) because diverse communities use more of the available space, thereby reducing the establishment of invaders. As species invasion rates rise with climate change (Intergov. Panel Clim. Change 2007) and some nonnative species become dominant as they fare better under warmer conditions (Sorte et al. 2010), the decreased invasibility conferred by diversity may be a key component of the resilience of coastal systems (Duffy 2008).

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Portfolio effects. At the ecosystem level, if the abundances of different species are negatively related or vary randomly, then increasing species diversity (and, perhaps concurrently, functional diversity) should increase the stability of ecosystem functioning. This is referred to as a portfolio effect (Hooper et al. 2005). For example, in an analysis of several large databases of fish catches, Worm et al. (2006) found that species diversity increases resistance and recovery from overexploitation. Fishery collapses were more common in species-poor ecosystems than in species-rich ecosystems. Furthermore, the average catches of noncollapsed fisheries were higher in species-rich ecosystems, and recovery from fishery collapse was positively correlated with fish diversity. The increased resistance, recovery, and productivity of more diverse fisheries may be partially due to fishermen's ability to switch more easily between target species as abundances shift—a social-ecological portfolio effect.

Clearly, diversity plays an important role in enhancing community stability over time, by increasing the chance that some species will be resistant over the short term, allowing species to compensate for one another, and by facilitating processes such as recruitment, which enhances recovery over longer timescales. Response diversity and functional redundancy are closely related and act synergistically to enhance resilience. For example, response diversity contributes to community stability only if the populations or species within the functional group can compensate for one another. Similarly, the benefits of functional redundancy are compromised if all species capable of replacing one another respond similarly to environmental fluctuations (Elmqvist et al. 2003). However, the net effect of diversity on recovery rates and overall community composition depends on the frequency and magnitude of disturbance. Thus, the increased frequency of extreme weather events associated with climate change may threaten even the most diverse communities.

Low-diversity functional groups play many key roles in marine ecosystems. For example, biogenic habitat provisioning is a functional role carried out by relatively few species in some systems (Bertness 2007, Micheli & Halpern 2005, Reusch 2002). The Atlantic coast's cordgrass-dominated salt marshes, Florida Bay's eelgrass meadows, and Chesapeake Bay's historically abundant oyster reefs provide important fisheries, water filtration, and habitat services (Jackson et al. 2001). Loss of such foundation species can severely compromise coastal systems' resilience to climate change and other stresses. Furthermore, the diversity of higher trophic levels is threatened by overexploitation (Myers & Worm 2003, Worm et al. 2006). Because of overfishing, many coral reefs have low functional diversity, particularly of herbivorous fishes, and are vulnerable to shifts to algal-dominated states (Burkepile & Hay 2008, Hoey & Bellwood 2009). Thus, particular attention should be paid to the diversity of species within key functional groups, such as foundation species, grazers, and top predators, to maintain ecosystem functioning in the face of climate change.

We still have much to learn about the roles of biological diversity in generating ecological resilience. First, the effects of diversity on community properties other than biomass and population abundance deserve more attention. The effects of diversity on many other ecosystem functions relevant to ecosystem service production, such as rates of nutrient cycling or bioturbation, are largely unknown (Solan et al. 2004). Similarly, the relative importance of species diversity and functional group diversity in different ecological contexts remains unclear. Finally, much of the empirical evidence of diversity effects on resistance and recovery comes from relatively short-term experiments (e.g., two years) and needs to be complemented with longer-term studies (e.g., decades). (See, however, Reich et al. 2012 for a terrestrial example of how diversity effects change with time.) This information will be critical to forecasting the role of diversity in ameliorating ecosystem responses to climate change over the next century. However, adaptation to climate change impacts by people and other species is already under way and will not pause while multidecadal studies are completed. In light of this changing social-ecological context, adaptive management

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strategies, which incorporate new knowledge of ecosystem functioning as it becomes available, will be critical (as we discuss below).

Connectivity Enhances Capacity for Recovery and Self-Organization

Another key component of resilience is the degree to which an ecosystem is capable of self-organization and recovery. Connections at multiple scales of biological organization enhance capacity for self-organization and recovery from disturbance. We find evidence that a broad range of connections is important, including interactions among species within a local community and connections among populations, communities, and ecosystems through both space and time (**Figure 2*b***). The strength and number of these varied connections determine their effect on the recovery and self-organization components of ecological resilience, as we describe below.

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Strength of species interactions. Recent theoretical and empirical work has demonstrated the skew toward weak interactions in food webs and highlighted their importance in maintaining community stability over time (Emmerson & Yearsley 2004). Weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer-resource interactions and facilitative interactions. In addition, weak interactions can generate negative covariances between resources, ensuring that consumers have weak consumptive influences on a resource when the resource is at low densities (McCann 2000). For example, the effect of weak predation by whelks on intertidal mussels switches in sign from negative to positive depending on the recruitment of barnacles (a secondary prey item for the whelk), and overall, weak predation is much more variable than strong predation in other ecological contexts (Berlow 1999). Such context-dependent weak interactions generate a variety of species' responses and contribute to patterns of self-organization, diversity, and stability at the seascape scale.

In contrast, ecosystems dominated by strong interactions are more vulnerable to disturbance because of the potential destabilizing effect of the loss of one key interacting species (Arnott & Vanni 1993, Crooks & Soule 1999, Estes & Palmisano 1974, Jackson et al. 2001, Menge 1976). For example, removal of a single strongly interacting species in a rocky intertidal system, such as the predatory sea star *Pisaster*, can result in greatly simplified lower-intertidal communities because the mussel *Mytilus californianus* competitively dominates all other sessile benthic organisms when freed from predation (Paine 1966). Similarly, disruption of strong nontrophic interactions, such as facilitation by the habitat-forming salt marsh species *Spartina alterniflora* (Bertness 1984) or symbiotic relationships between corals and zooxanthellae (Knowlton 1992), is likely to have community-wide effects.

Number of species interactions. Theory predicts that ecological resilience increases with the number of links per species in food webs (Dunne et al. 2002, Paine 1980). Ecosystems with few links are extremely sensitive to the removal of any given species, and many secondary extinctions may result (Dunne et al. 2002). In contrast, in highly connected food webs, the onset of secondary extinction is delayed. Marine food webs tend to be characterized by greater connectance (i.e., the fraction of all possible links among species, after Dunne et al. 2002) and longer food chains compared with terrestrial food webs (Bascompte et al. 2005, Dunne et al. 2004, Paine 1992). These characteristics could stabilize webs in the face of perturbations associated with climate change. However, few empirical tests of the influence of either connectance or food chain length have been conducted in marine systems, and thus the importance of these characteristics is an open question. (See, however, Long et al. 2011 for a recent test of both on the stability of a subtidal food web.)

Population connectivity. The movement of propagules, larvae, or adults among populations may reduce the risk of local extinctions because populations can be reseeded by individuals from other sites (Provan et al. 2009). In contrast, species that produce young that develop within meters of their parents are relatively isolated from nearby populations, and are at risk of local extinction because they cannot depend on propagule input from other populations. For example, California kelp forests are frequently subjected to major disturbances such as storms, grazer outbreaks, and high-temperature–low-nutrient water conditions caused by El Niño, all of which can cause massive localized mortality (Dayton 1985, Dayton et al. 1992). After such disturbances, kelp beds depend on spore delivery or drifting kelp from other beds for recovery. Similarly, for Australian corals, Underwood et al. (2007) found that recovery rates from bleaching were enhanced by immigration from unaffected sites, and that only those sites that were demographically connected to undisturbed sites recovered to pre-bleaching levels.

Ecosystem connectivity. The movement of organisms and organic materials between ecosystems is a ubiquitous and often essential component of community persistence (Mumby & Hastings 2008, Polis et al. 1997). For example, nutrient and larval delivery from oceanic waters can be a key bottom-up structuring element in intertidal communities (Menge 1992). Rocky shore filter feeders, including barnacles and mussels, benefit from increased food supply in areas of coastal upwelling, and these connections can enhance recruitment, reproductive capacity, and adult abundances in certain contexts. In mangrove ecosystems, sediment and organic matter inputs from rivers facilitate accretion processes and therefore enhance mangroves' capacity to keep up with sea level rise (Pernetta 1993). Although moderate levels of allochthonous inputs (i.e., inputs from outside the ecosystem) can stabilize food webs by providing an alternate prey resource (McCann et al. 1998), very high levels can have destabilizing effects by, for example, enabling consumers to deplete prey populations (Rosenzweig 1971). Thus, although the flow of materials between ecosystems may enhance resilience by facilitating recovery, the net effect of cross-ecosystem subsidies will depend on the magnitude of the subsidy. Moreover, further empirical tests are needed; our understanding of allochthonous inputs on marine communities comes primarily from theoretical models of food web dynamics.

Ecological memory (connectivity in time). Ecological memory refers to the species and habitats in a particular place that facilitate recovery following disturbance. Nyström & Folke (2001) identified three components of ecological memory: biological and structural legacies, link species, and intact support areas. Biological legacies are organisms or organic material that persist through disturbance and are incorporated into the recovering ecosystem. In mangrove ecosystems, for example, herbaceous species play an important role in facilitating mangrove recovery by trapping mangrove propagules and ameliorating soil conditions following disturbance (McKee et al. 2007). Structural legacies, such as coral fragments and rubble in coral reef systems or barnacle tests in rocky shore systems, play similar roles. Link species are those that disperse between disturbed and undisturbed patches, either actively (e.g., adult fish) or passively (e.g., invertebrate larvae or algal spores). For example, in the case of coral reefs, mobile herbivorous and predatory fish can transport symbiotic zooxanthellae between reefs (Muller-Parker & D'Elia 1997). Support areas are those left relatively intact following disturbance, and they can serve as refugia for mobile link species and as sources of larvae. For example, rocky intertidal cold spots on the US West Coast (Helmuth et al. 2002), created by the timing of low tides and fog, may serve as thermal refugia for intertidal organisms during heat waves and may also be sources of larvae, which can later recolonize highly disturbed areas. Coastal systems characterized by high functional diversity and habitat heterogeneity are more likely to include these components of ecological memory.

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Modularity. Modularity is the opposite of connectivity: It refers to the compartmentalization of populations in space and time (Levin & Lubchenco 2008). Modularity may contribute to an ecosystem's resistance to disturbance and its ability to regenerate following disturbance. For example, where populations are too closely connected, severe disturbances to one population (such as oil spills, hurricanes, or disease) may affect all populations (Allison et al. 2003). However, where populations are separated in space, disturbances to some will not impact all, and unaffected populations may provide important regional sources of larvae and other materials for recovery.

The importance of these different forms of connectivity depends on context-specific factors such as the frequency, magnitude, and extent of disturbance events. For example, although weak indirect interactions may stabilize ecosystems in response to relatively moderate fluctuations in resource supply, indirect interactions may also impede recovery following extreme disturbances such as oil spills. However, the relative importance of interaction strength, connectance, and other forms of connectivity is largely unknown. Trade-offs among the multiple forms of connectivity are likely (Levin & Lubchenco 2008).

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Ability to Adapt to the Changing Climate over the Next Century and Beyond

The ability of species and ecosystems to adapt to changing conditions, or their adaptive capacity, is an essential component of ecological resilience. Adaptive capacity in the face of a changing climate will include a combination of organism-level plasticity, species range shifts, and rapid evolution of traits better suited to new conditions (**Figure 2*c***) (Williams et al. 2008). Characteristics such as tolerance of environmental stress, dispersal ability, and potential for genetic change all contribute to these adaptive strategies. The relative importance of each of these strategies will depend on the species or ecosystem and its environmental context.

Tolerance of environmental stress and capacity to acclimate. The ability of an organism to maintain functioning in the face of increasing environmental stress depends on its acclimation capacity (Somero 2005). In many cases, phenotypic plasticity may be the most important component of adaptive potential because plasticity acts within a generation, whereas dispersal and evolutionary genetic change involve multiple generations (Hoffmann & Sgrò 2011). However, there are several constraints to plasticity. First, there are potentially large fitness costs associated with immediate plastic responses. Second, species that have evolved under fairly constant temperature conditions or live close to the limits of their environmental tolerances may lack the flexibility of gene expression needed for further thermal acclimation (Somero 2005). For example, Southern Ocean species die of acute heat stress when exposed to temperatures only a few degrees above their normal habitat temperatures (Peck et al. 2004, 2009). Surprisingly, several studies that have examined the acclimation capacity of congeneric rocky shore species living at different latitudes and shore heights have found that the most heat-tolerant congeners are least able to acclimate to increasingly warm conditions, probably because they are living closest to their physiological limits (Berger & Emlet 2007, Somero 2010, Stillman 2003). As we discuss below (see Evolutionary Potential), it is unclear whether these patterns translate to the metapopulation level—that is, whether populations living in more environmentally stressful regions tend to be less resilient to climate change.

Variation in thermal tolerances and capacity to acclimate among species within a community can have important effects on ecosystem structure and functioning (Menge & Sutherland 1987, Peck et al. 2009, Philippart et al. 2003). As the climate warms and species within different functional groups survive at different rates, the nature and magnitude of different ecosystem processes may change.

Dispersal ability. A species' ability to expand its range into more climatically suitable habitats is a critical component of adaptation to climate change (Parmesan 2006). The ability to disperse within and across habitats to track the changing climate will depend on reproduction and dispersal rates. For most marine species, the early life stages are the most motile. The dispersal distances of marine organisms range from centimeters to thousands of kilometers and are a function of oceanography, water temperature, food availability, and life-history traits (Kinlan & Gaines 2003, O'Connor et al. 2007). For example, macroalgae disperse much less widely than fish and some invertebrates (Kinlan & Gaines 2003). Similarly, mean larval duration varies significantly among biological communities: Approximately 80% of rocky intertidal organisms have widely dispersing larvae, whereas most sandy intertidal organisms have nonplanktonic, short-distance offspring (Grantham et al. 2003). Dispersal ecology will likely impact range expansion and other biogeographic patterns in the face of climate change. Some essential habitat-forming (or foundation) species like kelps and corals disperse short distances, thereby potentially limiting the establishment of communities in newly climatically suitable locations.

Evolutionary potential. As the changing climate imposes a new selection regime on Earth's biota, a species' evolutionary potential may increase its resilience to climate change. Increasing environmental stress will impose directional selection for resistance, particularly in species living close to physiological limits that may be exceeded in the coming decades, such as the intertidal porcelain crab (Stillman 2002). For example, an increased frequency of heat waves will impose selection by causing excess mortality and rapidly selecting for more heat-tolerant genotypes (e.g., of coral symbionts; Baker et al. 2004). In addition, changes in seasonality may select for distinct phenological patterns (Bijlsma & Loeschcke 2005). Evolutionary theory predicts that a species' capacity for "evolutionary rescue" in the face of rapidly changing environmental conditions depends primarily on population size, the quantity of genetic variance on which natural selection can act, and the organism's life span (Bell & Gonzalez 2009, Hoffmann & Sgrò 2011, Willi et al. 2006).

Evolution is responsive to climate variation and can occur on timescales relevant to current anthropogenic climate change (Skelly et al. 2007). For example, several studies have found evidence for the recent evolution of phenology (Edwards & Richardson 2004, Mackas et al. 2007, Philippart et al. 2003, Réale et al. 2003) and thermal tolerance (Grosholz 2001). Further, many marine species show geographic variation in thermal performance within their range, which may be evidence of localized evolution in response to climate variation and suggests the potential for future evolution. For example, Henkel & Hofmann (2007) found that the maximum temperature threshold for heat-shock protein synthesis in the kelp *Egregia* was higher in southern than in northern populations. Similar patterns have been shown in a rocky intertidal whelk (Sorte & Hofmann 2005), the killifish *Fundulus* (Fangue et al. 2006), and kelp crabs (Storch et al. 2009). More recently, Kuo & Sanford (2009) demonstrated that geographic variation in heat tolerance in the predatory snail *Nucella canaliculata* has a genetic basis. These patterns are evidence of past evolution, but they do not reveal the number of generations required to produce such divergence. Thus, although the potential for evolution exists in some species, it is unclear whether the rates of evolution characterizing whole marine communities can keep up with the rate of climate change. Far more empirical data are needed to test evolutionary potential across groups of species, especially those sensitive to environmental extremes.

Indeed, genetic limitations might prevent many species from evolving quickly enough to keep up with the changing climate. A small effective population size can limit evolutionary responses, as small populations often have high levels of inbreeding and low levels of genetic variation and are subject to genetic drift and demographic stochasticity (Willi et al. 2006). Evolution rates

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may decay over time owing to the loss of genetic variation as alleles become fixed. For example, Kelly et al. (2012) found that broadly distributed intertidal copepods were not able to evolve significantly higher thermal tolerances over the course of 10 generations of strong selection. Further, some marine organisms that have adapted to stable conditions, such as cold and well-oxygenated environments, may lack functional genes coding for proteins and regulatory systems required for coping with warmer conditions (Somero 2010). Finally, asymmetric gene flow from interior to edge populations may limit response to selection at range edges, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997). For example, Dawson et al. (2010) concluded that the northern range limit of an intertidal barnacle is limited by the migration load arising from a very high flow of maladaptive alleles into peripheral locations. Gene flow may act in combination with other factors like trait interactions (Angert et al. 2008) and demographic effects (Bridle et al. 2010) to constrain evolution. Thus, although evolutionary responses will be an important component of population- and ecosystem-level resilience to climate change, we expect that variation in both ecological and evolutionary responses by key taxa will likely result in a number of unexpected shifts in the structure and functioning of coastal marine ecosystems. These findings illustrate the need for more empirical studies that assess the relative importance of demography, plasticity, and genetic change for population persistence in a changing climate.

MANAGING FOR RESILIENCE TO A CHANGING CLIMATE

As climate change erodes ecological resilience, ecosystems become more susceptible to regime shifts and the loss of valuable ecosystem services. Through changes in temperature, ocean pH, and oceanography and the resulting shifts in species distributions and interactions, climate change impacts are reducing diversity, disrupting connectivity, and impeding adaptation (see sidebar Climate Change Effects on Resilience). Thus, two important questions arise: First, how can we detect losses in resilience? And second, how can management strategies enhance resilience?

Detecting Losses in Resilience and Ecosystem Functioning

Understanding the warning signals of impending regime shifts and thresholds is critical to maintaining ecosystem functioning. Yet most thresholds in real systems—particularly lakes, where

CLIMATE CHANGE EFFECTS ON RESILIENCE

Rising air and water temperatures, changes in ocean circulation, and increased storm frequency have the potential to disrupt ecological mechanisms that contribute to resilience. For example, warming air and water may lead to decreased response diversity and functional redundancy due to range shifts, extinctions, and invasions associated with these increased temperatures (e.g., Perry et al. 2005, Sorte et al. 2010, Southward et al. 2005). Warmer temperatures may increase feeding rates and thus interaction strengths (Sanford 1999) and may alter the timing of life-history events, leading to trophic mismatches (Edwards & Richardson 2004). Rising water temperatures may reduce population connectivity by reducing larval dispersal (O'Connor et al. 2007) and reproductive output (Wethey & Woodin 2008). Changes in circulation and increased storm frequency may reduce population connectivity by increasing offshore advection and sweeping larvae offshore, thereby decreasing larval dispersal to suitable habitats (Connolly & Roughgarden 1998). Lastly, as increasingly stressful conditions lead to declines in population size, adaptive capacity will be compromised for some species. Populations will become more susceptible to genetic drift and loss of diversity. As extreme events cause rapid selection for stress-tolerant genotypes, intense selection at one locus can decrease variability in the rest of the genome, thereby reducing the ability to respond to further climate changes (Hoffmann & Sgrò 2011).

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much of the ecological resilience work has been done—have been detected only after they have been crossed (Carpenter & Brock 2006). Direct evidence of thresholds among alternate states from controlled experiments is rare (Schröder et al. 2005, Thrush et al. 2009), although several indicators of impending shifts have been proposed, including increased temporal variability of key biological and physical variables (Carpenter & Brock 2006), increased return time from perturbations (van Nes & Scheffer 2007), and increased skewness in time series data (Guttal & Jayaprakash 2008). Unfortunately, gathering data for most of these indicators is resource intensive, and thus these approaches may be difficult to apply. Monitoring the underlying ecological components of resilience, such as species diversity or population size, may be a more tractable and efficient way for managers to track resilience over time.

In addition to indicators of impending regime shifts, considerable progress has been made in identifying reliable indicators of marine ecosystem functioning and resistance to disturbance, such as the proportion of predatory fish in a community and the biomass of detritivores (Essington & Punt 2011). When such indicators are linked to information on ecological thresholds, they can be used to develop targets and reference points to enable adaptive management, as we discuss below.

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Managing for Resilience

In the past decade, interest among policy makers, managers, and stakeholders in taking more integrated, ecosystem-based approaches to coastal and ocean management has grown (McLeod & Leslie 2009a). Marine ecosystem–based management efforts are place based, recognize the diverse linkages between humans and other components of the ecosystem, and focus on the range of benefits, or ecosystem services, that we receive from marine systems, including healthy fisheries, biodiversity conservation, renewable energy, coastal protection, and recreation. In contrast to traditional management measures, which often disregard ecological dynamics and interactions, ecosystem-based approaches, which include those focused on resilience, recognize the importance of multiple forms of diversity and connectivity in sustaining the resilience of socially desirable ecosystem conditions over varied spatial and temporal scales (Folke et al. 2004, Hughes et al. 2005, Leslie & Kinzig 2009). Ecosystem-based approaches include but are not limited to place-based management strategies, ecosystem-based climate adaptation and restoration efforts, and interdisciplinary research that generates the rich biophysical and socioeconomic information needed to proactively manage coupled human-ocean systems.

Place-based management. Place-based management approaches include coastal and marine spatial planning (CMSP), fully protected marine reserves, and other types of marine protected areas (MPAs). CMSP refers to efforts to proactively consider the interactions among and cumulative impacts of different human activities in coastal and ocean spaces (Foley et al. 2010). Although CMSP is a nascent effort in the United States, this comprehensive approach draws on a long tradition of marine and terrestrial conservation planning globally, including the implementation of MPAs for biodiversity conservation and other targeted goals (reviewed in Leslie 2005). For example, in Australia, the Great Barrier Reef Marine Park (GBRMP) includes a mosaic of fully protected marine reserves and other, less restrictive zones designated for particular uses. Australia recently conducted a management review of the GBRMP, and as a result increased the overall area of fully protected zones from 4% to 33% of the total park (Fernandes et al. 2005). Importantly, this review included consideration of connectivity among individual reserves and of the inclusion of a diversity of habitat types (and key species) present throughout the park. In these and other ways, the adaptive management approach of the GBRMP is emblematic of how knowledge of diversity, connectivity, and related characteristics of marine ecosystems can help guide conservation and management efforts.

Implementing fully protected (or no-take) marine reserves and other types of MPAs is one strategy for maintaining or increasing the multiple forms of diversity, connectivity, and adaptive capacity known to enhance resilience. In some cases, marine reserves are already being implemented with resilience principles in mind (see sidebar Case Studies of Managing for Resilience) (McLeod et al. 2009). For example, areas with high species diversity or many endemic species can be targeted for marine reserves to maintain functional redundancy and response diversity (**Table 1**). Kelp forests within reserves have been found to be more resilient to ocean warming than forests in fished areas because the diversity of predators in these fully protected reserves keeps grazers in check (Behrens & Lafferty 2004).

Protecting key environmental refugia—as is being done through the Nature Conservancy Reef Resilience program—may stabilize interspecific interactions and increase ecological memory, thereby enhancing the capacity for recovery following a disturbance. Similarly, protecting multiple sites of the same habitat type will reduce the risk of all MPAs being affected by the same disturbance and allow population connectivity to facilitate recovery (Allison et al. 2003, Green et al. 2009). Spacing reserves in the range of 10–100 km apart should facilitate replenishment via larval dispersal for many species following disturbance (Gaines et al. 2010). MPAs that incorporate multiple habitat types, such as mangroves, coral reefs, and seagrass beds, will enhance ecosystem connectivity (Mumby 2006).

Finally, marine reserves can explicitly enhance the adaptive capacity of coastal species (**Table 1**). Larger reserves, with larger populations of key species, may contribute to the maintenance of higher genetic diversity (Gaines et al. 2010). Reserves should aim to conserve several thousand (versus several hundred) individuals to ensure that evolutionary potential is maintained (Sgrò et al. 2011). Siting reserves along environmental gradients can enhance their long-term capacity to sustain large, genetically diverse populations, and can also allow for migration and maximize opportunities for in situ adaptation. Interconnected reserves will help increase population size, increase links to refuge areas, and facilitate in situ adaptive evolution by encompassing a range of habitats. Such climate-motivated reserve designs also enhance population and ecosystem connectivity on ecological timescales.

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CASE STUDIES OF MANAGING FOR RESILIENCE

The Nature Conservancy Reef Resilience program combines place-based knowledge of the environmental context (e.g., bathymetry, oceanography) of priority coral reefs and knowledge of where corals and their associated symbionts are more likely to be resistant to bleaching or perhaps better able to bounce back from such stresses (McLeod et al. 2009). For example, in designing and implementing a network of MPAs in Kimbe Bay, Papua New Guinea, practitioners incorporated resilience principles such as maximizing risk spreading (i.e., modularity), connectivity, and habitat diversity (Green et al. 2009). These principles have also been applied in other Pacific Islands, the Mesoamerican Reef, the Caribbean, and the Western Indian Ocean. Monitoring MPA networks as experiments over the next several decades will empirically test the effectiveness of using resilience principles to maintain ecosystem functioning, and will clarify the relative importance of protecting or enhancing different resilience components. Similarly, in Great South Bay in New York State, activities by the Nature Conservancy and partners have focused on restoring shellfish populations by protecting spawner sanctuaries. Restoring shellfish is anticipated to contribute to improved water quality and habitats for other species, as well as to provide economic benefits. (**http://www.coastalresilience.org**).

Table 1 Management strategies to enhance coastal marine ecosystem resilience

Resilience component	Ecological mechanism	Management strategies
Diversity	Functional redundancy	Limit overharvest; manage at multiple spatial scales; place reserves in areas of high species diversity and high habitat complexity
	Response diversity	Limit overharvest; protect heterogeneous habitats
Connectivity	High connectance	Distribute extraction across trophic levels to maintain intact interactions, or limit extraction
	Population connectivity	Create reserve networks; restore degraded habitats; prevent habitat fragmentation; protect replicate areas of the same habitat type
	Ecosystem connectivity	Protect ecologically connected habitats within an area (e.g., mangroves, coral reefs, and seagrass beds); limit land-based nutrient pollution
	Biological legacies	Limit postdisturbance extraction and extraction of highly resistant species; protect climate refugia and areas where populations include diverse age classes, including reproductive individuals that provide a propagule source
	Modularity	Space reserves to buffer against disturbance; protect climate refugia
Adaptive capacity	Plasticity	Protect climate refugia, where plasticity is highest; maintain genetic diversity and habitat heterogeneity
	Dispersal ability	Protect dispersal "corridors": place networks of reserves along climate gradients and protect landward edges of wetlands to facilitate landward migration
	Population size	Create large and/or connected reserve networks; manage for adequate effective population sizes
	Genetic variation	Manage for evolutionarily significant units; create large reserves across environmental gradients to sustain larger, more diverse populations; restore with individuals sourced from climatically diverse populations

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Ecosystem-based adaptation and restoration. Ecosystem-based climate adaptation and restoration efforts target system properties—particularly connectivity and adaptive capacity—that contribute to population and ecosystem resilience. Marine managers as well as scientists increasingly recognize that ecological resilience can play an important role in fisheries, water quality, coastal hazards mitigation, and other marine management goals (e.g., Commonw. Mass. 2009, Samhouri et al. 2012, US Comm. Ocean Policy 2004). For example, gear restrictions that limit bottom trawling can prevent habitat destruction and maintain habitat heterogeneity and ecological memory. Restoration projects that source individuals from climatically diverse locations can enhance adaptive capacity. Limits on coastal development will limit coastal erosion and allow for inland migration of wetlands, thereby protecting key habitats that serve as nursery and breeding grounds. Similarly, US government plans for recovery and restoration following the 2010 oil spill in the Gulf of Mexico highlight climate change effects on both ecological and social resilience as well as how these effects may be addressed by future restoration efforts (e.g., **http://www.coastalresilience.org**). Conservation nongovernmental organizations have also elevated resilience considerations, particularly in the marine realm (see sidebar Case Studies of Managing for Resilience). As the magnitude and scale of many climate change effects are uncertain, resource managers should opt for restoration strategies that will enhance ecosystem functioning under a wide range of potential future climate scenarios (Lawler et al. 2009).

Interdisciplinary research. Sustainability science—a transdisciplinary field of research dealing with the interactions between natural and social systems—recognizes the context dependency of

each of the resilience properties we discuss above. Not only do nonhuman species' adaptive capacity, demographic and ecosystem linkages, and other ecological and evolutionary mechanisms play a large role in whether and how a coastal ecosystem is resilient to climate change, but there are also critical linkages between the human and ecological domains that influence ecological resilience. Diverse examples from fisheries, wetlands, and water management illustrate the importance of linking management institutions across different spatial scales to ensure that the ecological components of resilience—which may well cross political and socioeconomic boundaries—are maintained (Liu et al. 2007, Wilson 2006). The research enterprise of sustainability science continues to grow (e.g., see Clark & Dickson 2003, Kates 2011), and the climate and fisheries sciences provide many examples of use-inspired research relevant to the marine science community in particular (Rosenberg & Sandifer 2009, Tribbia & Moser 2008). Engaging conservation practitioners, managers, and other stakeholders in the scientific process can be incredibly valuable, in terms of hypothesis generation and model validation as well as actual knowledge production (Stokes 1997).

Adaptive management. Regardless of the specific strategy employed, adaptive management is essential to maintaining ecological resilience in the face of climate change. Monitoring proxies of ecological resilience such as species diversity, population sizes, and genetic diversity can aid resource managers in tracking the efficacy of particular management strategies as well as changes in coastal marine ecosystems due to climate variability and exogenous drivers (see sidebar Case Studies of Managing for Resilience). Recent analytical advances can facilitate the monitoring of resilience proxies. For example, because of the difficulty of measuring adaptive genetic diversity, this form of diversity has not yet been considered a priority in most conservation planning. However, recent advances in genotyping techniques enable the estimation of adaptive genetic diversity in a range of organisms. For example, genome-wide scans across large geographic scales can enable the detection of genomic regions under selection (Sgrò et al. 2011).

CONCLUSIONS

Our oceans are peopled, and have been for millennia (Lotze et al. 2006, Shackeroff et al. 2009). However, the rate, intensity, and duration of climate change present a novel threat to these systems that permeates all levels of biological organization (Intergov. Panel Clim. Change 2007). The temporal scaling of global climate dynamics ensures that background environmental conditions will continue to fluctuate over at least the next century (Intergov. Panel Clim. Change 2007). Thus, a wide array of coastal marine ecosystem services on which we depend are at risk (Doney et al. 2012, Hoegh-Guldberg & Bruno 2010). Many traditional management strategies are not well equipped to deal with the effects of climate change because they are often sector or species specific and rely on data from a limited number of samples in space or time. In contrast, resilience- or ecosystem-based approaches emphasize the dynamic nature of ecosystem functioning—and human interactions within ecosystems—over time. Applications of resilience science are relatively new, but suggest that this perspective can advance marine conservation and management (Halpern et al. 2012, Leslie & Kinzig 2009).

Ultimately, managing for resilience will involve balancing trade-offs between its different components (Levin & Lubchenco 2008). For example, maximizing population connectivity may undermine adaptive potential by reducing the capacity for local adaptation. The relative importance of each resilience component will depend on context. For example, for a long-lived species in a rapidly changing habitat, managers may prioritize maintaining dispersal potential and population connectivity over genetic diversity, so as to facilitate a range shift rather than maintaining adaptive potential. Another challenge will be to balance the benefits of managing for ecological resilience with the associated social and economic costs.

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Although managing for resilience may provide a means of sustaining ecosystem services in the face of climate change, resilience could also be viewed as an ecosystem service itself (i.e., a form of ecological insurance). Climate change and other anthropogenic impacts often compromise the ecological mechanisms that contribute to resilience. Yet because ecosystem dynamics are often nonlinear, detecting impending losses in resilience and ecosystem functioning is difficult. A critical challenge for scientists is to develop and monitor a suite of ecosystem attributes that can be used in the short term to track resilience components (i.e., diversity, connectivity, and adaptive capacity, or proxies thereof) and to forecast changes in ecosystems and the services they provide.

Although managing for resilience is not easy, nongovernmental and governmental organizations around the world have recognized its importance and have made substantial headway toward implementing resilience-based approaches. Protecting the ecological mechanisms that allow ecosystems to resist, recover from, and adapt to climate change will help to ensure that coastal marine ecosystems persist and continue to provide the benefits that people value over the next century and beyond.

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SUMMARY POINTS

1. Biological diversity plays an important role in enhancing resilience by increasing the likelihood that some species and/or functional groups will be resistant to perturbation, allowing species to compensate for one another within a community, and facilitating ecological processes vital for recovery and adaptation.
2. Multiple forms of connectivity (e.g., among species, populations, and ecosystems) can stabilize ecosystems under moderately fluctuating environmental conditions and enhance recovery following more severe disturbances.
3. Adaptation to the changing climate will include a combination of organism-level plasticity, species range shifts, and rapid evolution of traits better suited to new conditions.
4. Ecosystem-based approaches to marine management and conservation, including those focused on resilience, emphasize the dynamic nature of ecosystem functioning—and human interactions within ecosystems—over time.

FUTURE ISSUES

1. The effects of diversity on community properties other than biomass and population abundance are largely unknown. The importance of diversity for ecosystem functions relevant to ecosystem service production, such as rates of nutrient cycling or bioturbation, requires more attention.
2. Understanding of multiple forms of connectivity (from food web structure to the flow of materials among ecosystems) is limited. Testing theoretical predictions in real ecosystems is essential.
3. Much remains to be learned about the relative importance of diversity, connectivity, and adaptive mechanisms in different marine systems. If the resilience framework is to effectively influence resource management, these elements must be investigated empirically in more systems and over longer timescales.

4. Further understanding of the relative importance of phenotypic plasticity and genetic variation in generating adaptive capacity in real ecosystems could help guide future strategies to manage for ecological resilience.
5. Assessment of MPAs and other management and conservation strategies should include monitoring of ecosystem attributes related to diversity, connectivity, and adaptive capacity. Identifying specific indicators related to each of these resilience elements remains a key challenge.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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