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Resilience, Robustness, and Marine Ecosystem-based Management

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Marine ecosystems provide essential services to humans, yet these services have been diminished, and their future sustainability endangered, by human patterns of exploitation that threaten system robustness and resilience. Marine ecosystems are complex adaptive systems composed of individual agents that interact with one another to produce collective effects, integrating scales from individual behaviors to the dynamics of whole systems. In such systems, small changes can be magnified through nonlinear interactions, facilitating regime shifts and collapses. Protection of the services these ecosystems provide must therefore maintain the adaptive capacities of these systems by preserving a balance among heterogeneity, modularity, and redundancy, tightening feedback loops to provide incentives for sound stewardship. The challenge for management is to increase incentives to individuals, and tighten reward loops, in ways that will strengthen the robustness and resilience of these systems and preserve their ability to provide ecosystem services for generations to come.

Keywords: complex adaptive systems, scale, resilience, robustness, ecosystem management

Humans and their societies depend on natural systems for a wide range of services that are essential for their well-being. For most of human history, these services have been readily available. It is little surprise, then, that present-day societies tend to take many of these natural services for granted (Daily 1997, Millennium Ecosystem Assessment 2005a, 2006a, 2006b, 2006c, 2006d, 2006e), even while the support systems that provide the services are being severely degraded (Vitousek et al. 1997, Lubchenco 1998). Fisheries and other resource systems have declined drastically (Pauly et al. 1998, 2002, Myers and Worm 2003, Millennium Ecosystem Assessment 2006f, 2006g, Worm et al. 2006) as a result of overfishing, bycatch, habitat destruction, nutrient and chemical pollution, and selective fishing on apex predators; oceans are warming and becoming more acidic (Orr et al. 2005, Royal Society 2005); and novel and reemergent diseases and other invading species have burgeoned as problems (Ward and Lafferty 2004).

In the face of these growing challenges to the abilities of human societies to achieve and maintain meaningful and productive lifestyles, we must direct attention to issues of sustainability. For ecosystem services to be sustained over time, the ecosystems providing them must be able to continue functioning in essential ways despite disruptions. In other words, they must be robust and resilient, concepts that have developed somewhat independently in diverse scientific communities to mean much the same thing: the capacity of systems to keep functioning even when disturbed. For the purposes of this article, the central question is this: how do we increase the robustness or resilience of the systems that provide critical ecosystem services, while overcoming the robustness or resilience of systems that yield undesirable phenomena?

Given the century-long history of theory on the dynamics of ecological systems (going back at least to the work of the great mathematician Vito Volterra) and the practice of managing those systems, we can pose two critical questions: (1) Why has management not been more successful? and (2) Why are we still uncertain about how best to manage crises arising from the magnitude of human impacts on our environment? The central problem is that both natural and socioeconomic systems are complex: they are characterized by multiple possible outcomes and by the potential for rapid change and major regime shifts due to slower and smaller changes in exogenous or endogenous influences (Levin 1999,

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Carpenter 2002). Indeed, they are complex adaptive systems in which the dynamics of interactions at small scales percolate up to shape macroscopic system dynamics, which then feed back to influence the smaller scales (Levin 1998, 2003). It is crucial, then, to understand the linkages among these scales, and to incorporate that knowledge into public awareness, management actions, and policy decisions.

The vulnerability of marine ecosystems, the value of the ecosystem services they provide, and the need for different approaches in understanding and managing human activities that affect oceans have received much recent attention. Reports from the Pew Oceans Commission (2003), the US Commission on Ocean Policy (2004), the Joint Ocean Commission Initiative (2006), the Millennium Ecosystem Assessment (2006f, 2006g), and Worm and colleagues (2006) draw attention to the seriously disrupted state of marine ecosystems, a result of climate change, coastal development, overexploitation of ocean resources, nutrient and chemical pollution from the land, and other anthropogenic influences. Disruption of marine ecosystems diminishes ecosystem services such as the provision of fish and other seafood, the maintenance of water quality, and the control of pests and pathogens. The collective conclusion of these reports is that if people wish to have safe seafood, stable fisheries, abundant wildlife, clean beaches, and vibrant coastal communities, priority must be given to protecting and restoring the coupled land-ocean systems that provide these services. Both the Joint Ocean Commission and the Pew Oceans Commission conclude that current public awareness, laws, institutions, and governance practices are insufficient to accomplish these goals.

A central recommendation of both commissions is to adopt ecosystem-based management (EBM), reinforcing earlier recommendations of the National Research Council (1999). The key challenges are to refine EBM further, and to develop a set of principles to guide management and policy. EBM for the oceans is the application of ecological principles to achieve integrated management of key activities affecting the marine environment. EBM explicitly considers the interdependence of all ecosystem components, including species both human and nonhuman, and the environments in which they live. EBM classically defines boundaries for management on the basis of ecological rather than political criteria, although certainly the political contexts of management must be considered. The goal of marine EBM is to protect, maintain, and restore ecosystem functioning in order to achieve long-term sustainability of marine ecosystems and the human communities that depend on them (Guerry 2005, McLeod et al. 2005, Rosenberg and McLeod 2005).

Marine ecosystems and socioeconomic systems are complex adaptive systems. To guide the design and implementation of marine EBM, it will be useful to draw on the knowledge and understanding that are emerging from the exploration of the resilience and robustness of complex adaptive systems. The articles in this special section of *BioScience* provide guidance about EBM by using the concepts of resilience and robustness as a lens for thinking about complex dynamic systems. Understanding how humans might enhance the robustness and resilience of the systems that provide critical ecosystem services, while thwarting the robustness and resilience of systems that yield undesirable phenomena, will be useful to society. This article summarizes the connections between human well-being and marine ecosystem services, explains why it is useful to think of marine ecosystems as complex adaptive systems, and describes resilience and robustness as they apply to ocean ecosystems.

What do we mean by resilience and robustness?

The concepts of robustness and resilience are widely used in the scientific literature, although there is considerable confusion about their meanings. The Resilience Alliance (*http://resalliance.org*) makes a distinction between *engineering resilience* (namely, "the rate at which a system returns to a single steady or cyclic state following a perturbation") and *ecological resilience* (namely, "the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures"). The latter definition, which reflects the focus of the Resilience Alliance, seems closest to that introduced by Holling (1973) in his seminal paper; but it is clear that the notion of resilience is sometimes interpreted in the general literature in the narrower sense of recovery from disturbance, and at other times in the broader sense of the maintenance of functioning in the face of disturbance. Within this article, we adopt the broader definition, and we do not distinguish it from robustness.

Parallel ideas have developed in other scientific communities. In materials science, two concepts are central: *stress,* or the force tensor applied to a system, and *strain,* or the deformation tensor that results from the application of the stress. These concepts have relevance for ecological systems as well, and failure to distinguish between stress and strain can lead to confusion. In the face of stressors, whether endogenous or exogenous, both the ability to resist deformation (strain) and the ability to recover from deformation are important. That is, it is important to recognize that there are two key aspects of what may be called robustness (or resilience): (1) resistance to change (as well as flexibility, the amount a system can be perturbed from its reference state without that change being essentially irreversible); and more generally, (2) the ability of the system to recover. Such a definition is also concordant with what in developmental biology is termed *developmental robustness*—namely, "the capacity to stay 'on track' despite the myriad vicissitudes that inevitably plague a developing organism" (Fox Keller 2002). In turbulent marine systems, for example, organisms may weather the waves (thereby achieving robustness) either by resisting fluid dynamical stresses with a rigid structure, as barnacles or corals do, or by going with the flow, as the flexible large kelp do. Considering these multiple aspects of robustness and resilience requires attention to the related concepts of resistance, recovery, and irreversibility, as developed in the article by Palumbi and colleagues (2008).

Whatever definition we choose, it is essential to identify the pattern or activity that is desirable to maintain—we must ask, "The robustness or resilience of what?" We are concerned simultaneously with a wide variety of natural and social systems. For some systems and activities, such as fisheries and sensible management practices, we seek to find ways to enhance resilience and robustness; for others, such as diseases and destructive patterns of overconsumption, resilience and robustness are impediments to achieving a sustainable future.

For the remainder of this article, we use the terms *robustness* and *resilience* interchangeably to mean the capacity of a system to absorb stresses and continue functioning. In considering robustness and resilience, scale is critical: what will work best over short timescales is not necessarily what will work best over the long term. Where natural selection has operated to increase the robustness of organisms within the constraints of particular environmental conditions, for instance, there is no reason to expect that robustness would be maintained if those conditions changed. Indeed, given that there are inevitable trade-offs in any process of selection, it is reasonable to expect that adaptation to one set of conditions may lead to disadvantages in changing environments. Similarly, what is best for a local community is generally not what will work best regionally or globally. Perhaps most important, robustness or resilience at the level of a whole system may be achievable precisely through the lack of robustness at the level of the individual agents that make up the system. Many diseases persist, despite our best efforts at management, because pathogens form complex adaptive systems in which robustness—of influenza, for example—at the level of subtypes is mediated through high mutation rates that allow the continual replacement of spent strains with novel ones, and at higher levels by reassortment events that create new subtypes. Thus, as we will explain further in the next section, diversity and the mechanisms that maintain it are essential aspects of the adaptive capacity of any resilient system. Similarly, achieving robustness typically requires the maintenance of sufficient variability at the level of the system's components, so that natural and other forms of selection can operate. That by itself is not sufficient, of course; there is no guarantee that individual selection will operate for the common good. An engineer attempts to optimize for properties such as robustness. In complex adaptive systems, in contrast, a different approach must be taken. An issue of fundamental interest is how different the robustness properties of complex adaptive systems are from systems that have been designed for robustness (Levin 1998). We turn to these and other related issues in the next section.

The example of influenza makes clear that not just spatial and temporal scales are important; so too is the organizational scale. That the robustness of an ensemble may rest upon the high turnover of the units that make it up is a familiar notion in community ecology. MacArthur and Wilson (1967), in their foundational work on island biogeography, contrasted the constancy and robustness of the number of species on an island with the ephemeral nature of species composition. Similarly, Tilman and colleagues (1996) found that the robustness of total yield in high-diversity assemblages arises not in spite of, but primarily because of, the high variability of individual population densities. Finally, the age-old debate in ecology as to whether diversity leads to stability is largely a semantic one (Levin 1999). Studies that focus on the densities of individual species find that more diverse assemblages are less stable by this definition (May 1972, 1973, Tilman and Downing 1994, Naeem et al. 1995), but it is no contradiction that such communities may be more robust regarding aggregate properties, such as species-abundance relations or nutrient cycling.

Ultimately, this dependence on context and level means that any management efforts must begin with careful consideration of the question, "The robustness of what?" In practice, this means identifying those aspects of ecosystems that are most precious in terms of the values that humans apply, and that brings into focus the importance of ecosystem services (Daily and Ellison 2002, Millennium Ecosystem Assessment 2005a, 2005b, 2006a, 2006b, 2006c, 2006d, 2006e).

Central themes in management, and throughout this special section, are the conditions under which robustness and resilience may be lost as a result of endogenous or exogenous influences. The dominant paradigm discussed here, borrowed from catastrophe theory (Thom 1975), is of a dynamical system characterized by multiple basins of attraction at any given point in time. Over fast timescales, such systems may be expected to approach (possibly dynamic) asymptotic states of lower complexity and dimensionality than the transient dynamics; over longer (slower) timescales, the shape of the dynamic landscape changes, and the stability of those asymptotic states may be compromised. The result may eventually, over even longer timescales, be a transition to a new asymptotic state. The changes may be subtle: erosion of adaptive capacity or buffering from the loss of biological diversity, say, may expose the system to the effects of novel perturbations, but the consequences may take a while to appear.

These concepts are directly relevant to our thinking about marine EBM and the goal of sustaining the ecosystem services provided by marine ecological systems. Since the term was first introduced (Ehrlich and Mooney 1983), the concept of "ecosystem services" has evolved (Daily 1997, Millennium Ecosystem Assessment 2006a, 2006b, 2006c, 2006d, 2006e). Ecosystem services are benefits that humans obtain from ecological systems. Four types of ecosystem services are now recognized: (1) provisioning services, such as food and habitat; (2) regulating services, such as the regulation of coastal erosion, climate, and outbreaks of pests and disease; (3) supporting services, such as primary production, sediment formation, detoxification and sequestration of pollutants, and nutrient cycling; and (4) cultural services, such as aesthetic, recreational, spiritual, religious, and other nonmaterial benefits (Millennium Ecosystem Assessment 2005a, 2006a, 2006b, 2006c, 2006d, 2006e). Mangroves, for example, provide nursery habitat; trap sediment; recycle nutrients; regulate diseases; protect land from coastal erosion; detoxify and sequester pollutants; provide food, fiber, and fuel; and offer recreational and other cultural benefits. The services, which vary according to the ecosystem, result from the interactions among the plants, animals, and microbes and their physical environment.

Coastal and marine ecosystems are affected by direct uses of those ecosystems (recreational and commercial fishing; aquaculture; other forms of recreation; drilling, extraction, and transportation of gas and oil; shipping; conversion of coastal habitats), as well as by upstream or upwind activities (agriculture, forestry, transportation, manufacturing, energy generation, etc.). As habitat is converted or fragmented, as species are lost, as biogeochemical cycles are altered, as introduced species and disease eliminate native species, as climate changes, and as oceans become more acidic, the functioning of ecosystems may be disrupted and the delivery of ecosystem services compromised. The challenge of EBM is to think holistically about the various factors that modify the functioning of ecological systems and about how to manage those activities in order to sustain the provision of their services over the long term.

Structure-function relationships

Although an engineering approach is insufficient for understanding the robustness of complex adaptive systems such as ecosystems and the biosphere, it can provide insights into what makes systems robust, and thereby provide a guide for management. Indeed, a fundamental challenge for control engineering is to extend the classical top-down approaches to develop a theory of optimal control of complex adaptive systems. For management, this means in part asking how the reward structure to individuals can be modified in ways to encourage behaviors that are in the common good.

Levin (1999) identifies a set of characteristics that are essential to sound management. In particular, with regard to robustness, the essential elements are diversity and heterogeneity, redundancy and degeneracy, modularity, and the tightness of feedback loops. These are not independent of one another; because of these trade-offs, and for other reasons that have nothing to do with trade-offs, the optimal robustness will typically be achieved at some intermediate level of each. Tight feedback loops, for example, may help to provide the reward structures that sustain systems, but they may also create the autocatalytic cycles that lead to the rapid breakdown of robustness. Thus, in arguing for robust management practices, we argue simply for considering these central elements, and finding the optimal trade-offs, both within each category and among categories.

Diversity and heterogeneity capture the adaptive capacity of a system, its ability to alter its composition in a changing environment. In evolutionary theory, Fisher's fundamental theorem of natural selection states that the rate of evolutionary change is proportional both to the selective differential and to the genic variance in the population. Without variance, there can be no adaptation; and without this adaptive capacity, populations are at risk. The same applies to changes at higher levels of organization—without variation, there can be no adaptive response. This use of the word "adaptive" should not be misconstrued: adaptation takes place in a complex adaptive system, but at levels below that of the whole system. There is no suggestion that such changes work to the benefit of the whole system; that remains to be examined, and the distinction is the principal reservation of evolutionary biologists about the romantic concept of Gaia (Lovelock 1979, Schneider and Boston 1991, Levin 1999, 2003).

It is well established that, at least in some circumstances, lowered diversity exposes ecosystems to catastrophic change. A classic example is agriculture, in which the low genetic diversity associated with preferred varieties makes systems highly vulnerable to pathogen outbreaks (Clay 2004); similar concerns have raised some red flags over aquaculture (Clay 2004). Agricultural systems, however, may not be entirely representative of natural systems in this regard, so investigation of the linkage between diversity and vulnerability to catastrophic change represents an important priority for research.

There is also evidence from marine ecosystems that higher diversity provides robustness (Millennium Ecosystem Assessment 2006a, 2006b, 2006c, 2006d, 2006e, Worm et al. 2006). In coral reefs in Jamaica (Jackson 1994, Jackson et al. 2001) and on rocky shores in Panama (Menge et al. 1986), removal of single species or single functional groups (such as herbivorous fishes) had little observable impact, because other species or functional groups (for example, other herbivores such as crabs, limpets, chitons, or urchins) could compensate for the function formerly performed by the removed species or group. Only when all groups were removed in either system (herbivores, historically, in the case of Jamaica; all consumers, experimentally, in the case of Panama) did a catastrophic change occur. A recent meta-analysis across multiple spatial and temporal scales in ocean ecosystems reinforces the conclusion that loss of biodiversity increases an ecosystem's susceptibility to abrupt change and is also likely to result in loss of ecosystem services (Worm et al. 2006).

Ehrlich and Ehrlich (1981), using the analogy of rivets on an airplane wing, called attention to the importance of having multiple copies of critical elements within ecosystems, so that the loss of a few rivets does not result in the loss of system functioning. Indeed, more generally, we are interested in the notion of functional redundancy, or what Edelman and Gally (2001) call "degeneracy," namely, the notion that multiple distinct elements perform the same function. Degeneracy captures features both of redundancy and of diversity; for example, having multiple different nitrogen fixers in a system means that if conditions change so that one is lost, the other may expand its role and fill the void. Though loss of redundancy may not be associated with immediate loss of function, the adaptive tolerance of the system will have eroded. Species in ecosystems, even those within a functional group, are not as similar to one another as are rivets on a plane. Nonetheless, they can perform overlapping functions; thus, through degeneracy (functional redundancy), one or more can compensate for the loss of others, as demonstrated experimentally in the Panama example noted above.

Modularity refers to the compartmentalization of the system in space, in time, or in organizational structure. The most evocative illustration of the importance of modularity is perhaps Herbert Simon's parable of the two watchmakers (Simon 1962), but many ecological examples exist to bring the lesson home. Simon compares two watchmakers, one of whom builds watches by first building modular components and later assembling them, and the second of whom simply builds the whole watch from scratch in a linear fashion. In the face of continual disturbances, the second watchmaker's work is never done, since he must start over again each time. Modularity, as practiced by the first watchmaker, confers robustness by locking in gains and compartmentalizing disturbances. Similarly, in epidemiology, it is well understood that diseases, especially sexually transmitted diseases, do not put all individuals at risk uniformly; rather, risk groups exist, with high mixing rates within these groups and lower mixing rates with other groups. Efforts at control therefore may attempt to capitalize on this modularity, containing the harm by minimizing the risk of transmission among groups. Such groups may be defined spatially, which is why so much attention in the battle against SARS (severe acute respiratory syndrome) was concentrated on minimizing intercity transport by airline travel. The importance of space, and of the compartmentalization of biodiversity into relatively isolated patches, is also central to theories of reserve design, as well as in forest fire management, in which the introduction of firebreaks is an effort to manipulate the compartmental structure of the forest.

More generally, the nature of the topological web of trophic and other ecological interactions has always fascinated ecologists (Paine 1980, Pimm 1982, Cohen 1989, Menge 1995). Paine, in his Tansley lecture to the British Ecological Society, elegantly develops the notion of tight modules, loosely connected to other modules, and their importance for the robustness of food webs (Paine 1980). The recent attention to small-world networks (large networks in which, because of their connectivity patterns, the distance between any two individuals is small; Watts and Strogatz 1998, Watts 1999) in a variety of settings has introduced a fascinating new set of tools for examining these topologies.

Recent theoretical work (Earn et al. 2000) elucidates the importance of the connectivity among subpopulations in determining the robustness of species, or of broader biological assemblages. Where populations are too tightly connected, insults to one affect all; modularity in the distribution of species allows species to fluctuate independently, buffering against unfavorable environmental conditions. Conversely, when populations are too loosely connected, stabilizing feedbacks do not operate effectively.

Attention to this suite of factors can provide helpful guides to management practice. For example, the management of Pacific salmon, which focuses on the "evolutionarily significant unit" (Waples 1992), involves choices about how much importance to accord particular subpopulations. The prevalent rules of thumb balance all three factors, choosing a few subpopulations to protect in each geographical area, but also emphasizing a diversity of subpopulations subject to different environmental regimes. Thus, diversity, redundancy, and modularity all enter into the equation (Ruckelshaus et al. 2008).

Finally, layered on top of these characteristics is the importance of tight feedback loops, which the spatial localization of interactions might engender. Modularity tightens feedback loops in general, but not necessarily with a concomitant increase in robustness. Tightening feedback loops can foster cooperation, but can also facilitate greed (Levin 2003). The lesson for management is that social norms that provide hope for equity in a global commons are essential.

Clearly, the concepts of resilience and robustness underpin effective EBM. The other articles in this special section expand on key concepts and empirical insights. Palumbi and colleagues (2008) examine the wealth of experimental, observational, and modeling information from marine ecology to understand the recovery, reversibility, and resistance of ecological systems. Hofmann and Gaines (2008) explore some of the powerful new technologies and tools available to provide novel insights into the dynamics of individuals, populations, communities, and ecosystems, ranging from DNA barcoding to satellite-based technology, acoustic sensing, and ecogenomics. Ruckelshaus and colleagues (2008) take on the challenge of applying much of the theoretical and empirical ecological information to real-world EBM decisions by analyzing key case studies and proposing general principles for implementation of EBM. The *Scientific Consensus Statement on Marine Ecosystem-based Management* (McLeod et al. 2005) summarizes for policymakers key areas of agreement about marine EBM. This collection will add significantly to our understanding of marine EBM.

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