Ecosystems in Action: Lessons from Marine Ecology about Recovery, Resistance, and Reversibility

STEPHEN R. PALUMBI, KAREN L. McLEOD, AND DANIEL GRÜNBAUM

The study of ecosystems in action, by measuring ecosystem recovery from disturbance, resistance to alterations, and the reversibility of ecosystem changes, highlights features of natural communities that contribute to resilience. Examples from marine intertidal and subtidal communities document the importance of species redundancy and complementarity in resistance and recovery, and they also show why recovery potential and resistance can differ from place to place within the same ecosystem. Whether a change is considered reversible may depend on the timescale of interest, and on whether fundamental new ecological processes have taken hold after a disturbance. By focusing on recovery, resistance, and reversibility as key components of resilience, marine ecologists have provided a much-needed empirical database about the response of the living world to human-mediated change.

Keywords: disturbance, sustainability, resilience, kelp forest, coral reef

In the face of natural or human disturbances, an ecosystem may be damaged and recover; it may resist the disturbance and remain fundamentally unchanged; or it may change irreversibly, persisting in a different state for a long period of time. All three of these features of ecosystem stability—recovery, resistance, and reversibility—are features of overall resilience or robustness (Levin 1999, Levin and Lubchenco 2008), are measurable features of ecosystems, and can serve as empirical targets for experimental and comparative studies.

These components of resilience, however, are nearly impossible to study in isolation. They are embedded in complex ecosystems, and as a result, their components must be studied within the context of their day-to-day function. Unlike the parts of a machine that can be broken apart for careful study in isolation, the components of resilience must be studied as they operate within functioning ecosystems.

Physicians are challenged to observe, diagnose, and repair living but damaged bodies. Similarly, ecosystem scientists must observe, diagnose, and repair living ecosystems while these ecosystems are in action. Mathematical models can greatly help researchers understand the behavior of real ecosystems, but field study of particular systems remains essential for understanding ecological functioning. Our goal here is to show how the study of ecosystems in action has revealed fundamental properties of resilience. Because the study of marine ecosystems in action has a long history (Paine et al. 1998, Levin and Lubchenco 2008), we can examine the lessons that have emerged from studying the responses of ecosystems to disturbance, and ask how that knowledge can illuminate fundamental ecological processes and inform future management plans.

The ecological stethoscope

The simple requirement that ecologists study ecosystems in action spawns enormous complexity in the design of ecological research programs and their interpretation. Especially in the context of recovery, reversibility, and resistance, observations of or experiments on living ecosystems are often the only way to increase our knowledge of the role of disturbance in natural systems, how environmental change will affect the delivery of ecosystem services, or how future environmental alterations might be expected to affect ecosystem dynamics. Placing an ecological stethoscope against the pulse of ecosystem recovery can tell us a huge amount about this process in the wild.

Stephen R. Palumbi (e-mail: spalumbi@stanford.edu) works with Hopkins Marine Station at Stanford University in Pacific Grove, California. Karen L. McLeod is with the Department of Zoology at Oregon State University in Corvallis. Daniel Grünbaum is with the School of Oceanography at the University of Washington in Seattle. © 2008 American Institute of Biological Sciences.

This information can have strong management implications, because it may signal the range of likely impacts from a given environmental change and inform choices among different management strategies. Unfortunately, however, information about ecological recovery is often incomplete or indirect.

The best information usually comes from the study of well-known ecosystems, where the component species, their interactions, and the environmental drivers of ecosystem change are relatively well studied. In many cases, the dynamics and history of well-studied ecosystems can resolve key questions for which scientists do not usually have even order-of-magnitude answers: If a system does recover, how long will it take? What level of disturbance precludes recovery? How will we know whether or not changes are reversible? In many cases, simple information about the scale of disturbances and the ecosystem response can provide key information to guide management. In other cases, it is possible to chart in detail the mechanisms of resistance to disturbance, or the mechanisms by which ecosystems recover.

Recovery from disturbance

Understanding how marine ecosystems respond to natural disturbance—and, just as important, how they recover from resulting changes—is critical to effective management. The balance between disturbance rates and recovery rates has long been known to be important in maintenance of community structure. If disturbance occurs at a rate that is faster than recovery, then ecosystems can change dramatically. In addition, a proper balance between recovery rate and disturbance rate is fundamental to ecological sustainability.

At the margins of land and sea, intertidal communities form a fringe of marine species stretching between the high and low tide marks. Rocky shores are frequently disturbed by the pounding of strong waves, which dislodges patches of sessile organisms such as mussels from their mooring (figure 1). The rate of recovery from disturbance events of different magnitudes and sources, such as wave exposure, changes in predator distributions, and physiological stress, has been particularly measurable in these environments, providing much insight into the role of disturbance in community structure (Paine and Levin 1981, Paine et al. 1998, Guerry 2005). Similar work on coral reefs, sea-grass beds, kelp forests, and other marine systems emphasizes that in some cases, partial recovery is the most natural community state.

Recovery rate. Because marine ecosystems can be space limited, when physical disturbance removes organisms, it frees up a limiting resource and affects the distribution of species. For example, after a boulder is rolled by intertidal waves, it can take one to two years for the boulder's substrate to recover its vertical zonation of plants and animals (Sousa 1984). From barnacles below to a forest of algae on top, the successional march that re-creates these spatial patterns varies with the amount of herbivory, the rate of settlement of sessile species, and the stability of the boulders themselves (Sousa 1984). Likewise, the regrowth of patches in mussel beds has been modeled as a balance between recovery and patch creation (Paine and Levin 1981). Other communities show similar patchy disturbance from fire, tree falls, hurricanes, landslides, or herbivore trampling, with similarly important balances between recovery rate and disturbance rate.

Recovery and productivity. More recently, comparisons of diverse ecosystems have focused on a different aspect of recovery: the importance of local productivity. In marine communities, for example, nearshore physical oceanography can change the amount of phytoplankton in the water, which alters the individual growth rates of filter-feeding invertebrates

Figure 1. Pounding surf along the US western coast (left) creates gaps in Oregon mussel beds (right) and provides lessons about recovery from disturbance. Photographs: J. Brock McLeod and Gary W. Allison.

such as mussels and barnacles (Menge et al. 1997). To what degree do such influences on productivity influence rates of intertidal recovery from disturbance? Where the delivery of phytoplankton and growth rates of mussels were higher, rates of recovery within experimentally cleared patches and in naturally occurring gaps in mussel beds were 10 to 15 times faster than in similar areas with lower productivity (Guichard et al. 2003). In this case, enhanced productivity arose from higher subsidies (e.g., phytoplankton) from the open ocean to intertidal ecosystems. The geographic mosaic of differing levels of upwelling creates a mosaic of subsidies, including nutrients and propagules, that can generate spatial variation in intertidal community recovery (e.g., Menge et al. 1997, 2003, Guichard et al. 2003).

This example shows that recovery rate can be fundamentally related to productivity, and that as rates of recruitment, growth, and survival increase, the recovery of populations within ecosystems increases. A positive relationship between increased productivity and recovery has been described in many ecosystems, from marine systems to freshwater to grasslands, sometimes with an explicit link between diversity and productivity (van Ruijven and Berendse 2007). The intertidal work emphasizes that other productivity-enhancing mechanisms besides diversity, such as subsidies or spatial variation in nutrient availabilty, can play a role in speeding recovery.

Disastrous lessons. One-time environmental disasters, such as oil spills, provide important lessons about the recovery of marine systems from disturbance. Ecologically important species can thwart simple recovery trajectories. The 1989 *Exxon Valdez* oil spill in Prince William Sound contaminated 1990 kilometers of shoreline with 40 million liters of oil. Sea otters, seabirds, harbor seals, macroalgae, and benthic invertebrates all experienced substantial and immediate mortality (Peterson et al. 2003). The recovery of the system was slowed by indirect interactions (Peterson 2001). On rocky shores, dramatic initial mortality of rockweed, a key provider of habitat in this environment, resulted in a cascade of indirect effects. For example, the loss of rockweed, coupled with losses of herbivorous and predatory gastropods, promoted blooms of ephemeral green algae and, later, an opportunistic barnacle species. The absence of rockweed also inhibited the recruitment of more rockweed, because juveniles of this species preferentially settle under the protective shield of adult plants. Even after the apparent recovery of rockweed, previously oiled shores experienced another round of mass rockweed mortality, most likely because the entire stand was of the same age. An important lesson from this story is that recovery can be delayed by complex and often indirect interactions among species (Peterson et al. 2003).

Long-term ecosystem shifts. In contrast to systems like the intertidal zone that experience frequent disturbances over short periods of time, embedded in a community recovering in a mosaic fashion, other systems experience longer, larger-scale cycles of change. Without long-term data on natural fluctu-

ations in ecosystems, this variability might be mistaken for ecosystem damage and recovery. For example, small ocean-going anchovies and sardines dominate fisheries in highly productive regions along the coasts of California, Peru, Chile, and Japan. Landings of these fish have varied by millions of metric tons annually over a 50-year cycle, such that when anchovies are abundant, sardines are less abundant, and vice versa (figure 2; Chavez et al. 2003). These flip-flops have been linked to alternating climate regimes that differ in ocean temperature, circulation, and nutrient availability. A single anchovy-sardine cycle might look like an ecosystem fluctuating wildly out of control, but viewed over a longer time frame, the succession of cycles depicts the natural range of variation present within the system. In this case, the ecosystem responds to changes in environment over large spatial scales, and what seems like recovery of a previously abundant stock may be a reflection of long-term environmental cycling.
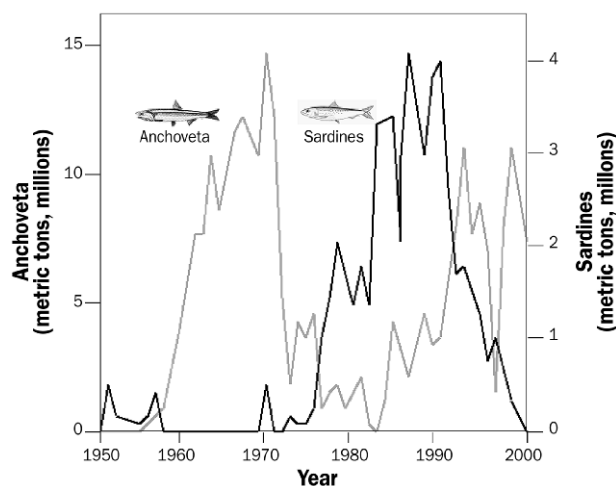

Figure 2. Anchoveta and sardine landings from Peru over the last 50 years. When anchoveta are abundant, sardines are less abundant, and vice versa. This natural variation has been linked to alternating climate regimes that differ in ocean temperature, circulation, and nutrient availability. Redrawn from Chavez and colleagues (2003).

Over even longer time frames, historical studies of ocean dynamics give a fascinating glimpse of the wild swings in fishery communities that have occurred over millennial timescales. In the northeastern Pacific, long-term data over the past two millennia include some periods, like the present, when anchovies and sardines cycle out of phase, and some in which anchovy and sardines vary in synchrony with one another (Finney et al. 2002). These data also show fundamental shifts in ocean productivity: the centuries from AD 300 to 1200 were more productive along the North American western coast than at other times (Finney et al. 2002). If productivity and recovery are related, then long-term shifts in the physical delivery of nutrients to ocean ecosystems might result in productivity changes that cascade down to spark changes in ecosystem recovery (see also Jacobs et al. [2004]).

In addition to these long-term, natural changes to ecosystem recovery patterns, anthropogenic changes may also be playing a growing role. For example, overfishing of fish stocks on their natural downswing may slow recovery. One such downturn doomed the sardine industry of Monterey's Cannery Row, immortalized in John Steinbeck's *Cannery Row* and *Sweet Thursday*. When fishing was near its peak and stocks were low, the Pacific Decadal Oscillation turned from a warm to a cool phase, slowing the recovery of sardine populations for decades (Chavez et al. 2003). In 1946, Ed Ricketts, a long-term marine biologist in Monterey and the model for "Doc" in *Cannery Row,* wrote concisely about the problem of adding the stress of fishing pressure to a sardine population that fluctuated naturally. When the sardines were at a natural low point, excess fishing "could conceivably sometime hit them so bad, when they were at a trough anyhow, that the margin by which they survive...would be wiped out completely, and they'd go down" (Rodger 2002).

Future worry surrounds the possibility that climate change could affect upwelling patterns or ocean pH, further pushing ecosystems from their long-term norms. In the midst of natural variation, it is critical to understand how human activities interact with natural cycles to influence the frequency or strength of recovery. If communities are normally in a balance of disturbance and recovery (as in Paine and Levin [1981]), then increased disturbance from human sources may push ecosystems to a less recovered state (figure 3). Increasing the disturbance rate or magnitude of disturbance events could knock an ecosystem out of its normal balance. Likewise, slowing the recovery rate through reductions in diversity or productivity can have similar effects. Detecting when ecosystems are far from their normal disturbance-recovery balance often requires long-term data, because some disturbance-recovery cycles are very slow, and only long-term data show the types of natural ecosystem variation that typically occur in a given system.

Resistance

Resistance to ecological change is usually studied in its absence, when a system finally changes in the face of ecosystem alteration. These studies often show that change occurs more quickly when ecological redundancy is low and the ecological role of key species cannot be replaced by other species within the ecosystem. Particularly in marine systems, recent human removal of key species, such as top predators, can dramatically reduce redundancy and therefore alter the ability of ecosystems to resist ecological change. The limits of resistance to disturbance have important lessons to teach us about the potential future of marine ecosystems in the face of an increasingly human-dominated world.

Diversity and resistance. The Bristol Bay salmon fishery targets sockeye salmon, but the salmon are actually an amalgamation of differentially adapted populations spawning in different places at different times. Variation in total yield in this regional fishery has been buffered by compensatory changes in production in different stocks (figure 4; Hilborn et al. 2003). For example, before about 1950, the major yield was from the Naknek-Kvichak area, with the Egegik fishery contributing less than 20%. By contrast, after the Pacific Decadal Oscillation change of the mid-1970s, the Egegik stock rose to dominate the fishery, and the other two areas provided much less. Though there are still large year-to-year changes (figure 4), the fishery would have been much smaller without Naknek-Kvichak before 1950 or without Egegik after 1980. The regional total is much more stable when all three spawning populations remain in the system.

The resistance of total catch to environmental change derives from the diversity of the spawning population. At different times and places, different spawning populations contribute strongly to the next generation. In most years, spawning is favored in at least one habitat, so the mixed reproductive strategies of the entire set of populations allows maintenance of high catch rates despite changes in the environment. The key feature of this system is that similar populations are slightly different from one another and can therefore react slightly differently to the same environmental shift. This ecological complementarity results in resistance to disturbance when the ecological response of each group to disturbance differs from that of the other groups.

Complementarity can sometimes help more highly diverse ecosystems to resist invasion. When sessile invertebrate communities are artificially constructed from a larger num-
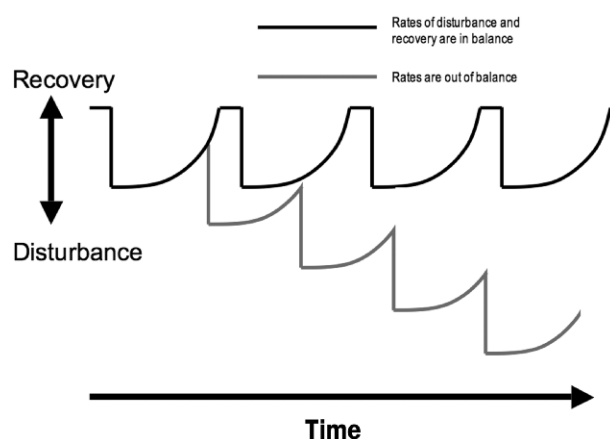

Figure 3. A conceptual model of the balance between disturbance and recovery rates in natural ecosystems. Recovery after disturbance events can return an ecosystem to its original state (black line) if disturbance is well spaced in time or if recovery is fast. If disturbance becomes more frequent or more severe, ecosystem health or quality can drop lower and lower with every incomplete recovery (red line). In some cases, ecosystem recovery itself may be impaired as the ecosystem ratchets down, much as the human immune system gradually decays and collapses during HIV infection. Just as a human body converts to AIDS, ecosystems under human disturbance may covert to acquired ecosystem deficiency syndrome.
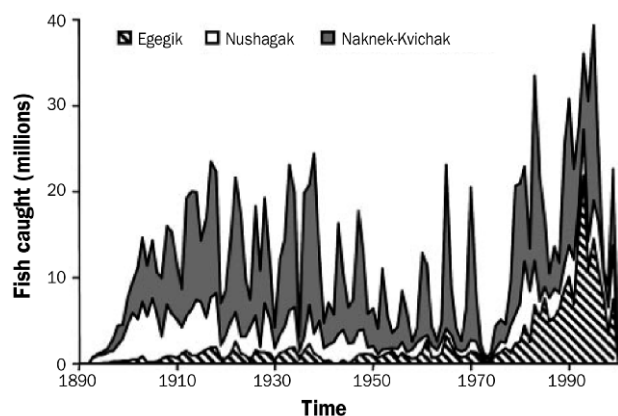
Figure 4. Fisheries yield of salmon from Bristol Bay, Alaska, showing the varying contributions of salmon from three major regions of the bay. Slightly different spawning stocks in these regions reacted differently to environmental change across the last century, particularly after 1977. Though variability in stocks from year to year is still high, the long-term yield across the three regions is more stable because all three stocks contribute to the regional totals. Redrawn from Hilborn and colleagues (2003).
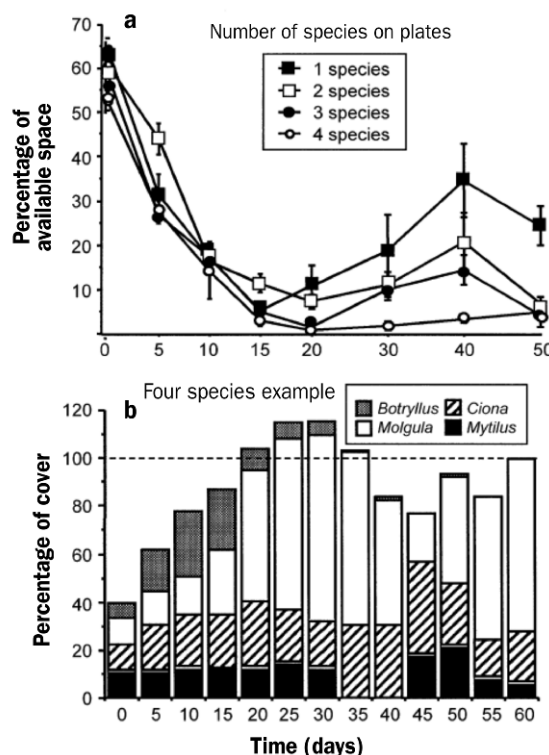

Figure 5. Space occupation of marine fouling panels that were grown with one to four native species of sessile invertebrates. (a) Panels grown with four species show higher and more consistent space occupation than species grown with one to three species. By contrast, panels with fewer species show large swings in space occupation, especially after about day 20, that open up these communities to invasion. (b) An example of the total space occupation of panels grown with four native species. The combination of space occupied by all four species varies less than it would if only one, two, or three species were in the system. Redrawn from Stachowicz and colleagues (2002).

ber of species, fewer invasive species settle and grow among them (Stachowicz et al. 1999, 2002). The mechanism of increased resistance appears to be related to the same feature that was important in Bristol Bay salmon: different native species occupy space and reproduce in slightly different ways. Over a summer growing season, communities with many species show more consistent use of space, providing few open areas for nonnative species to invade (figure 5). At all times during the season, one or another of the native species is spatially dominant. When few species inhabit the system, there are weeks when no species is spatially dominant, and thus they leave up to 30% open space available for invaders (see, e.g., figure 5a after day 20). In this case, the slightly different way in which sessile species use space is a key part of ecological resistance to invasion.

Over larger spatial scales, more highly diverse marine ecosystems show a smaller fraction of fished species that have commercially collapsed, and a higher rate of recovery of collapsed species, than large marine ecosystems with less diversity (figure 6; Worm et al. 2006). Ecosystems in which more than 20% of more of the collapsed stocks have recovered are all high-diversity ecosystems. The lowest-diversity ecosystems show less than 10% of their stocks recovered (figure 6). Though these patterns have yet to be explained mechanistically, one possibility is that the ability of fishers to switch among alternate targeted species is greater in highly diverse ecosystems, reducing the rate at which species collapse. This is essentially a redundancy mechanism. Alternative explanations include the younger age of many industrialized fisheries in the high-diversity tropics; however, this latter explanation does not seem capable of explaining why recovery may increase

with diversity. In this case, lower fishing pressure on scarce stocks may prevent them from being fished to as low a point as they would be in less diverse settings. The faster rebound of overfished species in high-diversity ecosystems deserves greater scrutiny and testing.

Diversity within species can also be important. In the Baltic Sea, large, ancient, genetically identical clonal patches of the sea grass *Zostera marina* spread to form the basis for a diverse benthic community of invertebrates and fish. Experimental patches constructed to have more clones generally grew faster, produced about twice the biomass, hosted 50% more invertebrates, and better resisted disturbance due to extreme warm weather (Reusch et al. 2005) than patches with little clonal diversity. In these and other cases, diversity per se probably is not the key; rather, it is likely that a combination of slightly different local adaptations by different genotypes or species allows higher combined productivity or stability in
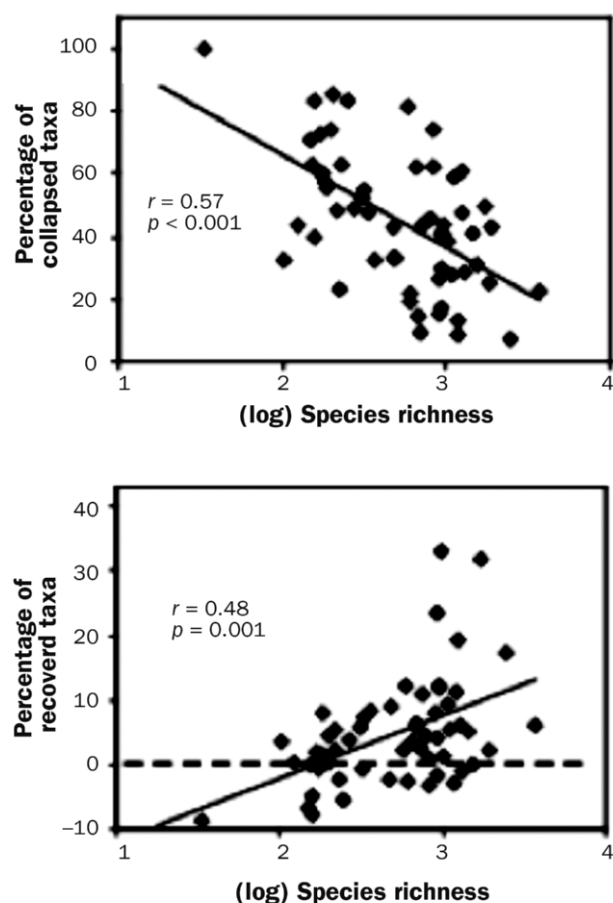
Figure 6. Upper panel: Proportion of collapsed fish and invertebrate taxa within large marine ecosystems as a function of the fish species diversity in those ecosystems. High-diversity ecosystems show a much lower proportion of collapsed species. Collapse was defined as a reduction to less than 10% fishing yield of a species from its maximum fishing yield. Lower panel: Percentage recovery of fish and invertebrate taxa 15 years after their collapse. Collapsed species in large, high-diversity marine ecosystems recover more completely than those in lower-diversity ecosystems. Redrawn from Worm and colleagues (2006).

the face of disturbance. The mechanisms of resistance attributable to diversity are a critical focus for future research.

Do marine ecosystems resist overfishing? In the past few years, massive changes in oceanic ecosystems have been recorded: a number of large consumers—whales, turtles, sharks, and pelagic fish—are at tiny fractions of their former abundances (Jackson 1997, Myers and Worm 2003, Roman and Palumbi 2003). Lessons from sea otters suggest that the oceans may not be resistant to these changes, especially if they severely reduce ecological redundancy. For example, there are numerous species of great whales, but all of them were severely depleted by whaling, and so an entire ecological functional

group has been reduced. Similar arguments seem to apply to sharks and other pelagic fish; virtually all species with large body sizes have been culled from the world's oceans (Jackson et al. 2001). If lessons about the link between reduced redundancy and ecosystem shifts are correct, where are the oceanwide ecological effects?

Oddly enough, few researchers are looking for these effects. Lobsters in the Gulf of Maine live with less risk from large, carnivorous fish since the collapse of the groundfish species, and in these waters, lobster populations show increased juvenile survival (Steneck et al. 2004). But in this case, human hunting of lobsters keeps adult numbers from booming, so the system seems more stable than it really is. One study has found increases in medium-sized fish that are normally prey to sharks, which have been commercially overfished (Myers and Worm 2005). In a follow-up (Myers et al. 2007), the 90% decline in abundance of sharks that usually consume rays is associated with large-scale increases in ray populations (figure 7). One extra step in this ecological cascade is apparent as well. Rays have quadrupled in abundance in the coastal estuaries of North Carolina, and are now a major predator on scallops there. What was a productive scallop fishery has declined dramatically in the past decade as cownose ray populations have skyrocketed (figure 7).

Other cascades are less well known, but could be an important part of today's ocean ecosystems. Gray whales play an important role in Arctic ecosystems because they bulldoze shallow sediments while feeding on benthic amphipods. New genetic estimates of gray whale population sizes before whaling peg the former abundance of this species at 3 to 5 times today's level (Alter et al. 2007). At these levels, the sediment transport impact of gray whales would be 12 times the sediment contribution of the Arctic's largest river, the Yukon, and would provide food subsidies to a million seabirds. The ecological impact of large whale populations in the past is largely unknown, but could present a primary opportunity for understanding the ecology of the natural oceans before major hunting by humans.

Why are ecosystem-wide impacts of heavy fishing so difficult to document? Are current ocean ecosystems highly resistant to the large changes that have occurred recently? Another hypothesis is that the effects are hidden by other anthropogenic impacts. The increase in fishing pressure over the past century may have masked increases in intermediate-level fish species around the world. Given the propensity of fishing operations to remove virtually all large vertebrates from the seas, these operations may have resulted in many ecosystem responses, including increases in some medium-sized fishes. Whether human consumers have eaten the evidence of these responses before they could be documented remains to be discovered.

Reversibility and changes to ecosystem rules

Although in some instances ecosystems resist disturbance or recover from it, in other cases systems appear to have profoundly changed, shifting to an alternative (and potentially
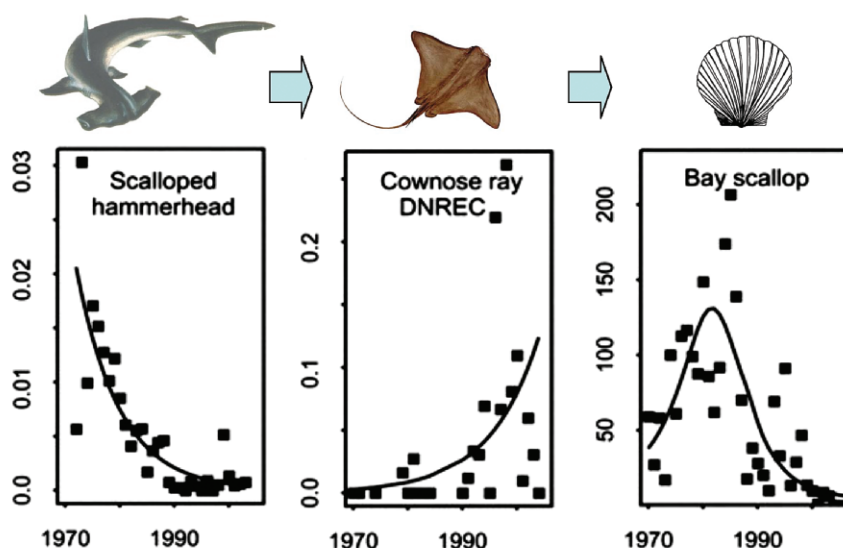
Figure 7. A cascade of fishing effects along the eastern coast of North America. Since 1970, fishing for large sharks has severely reduced their population levels, and some of their prey, such as the cownose ray, have increased dramatically. Once the rays' abundance significantly increased, after about 1980, the abundance of one of their major food sources, the bay scallop, plummeted. Redrawn from Myers and colleagues (2007), with animal logos adapted from www.tomzap.com *and* www.ncfisheries.net.

One possible explanation is that the urchins do not reproduce well when they are rare—the fertilization and larval settlement of these animals is impaired at low adult densities. Therefore, the potential rapid recovery of sea urchins has not occurred, and the shift from corals to algae has been irreversible, even in marine reserves with higher abundances of herbivorous fish. In this example, the sequential removal of all major herbivores exhausted ecological redundancy. Once large herbivores such as parrotfish were removed, smaller herbivores such as surgeonfish were also targeted. Sea urchins provided the last of the herbivory "services" on the reef, and their death left no major consumers of algae.

Other studies also emphasize the importance of multiple species. Experimental evidence from the intertidal zone in Panama also shows that the sequential reduction of redundancy can push an ecosystem into a new state. Crustose coralline algae remained resilient to the removal of various combinations of four functional groups (large fishes, small fishes and crabs, herbivorous mollusks, and predatory gastropods). However, the removal of all four functional groups resulted in rapid invasion by green algae (Menge and Lubchenco 1981).

The important role of redundancy arises in many studies of ecosystem resilience. When only a small number of species play major ecological roles, ecosystems can be particularly vulnerable if they are removed. Sea otters along much of the western coast of the United States are strong determinants of the density of kelp forests. Coastwide removal of otters by fur traders in the 19th century resulted in an explosion of herbivores, primarily sea urchins and abalone. The former species chewed into the extensive kelp beds of the western coast, enormously reducing their extent (see Estes and van Blaricom [1988] for a review). The return of otters in the last few decades reversed the kelp decline, but the pendulum is starting to swing back again in Alaska, where orcas eat otters (Estes et al. 1998). Thus, the kelp ecosystem has swung back and forth from kelp to urchin domination as the fortunes of a single species have waxed and waned. In southern California, where there are more species of urchin predators, such as California sheephead or spiny lobsters (e.g., Byrnes et al. 2006), higher ecological redundancy could conceivably buffer the ecosystem from otter-caused ecological gyrations. Unfortunately, human impacts on these other predators may be preventing such buffering. The lesson here could be that natural or perturbed ecosystems with low redundancy are especially sensitive to disturbances, and that even highly

undesirable) state. Studies of these heavily changed ecosystems are more than ecological obituaries. Studies of ecological alternative states in marine and terrestrial systems (e.g., Knowlton 1992, 2004) suggest that once the mixture and abundances of certain species deviate enough from the natural state, recovery is slowed or comes to a standstill. In some cases, these alternative states can last for a long time even if no further disturbance affects the ecosystem. Can researchers or managers tell how close an ecosystem is to such wholesale collapse? What factors can reverse these "stable" changes?

A role for redundancy. Over the past few decades in Jamaica, the cover of live coral has declined, while that of algae has increased substantially (Hughes 1994). Human removal of herbivorous and predatory fish, as well as nutrient input from sedimentation and sewage, contributes to the persistence of this altered community. But these impacts existed before reefs declined in the mid-1980s. The straw that most likely broke the camel's back was the demise of the long-spined sea urchin (*Diadema antillarum*), which had become the principal herbivore on Caribbean reefs after the elimination of most of the herbivorous fish. A catastrophic pathogen outbreak between 1982 and 1984 eliminated 99% of these urchins throughout the Caribbean. Thus, it appears that the removal of the last major herbivore resulted in a shift from coral-dominated to algae-dominated reefs. Is this change irreversible? Twenty years after the sea-urchin disease burnt itself out, the urchin populations are only slowly recovering.

redundant systems may collapse if anthropogenic pressure is high enough.

Reversing the irreversible. If the erosion of redundancy can sometimes move ecosystems toward wholesale change, what information is available about when and why such changes are reversible? One lesson from Jamaica is that recovery is impeded when a previously abundant species has become rare and cannot rebound (Knowlton 2004). In the Jamaican example, ecologically pivotal sea urchins are probably experiencing lowered reproduction at low densities because of fertilization failure, keeping their numbers from rebounding despite a surfeit of food. Similarly, the removal of settlement cues, low juvenile survival in the absence of adults, a higher per capita predation rate, or even a lack of mates may impair the recovery of a formerly abundant species (Knowlton 2004). If such a species or species group is crucial to community structure, an ecosystem may persist in an altered state until the species or group increases in abundance.

In other cases of deep disturbance and irreversible change, new ecological players may enter the system and prevent a rapid return to a former state. Marine diseases represent a new class of marine invaders that may be resetting the ecological rules. Coral communities in the Caribbean and elsewhere have experienced rapid growth in the prevalence and severity of pathogen outbreaks (Harvell et al. 2002). The combined effects of physiological stresses such as increased water temperature, nutrient loading, and virulence of pathogens have resulted in the outbreak of diseases, which often cause widespread death.

Disease-induced mortality is usually not equivalent to mortality caused by predators. The population dynamics of most urchin predators, for example, are slower than or similar to the dynamics of the urchins themselves. Pathogens, in contrast, have generation times as short as days, and can show much more rapid population dynamics. Consequently, the magnitudes and spatiotemporal scales of population fluctuations can shift dramatically when populations are regulated by predatory pathogens rather than by longer-lived predators such as otters.

A recent experimental investigation of the processes underlying the reversal of alternative states in Australian coral reefs highlights the importance of expecting the unexpected when it comes to understanding reversibility—in this case, the role of a single, rare species. Bellwood and colleagues (2006) experimentally triggered a phase shift to algal dominance by simulating overfishing of herbivores in large exclusion plots on the Great Barrier Reef over three years. Surprisingly rapid reversal of the phase shift, within eight weeks, was driven by a single, rare spadefish species (*Platax pinnatus*), a species previously thought to feed on invertebrates. Forty-two other local herbivorous fish species had little effect on macroalgal cover, and thus, in this case, biodiversity did not contribute to ecosystem recovery. An important lesson from this work is that the species that prevent phase shifts from occurring in

the first place (e.g., parrotfish or surgeonfish) may not be the ones that eventually contribute to reversing those shifts.

Is there a time limit on reversibility? In real ecosystems, slow recovery may eventually lead to reversibility, but a slow march back to a former ecosystem state may be difficult to detect unless long-term data are available. The 20-year absence of sardines from Monterey was long enough to see the canneries there dismantled and the entire human economy of the area changed, but sardines are once again a fishing target in this area, although at lower levels than before. The ecosystem changes induced by 18th- and 19th-century sea-otter hunting were reversed in the 20th century when otter populations began to expand.

Few ecosystem states are likely to be truly permanent, because environments change over decadal, century, and millennial timescales (e.g., Finney et al. 2002). A challenge is to distinguish between ecosystems that can recover after a long time, when conditions allow, and those that require further human intervention. An ecosystem recovery that requires a millennium to occur is, for all intents, an irreversible change, whereas one that requires a decade might be classified differently.

A different question about reversibility is whether an ecosystem will quickly revert to its former state if the disturbance that changed it is halted. If the ecological mechanisms that determined the fundamental distribution and abundance of species are so severely overturned by a disturbance that these mechanisms cannot restart, then reversibility is in doubt. But if these mechanisms are working, even slowly, after the disturbance retreats, then perhaps this could be classified as a slow recovery rather than an irreversible decline. Ecologists and managers may need to use the term "reversible" differently: ecologists need to think over long timescales to understand the way ecosystems are controlled, whereas managers need to think over the timescale of human generations.

Lessons for management and prediction

From observations of ecosystems and their responses to disturbance, the picture of resilience that is emerging may make ecosystem management more tractable. Ecological redundancy seems to buffer systems if the role of critical species can be taken over by other species in the same ecosystem. In such cases, ecosystems with high redundancy resist disturbance, recover more quickly, or are less likely to be changed irreversibly. A second key lesson from studying ecosystems in action in that species complementarity also plays a major role. For example, different sessile species use space in slightly different ways (figure 4), and this complementarity protects bottom-dwelling communities against invasion. Another is that higher productivity may help increase recovery rates or resistance to major shifts in ecosystem state. Productivity may be related to biodiversity, but there are cases in which physical delivery of nutrients (by upwelling, for example) may play a more controlling role.

Redundancy, complementarity, and productivity have been seen to increase with greater levels of natural diversity in some circumstances (van Ruijven and Berendse 2007). By contrast, disturbance can diminish diversity, and in many cases may reduce productivity, redundancy, and complementarity to levels that subject an ecosystem to dramatic shifts in composition. When diversity plays a central role in these beneficial ecosystem properties, diversity maintenance may be an important mechanism for ecosystem management (Loreau 2004). Management to bolster diversity may be effective in these cases, if such management is possible. For example, management of lobsters as sea-urchin predators may take on greater significance when lobsters are the only predators left (e.g., in southern California). However, different ecosystems have very different levels of productivity, redundancy, and complementarity, and there is no single diversity formula that can be used to monitor the degree of disturbance within all ecosystems. It may also be that some ecosystems with naturally low diversity are intrinsically less diverse, have different resilience properties (e.g., figure 6), and need to be managed differently.

Recovery varies from place to place within an ecosystem, and may generally be higher under conditions that favor high colonization rates and high survival. In oceanic settings, the connections among ecosystems (e.g., between intertidal and pelagic ecosystems) may play a strong role in differences in recovery potential. Identifying areas in which recovery is intrinsically faster may help managers decide on spatial patterns of protection. An important debate may be looming about whether high-resilience areas are more deserving of protection or more able to absorb high human impact.

Careful study of complex marine ecosystems also reveals that indirect effects among species can sometimes delay recovery. This is especially true if the dominant ecological processes acting within a community are overturned by a disturbance event, or if new agents, such as disease, fundamentally change the ecosystem rules. Whether such changes in ecosystems are irreversible or merely require decades or centuries for recovery may not be a practical distinction. Rather, researchers and managers need to identify the ecological mechanisms that should be restored in order to speed recovery. These mechanisms may focus our attention on the ability of previously abundant species to increase when they are rare, or on ways to reduce the domination of previously rare species that have increased after disturbance.

There are many crucial caveats about using ecosystems in action to understand recovery. Natural disturbances tend to be relatively short in duration, while anthropogenic disturbances increasingly tend to be nearly permanent. Thus, our current knowledge is generally skewed toward shorter-term disturbances, and such lessons may not apply directly to chronic disturbances. In addition, ecosystems are unique and ever changing, and generalizations about how they function in the face of disturbance will almost certainly have important exceptions. Other approaches can also provide insight complementing the observations described here. Experiments on laboratory or artificial ecosystems, mathematical models, and even analogies to complex engineering systems that require resilience, such as power grids, can help.

In this article we have split the concept of resilience into three components that can be studied within functioning ecosystems and shown how these three components play a major role in responses to disturbance. Managing for resilience may require equal attention to each of these three elements, or there may be cases in which one or another is more important. One interesting result is that productivity and diversity seem to play major roles in the elements of resilience. While we recognize the limits of any management plan that spans ecosystem types and localities, a strong focus on maintaining ecosystem diversity and productivity at natural levels may be a way to begin management for resilience.

Of course, infinite knowledge about ecosystem recovery, reversibility, and resistance will not matter unless it is applied to enhance management of human activities in our human-dominated world. Moreover, the management implications of such ecological knowledge are difficult to assess. Ecologists have traditionally focused on getting the information needed to develop better management plans. Much less attention has been focused on the ways to use this knowledge in the future. The promise of ecology, and the substance of its contract with society (Lubchenco 1998), is to use knowledge to help deliver a livable planet (Palmer et al. 2004). If ecosystem resilience is to be a powerful mechanism to help that delivery, we need to understand its scientific basis much more thoroughly. And we need to apply it quickly.

Acknowledgments

References cited

Alter SE, Rynes E, Palumbi S. 2007. DNA evidence for historic population size and past ecological impacts of gray whales. Proceedings of the National Academy of Sciences 104: 15162–15167. doi:10.1073/pnas.0706056104

Bellwood DR, Hughes TP, Hoey AS. 2006. Sleeping functional group drives coral-reef recovery. Current Biology 16: 2434–2439.

Byrnes J, Stachowics JJ, Hultgren KM, Hughes R, Olyarnik SV, Thornber S. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. Ecology Letters 9: 61–71.

Chavez FP, Ryan J, Lluch-Cota SE, Niguen M. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science 299: 217–221.

Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473–476.

Estes JA, van Blaricom G, eds. 1988. The Community Ecology of Sea Otters. New York: Springer.

Finney BP, Gregory-Eaves I, Douglas M, Smol J. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2000 years. Nature 416: 729–733.

Guerry AD. 2005. Icarus and Daedalus: Conceptual and tactical lessons for marine ecosystem-based management. Frontiers in Ecology and Evolution 3: 202–211.

Guichard F, Halpin PM, Allison GW, Lubchenco J, Menge BA. 2003. Mussel disturbance dynamics: Signatures of oceanographic forcing from local interactions. American Naturalist 161: 889–904.

Harvell CD, Mitchell CB, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD. 2002. Ecology: Climate warming and disease risks for terrestrial and marine biota. Science 296: 2158–2162.

Hilborn R, Quinn TP, Schindler DR, Rogers DE. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100: 6564–6568.

Hughes TP. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551.

Jackson JBC. 1997. Reefs since Columbus. Coral Reefs 16: S23–S32.

Jackson JBC, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.

Jacobs D, Haney T, Louie K. 2004. Genes, diversity and geological process on the Pacific Coast. Annual Review of Earth and Planetary Sciences 32: 601–652.

Knowlton N. 1992. Threshold and multiple stable states in coral reef community dynamics. Integrative and Comparative Biology 32: 674–682.

———. 2004. Multiple stable states and the conservation of marine ecosystems. Progress in Oceanography 60: 387–396.

Levin SA. 1999. Fragile Dominion: Complexity and the Commons. Reading (Massachusetts): Perseus.

Levin SA, Lubchenco J. 2008. Resilience, Robustness, and Marine Ecosystem-based Management. BioScience 58: 27–32.

Loreau M. 2004. Does functional redundancy exist? Oikos 104: 606–611.

Lubchenco J. 1998. Entering the century of the environment: A new social contract for science. Science 279: 491–497.

Menge BA, Lubchenco J. 1981. Community organization in temperate and tropical rocky intertidal habitats: Prey refuges in relation to consumer pressure gradients. Ecological Monographs 51: 429–450.

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strubs PT. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94: 14530–14535.

Menge BA, et al. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences 100: 12229–12234.

Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280–283.

———. 2005. Extinction, survival, or recovery of large predatory fishes. Philosophical Transactions of the Royal Society B 360: 13–20.

Myers RA, Baum J, Shepherd T, Powers S, Peterson C. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315: 1846–1850.

Paine RT, Levin SA. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. Ecological Monographs 51: 145–178.

Paine RT, Tegner MJ, Johnson BA. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535–545.

Palmer M, et al. 2004. Ecology for a crowded planet. Science 304: 1251–1252.

Peterson CH. 2001. The "Exxon Valdez" oil spill in Alaska: Acute, indirect, and chronic effects on the ecosystem. Advances in Marine Biology 39: 3–103.

Peterson CH, Rice SD, Short JW, Esler D, Bodkin JL, Ballachey BE, Irons DB. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302: 2082–2086.

Reusch TBH, Ehlers A, Hämmeli A, Worm B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences 102: 2826–2831.

Rodger KA, ed. 2002. Renaissance Man of Cannery Row: The Life and Letters of Edward F. Ricketts. Tuskaloosa: University of Alabama Press.

Roman J, Palumbi SR. 2003. Whales before whaling in the North Atlantic. Science 301: 508–510.

Sousa WP. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353–391.

Stachowicz JJ, Whitlatch RB, Osman RW. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577–1579.

Stachowicz JJ, Fried H, Whitlatch RB, Osman RW. 2002. Biodiversity, invasion resistance and marine ecosystem function: Reconciling pattern and process. Ecology 83: 2575–2590.

Steneck RS, Vavrinec J, Leland AV. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems 7: 323–332.

van Ruijven J, Berendse F. 2007. Productivity relationships: Initial effects, long-term patterns and underlying mechanisms. Proceedings of the National Academy of Sciences 102: 695–700.

Worm B, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314: 787–790.