

New paradigms for supporting the resilience of marine ecosystems

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Resource managers and scientists from disparate disciplines are rising to the challenge of understanding and moderating human impacts on marine ecosystems. Traditional barriers to communication between marine ecologists, fisheries biologists, social scientists and economists are beginning to break down, and the distinction between applied and basic research is fading. These ongoing trends arise, in part, from an increasing awareness of the profound influence of people on the functioning of all marine ecosystems, an increased focus on spatial and temporal scale, and a renewed assessment of the role of biodiversity in the sustainability of ecosystem goods and services upon which human societies depend. Here, we highlight the emergence of a complex systems approach for sustaining and repairing marine ecosystems, linking ecological resilience to governance structures, economics and society.

Marine environments worldwide are in serious decline, primarily as a result of over-harvesting, pollution, and the direct and indirect impacts of climate change [1–9]. In many locations, anthropogenic stresses and climatic changes have caused dramatic shifts in species composition, known as phase or regime shifts, which are often long lasting and difficult to reverse [10–12]. Familiar examples include phase shifts on coral reefs [13–15] and in kelp forests [16,17] following declines in crucial canopy-forming species, and the collapse of many coastal and oceanic fisheries [9,18] (Figure 1). Emerging theories and new multi-disciplinary approaches point to the importance of assessing and actively managing resilience; that is, the extent to which ecosystems can absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states [12,19–22]. The capacity of ecosystems to regenerate following disturbance depends on sources of resilience that operate at multiple scales [21,22]. The concepts of alternate states, resilience and scale are also increasingly prevalent in economics and social science, and in developing theory for linked social–

ecological systems (SESs; see <http://www.resalliance.org>). Here, we argue that anticipating and preventing unwanted regime shifts (or, conversely, promoting desirable ones) in an SES context will require an improved understanding of the dynamic and complex processes that support or undermine resilience, and of the socio-economic drivers and governance systems that shape the use of living marine resources [21–23].

The long-standing approach to management of marine resources is based on a flawed conceptual model: the ‘optimal’ harvesting of targeted stocks in systems that are assumed to be reasonably stable. An emerging approach rejects this paradigm in favor of management practices that recognize coupled SESs that are characterized by complex dynamics and thresholds, with multiple possible outcomes and inherent uncertainties [10–12]. Social science has conventionally focused on common pool or communal marine resources, particularly issues of tenure and property rights, with important lessons for institutional design and governance at multiple social scales [23,24]. However, there is increasing recognition that understanding the social, legal and economic aspects of resource management is insufficient for sustainable outcomes unless coupled with a deep understanding of ecology. For example, the mobilization of Belizian coastal fishermen into cooperatives, which was socially desirable and economically successful, led ultimately to excessive harvesting of stocks of lobster and conch [25]. In a familiar sequence that reoccurs globally, overfishing led to greater catch-per-unit-effort, sequential depletion of stocks, and a loss of social–ecological resilience [1,2,15–18].

The increased recognition that humans are a crucial part of dynamic ecosystems and, simultaneously, are dependent on their environment for societal and economic development, has spurred the beginnings of a fusion between mainstream marine ecology, fisheries biology and the social sciences [26–28]. For example, fisheries science is gradually becoming more ecological, moving from the traditional approach based on the assessment of the maximum sustainable yield of individual species at a single broad scale, to multi-species stock analyses and a more general focus on ecosystem-based management at

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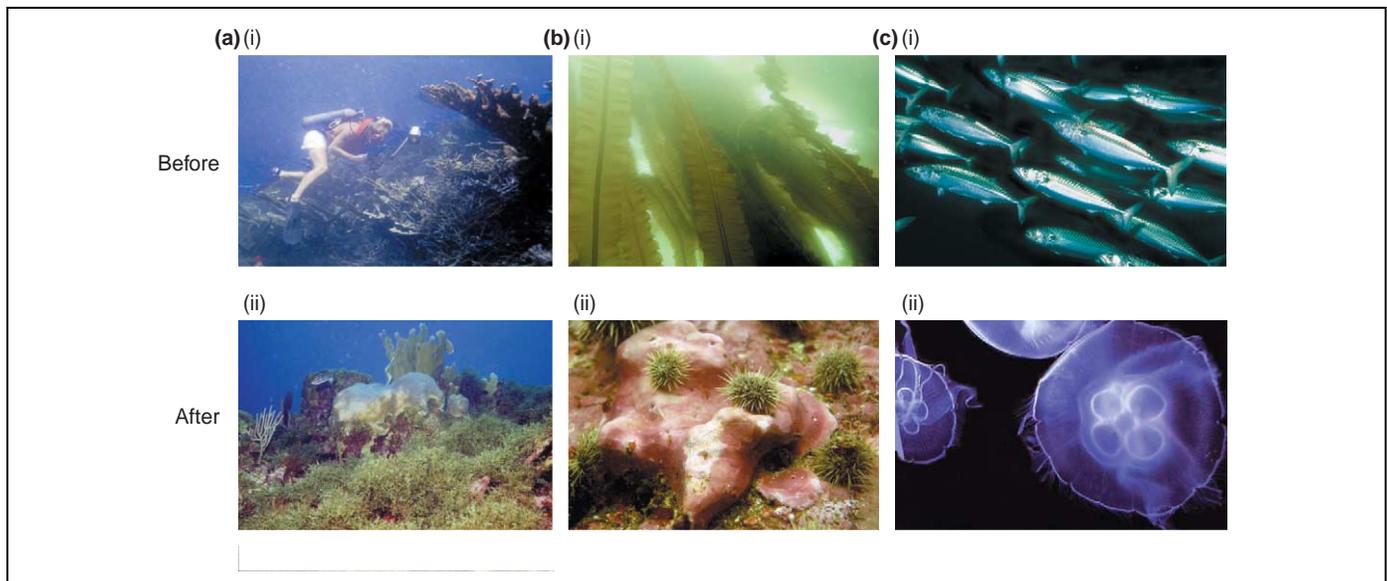


Figure 1. Three examples of alternate states in marine ecosystems. **(a)** Tropical coral reefs, (i) assemblages dominated by corals *Acropora palmata* and *A. cervicornis* in the Caribbean in 1979, and (ii) the same reef, degraded and smothered by fleshy seaweed *Dictyota* spp two decades later; **(b)** temperate and boreal rocky reefs, (i) kelp-dominated systems (*Alaria fistulosa*) in the Aleutian Islands, and (ii) over-grazed sea urchin *Strongylocentrotus polycanthus* barrens; **(c)** temperate coastal pelagic systems, (i) predatory fishes *Scombrus scombrus*, and (ii) overfished, depleted food chains, dominated by planktonic jellyfishes *Aurelia aurita*. By definition, phase shifts among alternate states constitute profound and often sudden changes in species composition, with major economic and social consequences. [Photography by T.P. Hughes (a) and R.S. Steneck (b). (c) reproduced with permission from E. Svendsen. (cii) reproduced with permission from R. Lumiaro].

multiple scales [28]. In its narrowest sense, ecosystem-based management extends the focus of resource management beyond target species to include the impacts of fishing on non-target species (caught as bycatch) or the effects of fishing gear on benthic habitats [29,30]. More broadly, ecosystem-based management reverses earlier single-species approaches by striving to support ecological processes that sustain the delivery of harvestable resources, recognizing the important and diverse ecological roles of fishes and other target species in the dynamics of complex ecosystems at multiple scales [31–33].

In tandem with these trends, marine ecology is developing novel paradigms and new conceptual models that encompass larger spatial and temporal scales, and incorporate the role of history and nonequilibrium dynamics in the tempo and mode of ecosystem change [1,8,10,12,20,34–40]. As a consequence, ecology has become more relevant for resource management. In effect, fisheries and ecological science are converging, from opposite directions, toward a multi-scale process-oriented perspective on the dynamics of marine ecosystems. The explosion of recent studies of marine no-take areas (NTAs; no-fishing refuges or sanctuaries) has also brought ecology and fisheries science closer and encouraged a more experimental, proactive and socio-economic approach to ecosystem management [41,42]. Fundamentally, NTAs are large-scale ecological experiments that exclude a top predator (recreational, subsistence and/or commercial fishers), with profound social and economic implications. The traditional view of NTAs as primarily a fisheries management tool [43] is waning, with an increasing emphasis on their broader utility for managing biodiversity, trophic structure and function, and ecosystem resilience [15,20,44,45]. For example, increasing concern about the combined impacts of fishing, pollution and climate change on the resilience of Australian coral reefs

was a major factor in establishing over 100 000 km² of new NTAs during 2004 [15].

Here, we highlight two important aspects of SESs that should be addressed to ensure the sustainable use and conservation of living marine resources; (i) the temporal and spatial scale of ecosystem dynamics and management; and (ii) the importance of biodiversity in the functioning and resilience of marine systems. We conclude with a blueprint for developing novel institutional frameworks for the future governance of marine systems.

The importance of scale

Developing marine policy and managing natural resources requires multi-scale ecological and social information. Traditionally, most ecological studies are brief and localized. However, the need for advice on how to cope with the impacts of environmental degradation, climate change and widespread overfishing is a major driver of an accelerating trend for the scaling-up of marine ecological studies. For example, the history of ecosystems (i.e. how they got to be in their current condition) is an important aspect of temporal scale that has far-reaching consequences for research and resource management [1,8,46–49]. If we ignore history and are unaware of trajectories of change, then a system is more likely to be falsely perceived as being stable and pristine [40]. In recent years, ecologists have focused increasingly on the cumulative and interactive effects of sequences of events, rather than concentrating solely on the most recent insult that leads to ecosystem collapse [1,15,16,20]. Nonetheless, most researchers still view resilience in terms of recovery from the most recent single disturbances, such as a storm or hurricane, to a single equilibrium. By contrast, social-ecological resilience focuses on absorbing recurrent perturbations, and on coping with uncertainty and risk, recognizing that disturbance and change are an integral

component of complex SESs [21,22,50]. Consequently, the timeframe for understanding and managing SES resilience is often much longer than the conventional one–three years of most ecological studies. For example, it is sobering to consider that, in the timeframe required for comprehensive regeneration of fish stocks in coral reef NTAs (>20 years), the human population size of developing countries is likely to double [51].

Overfishing and climate change have reduced the average life span of many marine species, producing unstable systems that are more responsive to pulses of recruitment and short-term environmental fluctuations, and less capable of supporting sustained exploitation [1,9,51]. Furthermore, distortions of food webs induced by selectively removing highly interactive top predators or major herbivores [52] have further undermined the resilience of many marine systems. For example, on many coral reefs, removal of fishes has led to massive increases in the number of their prey. In particular, removal of herbivorous parrotfish and surgeonfish can promote blooms of macroalgae that replace corals (Figure 1a). On some reefs, reduced levels of predation and competition from fishes have triggered unsustainably high populations of grazing sea urchins. This phase shift is unstable because of emergent diseases that cause mass mortalities of sea urchins [3], and because bioerosion of the substrate by sea urchin feeding can exceed the accretion rate of the reef [53]. In kelp forests worldwide, depletion of fish and lobster stocks has also led to increased abundance of sea urchins, promoting phase shifts to overgrazed urchin barrens (Figure 1b) [16,32,33]. In coastal seas, the collapse of pelagic fisheries and nutrient additions has contributed to unprecedented plankton blooms [47,54]. In the North Atlantic, the collapse of ground fish stocks has led to a precarious economic reliance on lobsters and other crustaceans that have been released from their major predators [17]. A disease outbreak in lobsters, similar to die-offs of tropical and temperate sea urchins [3,33] would have devastating social and economic impacts on coastal communities. In all these examples, the erosion of resilience, associated with the simplification of food chains, is driven by market demands (Box 1).

The spatial scale of dispersal of larvae, pollutants and exotic species is crucial for our understanding of the dynamics of marine systems and for sustaining SES resilience (Figure 2). Traditionally, marine ecologists have assumed that local populations are open and that the production and supply of larvae, although often highly variable, is effectively inexhaustible. A corollary of this expectation is that damaged ecosystems will recover to equilibrium conditions given sufficient time (Box 1). However, larval dispersal is surprisingly limited for many coastal species [55] and, consequently, the local loss of reproductive adults (e.g. through overfishing, disease or climate change) can disrupt stock–recruitment relationships [56]. Self-seeding populations on remote islands or reefs are particularly vulnerable [57]. Conversely, species with long-distance dispersal should be more resistant to habitat fragmentation, leading to a

Box 1. Regeneration and hysteresis

What are the prospects for the recovery of damaged marine ecosystems? Marine organisms have many adaptations for coping with recurrent natural disturbances. However, chronic human impacts are analogous to press experiments, in which a manipulation is sustained. Consequently, a return to original conditions is impossible unless the major ongoing drivers (e.g. runoff of sediment, excess nutrients and fishing pressure) are reduced. Many conservation and management practices imagine that if current stressors can be relieved, the ecosystem will automatically revert from an altered state to its original wilderness condition within a few years or decades. This approach ignores the recent emergence of a wealth of archeological and historical information about the profound changes wrought to marine ecosystems by human activities, especially harvesting [1,2,46–49,74]. Moreover, marine ecosystems exhibit varying degrees of hysteresis; that is, their recovery follows a different trajectory from that observed during decline. Some systems have changed to the extent that they can effectively no longer converge to the original assemblage [10,75]. From a complex systems perspective, they have crossed a threshold into a new state or domain of attraction that precludes return to the original state. The consequences for management are profound: it is easier to sustain a resilient ecosystem than to repair it after a phase shift has occurred.

Changes in species composition during recovery arise, in part, because of differences in life histories. For long-lived marine species (e.g. whales, turtles, dugongs, sharks and reef-building corals), recovery following controls on overfishing or pollution is necessarily slow [49,76]. For example, populations of the seacow *Dugong dugong* have declined by 97% over the past three decades along 1000 km of coastline in tropical Queensland, Australia (http://www.gbrmpa.gov.au/corp_site/info_services/publications/sotr/index.html). Assuming that hunting, incidental netting and habitat degradation can all be curbed, recovery of this species back to the levels of the 1970s (which were already severely depleted) will take at least 120–160 years, constrained by the limited annual growth rate of seacow populations of 2–3%. Similarly, recovery from increasingly frequent episodes of coral bleaching has favored short-lived species that can quickly recolonize after disturbances [20]. All of the major fishing grounds worldwide have also seen a shift to weedier, fast-growing species that are inherently less resilient and more prone to environmental fluctuations [54,71,72].

Alternate ecological states can be maintained by density-dependent mortality (e.g. owing to altered predator–prey ratios) or by density thresholds required for reproductive success [77,78]. For example, regeneration of coral reefs can be inhibited by a surfeit of coral predators, by recruitment failure, and by blooms of toxic or structurally resilient algae that resist herbivory and smother juvenile corals. The concept of hysteresis recognizes that localized short-term reductions of human impacts will not ensure recovery to a pristine state. Similarly, the lack of recovery of collapsed fisheries a few years after fishing has eased does not prove that something else must have caused the decline [75,79].

filtering effect that selectively impacts on species with limited dispersal abilities (Figure 2).

Even where local populations are highly interconnected by multiple sources of larvae, if too many patches of habitat degrade, the remaining healthy ones can catastrophically collapse, once a critical threshold is passed [58]. From a complex-systems perspective, the small-scale degradation of each patch represents a phase shift (e.g. when algae replace corals on a single reef). Furthermore, the dynamics of individual patches can propagate through larval dispersal to much larger scales, potentially leading to a phase shift of the entire system [41,58,59]. We speculate that a system-wide collapse is currently unfolding in the Caribbean, where the last few relatively intact

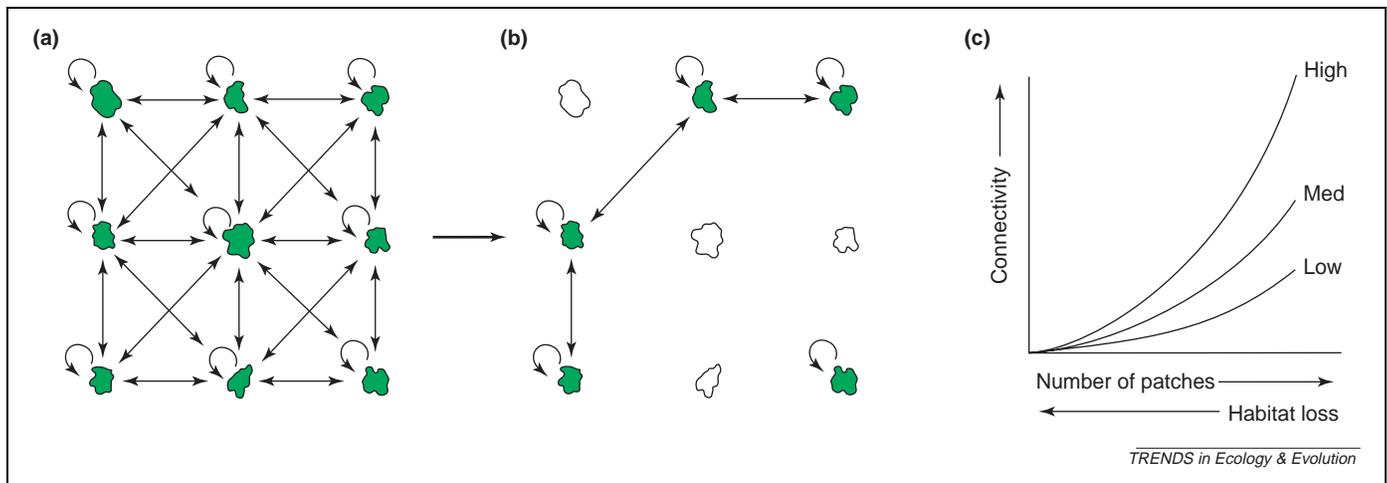


Figure 2. A graphic model of larval dispersal among patches of habitat, a key process for maintaining marine populations and ecosystems. Arrows depict potential dispersal pathways among adjacent patches and self-seeding within patches. **(a)** An intact system with high connectivity. **(b)** A damaged ecosystem, showing reduced larval connectivity caused by habitat fragmentation and loss of brood stock. **(c)** The non-linear relationship between habitat loss and the strength of larval connections for species with high, medium and low dispersal abilities. Species with limited dispersal are more vulnerable to recruitment failure.

coral reefs are increasingly vulnerable to degradation [3,7,60]. Importantly, because system-wide collapse is an emergent property of small-scale dynamics, even the most rigorous management of remnant areas could be too little, too late. The important lesson for conservation is that multi-scale dynamics requires multi-scale management, not just small-scale meddling.

Efforts at management, restoration, and mitigation in marine ecosystems are often mismatched to the scales of ongoing damage and change. Temporally, intervention efforts often come late, because warning signs were unrecognized or unheeded, and they are frequently aimed solely at the latest event. Spatially, management is often small scale and fragmented. Fortunately, there are grounds for optimism as our understanding of the processes that drive the resilience of marine ecosystems improves.

Resilience, ecosystem function and biodiversity

Resilience-based management represents a novel and timely approach to the stewardship of ecosystems [10–12,19–22,61–64]. Currently, the health of an ecosystem is typically measured by monitoring abundances of a few conspicuous species. The weakness of this approach is that the mechanisms driving temporal or spatial variation in abundance are often poorly known, and the consequences of changes in these few species to the ecosystem as a whole are rarely considered. Developing new metrics that are process oriented and that account for ecosystem dynamics is an urgent priority for improved stewardship of marine resilience (15). An emerging approach highlights the importance of key processes undertaken by crucial functional groups (i.e. collections of species that perform a similar function, irrespective of their taxonomic affinities) [65]. This perspective shifts the focus from conservation of targeted (often, commercially important) species to active management of functional groups that support essential processes and sustain ecosystem services, such as fisheries. The fundamental difference from traditional fisheries management is that a focus on functional groups recognizes the importance of

ecological roles and species interactions (including the role of humans) for sustaining ecosystem resilience across temporal and spatial scales.

Recognition of functional groups provides a deeper understanding of the role of biodiversity in ecosystem processes. An important issue is whether high species richness confers greater resilience to marine ecosystems, as suggested by some small-scale experimental studies of biodiversity and ecosystem function [66]. Certainly, depauperate marine assemblages are often functionally compromised, and richer biotas are more likely to have greater levels of functional redundancy [15–17]. Recent comparisons of species-rich and naturally depauperate marine systems indicate that higher biodiversity can afford a degree of ecological insurance against ecological uncertainty. For instance, high-diversity kelp forest systems off the west coast of North America are more resilient than are their depauperate counterparts off the east coast [16,17]. However, if all species within a functional group respond similarly to pressures such as overfishing or pollution, then higher biodiversity will not afford additional protection [62]. For example, the low-diversity coral reefs of the Caribbean undoubtedly have lower functional redundancy than do most reefs in the Indo-Pacific; nevertheless, coral reefs worldwide are threatened by severe overfishing and climate change [67].

A new framework for adaptive governance

Maintaining social–ecological resilience and successfully managing the delivery of ecosystem goods and services requires an ability to detect and react to ecological feedbacks [21]. Many customary forms of resource management (e.g. seascape tenure and taboos) successfully respond to these feedbacks and prevent or reduce over-exploitation [24,68]. However, in a global marketplace, providing an institutional framework for improved linkages between dynamic ecological and social systems is arguably the biggest challenge facing the sustainability of marine ecosystems [24]. Currently, feedbacks from damaged ecosystems are often masked by selling off natural capital to maintain short-term incomes (i.e. by

mining resources until they become economically unviable). Economic substitutions through serial depletion of resources temporally or spatially also mask ecological decline. Similarly, new technologies (e.g. improvements in fishing gear, storage and transport), increased industrialization and greater mobility of fishing fleets all conceal declining stocks and unprecedented levels of environmental damage by attempting to maintain supply to burgeoning markets [69–71].

Restoring ecosystems and reducing fishing pressure to enable the rebuilding of stocks and to improve governance will depend crucially on the creation of institutional frameworks that align the marketplace and economic self-interest with environmental stewardship and conservation. Developing institutions that interact across multiple scales to reinforce and balance each other is a major challenge. Such institutional frameworks are beginning to emerge through pioneering efforts to implement ecosystem-based approaches to management of large-scale seascapes, such as the Great Barrier Reef system in Australia. We propose that successful approaches to SES management will require four key attributes:

- *Embracing uncertainty and change.* A well functioning SES must develop resilience for dealing with external change, such as climate effects, evolving market demands, or changes to economic subsidies and government policies. A resilient SES could make use of disturbances as opportunities to transform into more desired states [12], whereas vulnerable systems might be overwhelmed by such events. The 2004 Boxing Day tsunami in south Asia is a clear example of a profound disturbance to SESs (Box 2).
- *Building knowledge and understanding of resource and ecosystem dynamics;* Supporting resilience requires an understanding of ecosystem processes and functions. Here, we have stressed scale issues and the functional roles of biodiversity for discerning crucial components of marine resilience. Management of complex adaptive systems might also benefit from the combination of different knowledge systems, including traditional knowledge [21,68].
- *Developing management practices that measure, interpret and respond to ecological feedback.* Successful management must continuously test, learn, and modify its activities and understanding for coping with change and uncertainty in complex systems [21,72]. We predict that the nascent fusion between ecology, fisheries science and social sciences will lead to further development of management that is proactive and adaptive. Already, we see the emergence of an experimental approach, based on iterative cycles of appropriately scaled manipulations (such as NTAs) that provides information, understanding and learning for renewed intervention [22]. Knowledge of ecosystems should evolve with the institutional and organizational aspects of management.
- *Supporting flexible institutions and social networks in multi-level governance systems.* An adaptive governance framework relies crucially on the collaboration of a diverse set of stakeholders operating at different social and ecological scales [72]. The sharing of management

Box 2. Social–ecological resilience, phase shifts, and the 2004 tsunami

The tragic human toll of the Boxing Day tsunami provides a stark example of the linkages between society and ecology, and of their entwined resilience in the face of rare catastrophes. In many developing countries, poverty is a key constraint on management options for sustaining resource use and attaining conservation goals [80]. For example, coastal mangroves in many highly populated areas have been reduced to small remnants, harvested and cleared to create living space for crowded coastal settlements, to provide easier access to beaches for the tourism industry, and to generate new sites for prawn farming. The decline in mangroves has greatly diminished the supply of the ecosystem services that they once provided, such as timber, firewood and the provision of nurseries and habitat for numerous fisheries. Furthermore, clearing has largely removed an important mechanical buffer against modest wave energy and run-off of land-based pollutants. Similarly, fish stocks in south Asia are critically depleted by subsistence fishing and industrial-scale extraction. Nearshore coral reefs, seagrass beds and associated habitats have been degraded to varying extents throughout the region. From a social perspective, the financial capital and infrastructure (schools, hospitals, transport systems, communication) of the region is under-developed. Furthermore, in tsunami-devastated Aceh and Sri Lanka, ongoing civil unrest erodes social capital and precludes collective action. All of these characteristics undermine resilience and make for a vulnerable social–ecological system.

The tsunami can be viewed as an external disturbance that has the potential to move a complex social–ecological system to a new SES state that is either more or less desirable than the one existing before. The local, regional and global response to the tsunami will determine whether the system has the potential to develop alternative paths and new trajectories. Beneficial outcomes could include reform of civil liberties, land use and property rights, improved governance, reduction of poverty and restoration of coastal ecosystems. Key components of resilience are likely to include leadership and insight, sustained mobilization of national and international aid, cultural and ecological diversity, development of multi-scale social networks, and the resolution of local civil unrest. It is clear that a narrow focus solely on restoration of coastal ecosystems is doomed to failure, unless the social costs and benefits of conservation efforts are addressed simultaneously.

power and responsibility can involve multiple institutional linkages among user groups or communities, government agencies and non-governmental organizations, from local to international levels. Developing fishing rights and incentives that are consistent with multi-scale ecological drivers is a major challenge. Institutions that manage fisheries at a very broad scale are likely to ignore local heterogeneity (e.g. spawning aggregations that are readily targeted to extinction) and thereby inadvertently provide incentives for localized hit-and-run harvesting. Conversely, institutions that are narrowly concerned with a particular locality or a particular species are susceptible to external drivers (e.g. recruitment failure, climate change and market demands) that operate predominantly at larger scales.

Conclusions and future directions

In conclusion, the key element in SES resilience-based management is the recognition of the linkages between the environment and people. Natural resources are too valuable, economically, culturally and aesthetically, to be squandered. Furthermore, restoring marine and

terrestrial ecosystems after they have degraded is much more difficult than maintaining them in good condition. New paradigms, perspectives, policies and governance systems are urgently needed to safeguard ecological systems for societal development and future generations. The developing concept of adaptive governance, informed by a clearer understanding of resource and ecosystem dynamics, provides a new paradigm for responding to multi-scale environmental feedbacks and for managing resilience to ensure sustainable resources. As outlined here, adaptive governance of linked social–ecological systems provides a radical new framework for developing a more mature ecosystem-based approach to management of the world's oceans [21,24,73].

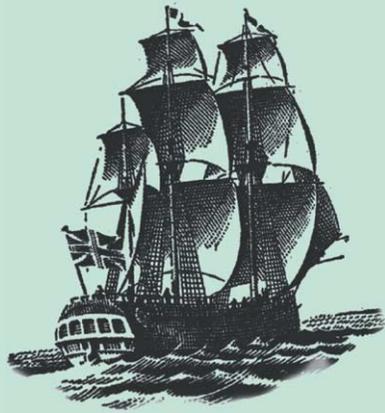
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