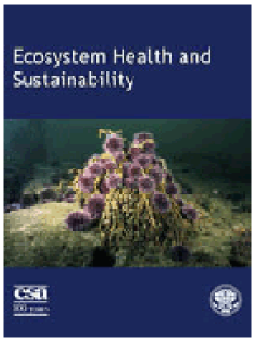


Taylor & Francis
Taylor & Francis Group

Ecosystem Health and Sustainability

ISSN: 2096-4129 (Print) 2332-8878 (Online) Journal homepage: https://www.tandfonline.com/loi/tehs20

Principles for managing marine ecosystems prone to tipping points

Kimberly A. Selkoe, Thorsten Blenckner, Margaret R. Caldwell, Larry B. Crowder, Ashley L. Erickson, Timothy E. Essington, James A. Estes, Rod M. Fujita, Benjamin S. Halpern, Mary E. Hunsicker, Carrie V. Kappel, Ryan P. Kelly, John N. Kittinger, Phillip S. Levin, John M. Lynham, Megan E. Mach, Rebecca G. Martone, Lindley A. Mease, Anne K. Salomon, Jameal F. Samhouri, Courtney Scarborough, Adrian C. Stier, Crow White & Joy Zedler

To cite this article: Kimberly A. Selkoe, Thorsten Blenckner, Margaret R. Caldwell, Larry B. Crowder, Ashley L. Erickson, Timothy E. Essington, James A. Estes, Rod M. Fujita, Benjamin S. Halpern, Mary E. Hunsicker, Carrie V. Kappel, Ryan P. Kelly, John N. Kittinger, Phillip S. Levin, John M. Lynham, Megan E. Mach, Rebecca G. Martone, Lindley A. Mease, Anne K. Salomon, Jameal F. Samhouri, Courtney Scarborough, Adrian C. Stier, Crow White & Joy Zedler (2015) Principles for managing marine ecosystems prone to tipping points, Ecosystem Health and Sustainability, 1:5, 1-18, DOI: 10.1890/EHS14-0024.1

To link to this article: https://doi.org/10.1890/EHS14-0024.1

Principles for managing marine ecosystems prone to tipping points

Kimberly A. Selkoe,[1,2,17] Thorsten Blenckner,[3] Margaret R. Caldwell,[4] Larry B. Crowder,[4] Ashley L. Erickson,[4] Timothy E. Essington,[5] James A. Estes,[6] Rod M. Fujita,[7] Benjamin S. Halpern,[1,8,9] Mary E. Hunsicker,[1] Carrie V. Kappel,[1] Ryan P. Kelly,[10] John N. Kittinger,[11] Phillip S. Levin,[12] John M. Lynham,[13] Megan E. Mach,[4] Rebecca G. Martone,[4] Lindley A. Mease,[4] Anne K. Salomon,[14] Jameal F. Samhouri,[12] Courtney Scarborough,[1] Adrian C. Stier,[1] Crow White,[15] and Joy Zedler[16]

[1]National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101 USA
[2]Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii 96744 USA
[3]Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, 10691 Stockholm, Sweden
[4]Center for Ocean Solutions, Stanford Woods Institute for the Environment, Stanford University, 473 Via Ortega Room 193, Stanford, California 94305 USA
[5]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195 USA
[6]Department of Ecology and Evolutionary Biology, 100 Shaffer Road, University of California, Santa Cruz, California 95060 USA
[7]Environmental Defense Fund, 123 Mission Street, 28th Floor, San Francisco, California 94105 USA
[8]Bren School of Environmental Science and Management, University of California, Santa Barbara, California 93106 USA
[9]Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY United Kingdom
[10]School of Marine and Environmental Affairs, University of Washington, 3707 Brooklyn Avenue NE, Seattle, Washington 98105-6715 USA
[11]Conservation International, Betty and Gordon Moore Center for Science and Oceans, 7192 Kalanianaʻole Highway, Suite G230, Honolulu, Hawaii 96825 USA
[12]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112 USA
[13]Department of Economics, University of Hawaii at Manoa, Honolulu, Hawaii 96822 USA
[14]School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada
[15]Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, California 93407 USA
[16]Botany Department, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. As climatic changes and human uses intensify, resource managers and other decision makers are taking actions to either avoid or respond to ecosystem tipping points, or dramatic shifts in structure and function that are often costly and hard to reverse. Evidence indicates that explicitly addressing tipping points leads to improved management outcomes. Drawing on theory and examples from marine systems, we distill a set of seven principles to guide effective management in ecosystems with tipping points, derived from the best available science. These principles are based on observations that tipping points (1) are possible everywhere, (2) are associated with intense and/or multifaceted human use, (3) may be preceded by changes in early-warning indicators, (4) may redistribute benefits among stakeholders, (5) affect the relative costs of action and inaction, (6) suggest biologically informed management targets, and (7) often require an adaptive response to monitoring. We suggest that early action to preserve system resilience is likely more practical, affordable, and effective than late action to halt or reverse a tipping point. We articulate a conceptual approach to management focused on linking management targets to thresholds, tracking early-warning signals of ecosystem instability, and stepping up investment in monitoring and mitigation as the likelihood of dramatic ecosystem change increases. This approach can simplify and economize management by allowing decision makers to capitalize on the increasing value of precise information about threshold relationships when a system is closer to tipping or by ensuring that restoration effort is sufficient to tip a system into the desired regime.

Key words: *critical transition; ecosystem-based management; marine spatial planning; nonlinear relationships; restoration ecology; stakeholder engagement.*

Citation: Selkoe, K. A., et al. 2015. Principles for managing marine ecosystems prone to tipping points. Ecosystem Health and Sustainability 1(5):17. http://dx.doi.org/10.1890/EHS14-0024.1

Manuscript received 14 December 2014; revised 3 March 2015; accepted 4 March 2015; final version received 22 April 2015; published 15 July 2015.

[17] **E-mail:** selkoe@nceas.ucsb.edu

Introduction

Ecosystems sometimes undergo large, sudden, and surprising changes in response to stressors. Theory and empirical evidence suggest that many complex systems have system boundaries (also called thresholds or tipping points; see Table 1) beyond which the system will rapidly reorganize into an alternative regime (Lewontin 1969, Holling 1973, Sutherland 1974, May 1977, Scheffer et al. 2001, Scheffer and Carpenter 2003, Folke et al. 2004, Petraitis et al. 2009). Tipping points can be quantified as zones of rapid change in a nonlinear relationship between ecosystem condition and intensity of a driver (Fig. 1, Table 2). For those who have witnessed collapsing fish stocks, cascading effects of eutrophication or overfishing, or climate-driven shifts in food webs, such tipping points may be intuitively understood. Nevertheless, rapid ecological shifts may surprise us, particularly when we have assumed linear, additive, and gradual ecological responses to impacts of human uses or natural drivers. Unanticipated ecological changes can be socially, culturally, and economically costly (Doak et al. 2008, Scheffer et al. 2009, Travis et al. 2014). For instance, in many aquatic systems, gradual increases in nutrient loading may have limited impacts on aquatic and marine ecosystems until a threshold nutrient level is reached, creating harmful algal blooms and oxygen-depleted zones that threaten water quality, human health, and animal life (e.g., Rabalais et al. 2010, Johannessen and Miles 2011, Michalak et al. 2013). However, for decades, water quality managers assumed constant, linear relationships between sewage discharge and impacts on local waterbodies, such as Lake Washington in Seattle, Washington, USA, and Tampa Bay, Florida, USA (Edmondson and Lehman 1981, Greening and Janicki 2006). Many such waterbodies have since tipped rapidly from clear-water, productive ecosystems to algal-dominated environments that pose health risks, compromise recreation, and threaten aquatic life. Given increasing evidence and understanding of complex system behavior and ecosystem tipping points, scientists, managers, stakeholders, and policymakers may benefit from new or renewed consideration of how plans and strategies can account for possible tipping points, whether the context is ecosystem-based management, environmental restoration, single-sector management (e.g., fisheries), or comprehensive spatial planning.

Our focus here is on managing marine systems prone to tipping points, but the issues and solutions we discuss are relevant to any setting in which ecosystems are likely to exhibit tipping points. A recent synthesis of managed ecosystems showed that, in a variety of settings, management strategies that include monitoring ecosystem state and identifying measurable tipping points tend to be more effective in achieving stated conservation and management goals than strategies that do not consider possible tipping points (Kelly et al. 2014*b*). As a precursor to tackling implementation, this study lays out the motivations and principles for acknowledging and addressing the potential for tipping points in marine ecosystems. Although many of these ideas have been articulated individually elsewhere, we synthesize them in a cohesive, accessible format, supported by theory (Table 2) and applied specifically to marine natural resource management. Our focus on marine tipping points complements recent efforts to list key challenges of applying resilience theory to social-ecological systems (Walker and Salt 2012) and principles for enhancing resilience of ecosystem services (Biggs et al. 2012). Our approach is inspired by similar efforts to translate broad scientific insights and management ideals into specific planning guidelines by articulating principles of ecosystem-based management and marine spatial planning (Leslie and McLeod 2007, Foley et al. 2010).

Seven Principles for Managing Ecosystem Tipping Points

In a series of five workshops held in 2013 and 2014 with subsets of the coauthors and a dozen other scientists, marine managers, stewards, and policymakers (see *Acknowledgements*), we sought to generate and then prioritize a short list of principles for managing marine ecosystems prone to tipping points. We began by articulating fundamental traits of ecological and social-ecological tipping points, derived from ecological resilience theory, that participants felt were most relevant to management (Table 2). We describe these traits using examples from marine systems. Next, we discuss the significance of these traits for management of social-ecological systems in marine and coastal settings. Management principles were generated through group discussion and drawn from existing literature on application of theory to management practice (Table 3).

1. Tipping points are common

The ecological literature provides numerous examples of nonlinear relationships between predictor and response variables, including responses exhibited at individual, population, species, and ecosystem levels. Examples of fundamental, ubiquitous, nonlinear responses include density dependence, such as the logistic curve of population growth, the Allee effect (i.e., accelerating likelihood of local extinction as population density falls below a minimum threshold; Stephens et al. 1999, Dulvy et al. 2003), and the relationship of per capita consumption rate to food availability (Holling 1959, Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). Dose-response curves are also pervasive in physiology, and some can cascade to ecosystem-level responses (e.g., Salazar and Salazar 1991, Fairchild et al. 1992, Meador et al. 2002, Karnosky et al. 2005, Lockwood et al. 2005). A recent synthesis of empirical studies in pelagic marine systems provides further support for the ubiquity of threshold responses (M. E. Hunsicker et al., *unpublished*

Table 1. Foundational concepts behind the theory of tipping points.

Term	Definition
Cross-scale interactions	Processes at one spatial or temporal scale interact with processes at another scale, resulting in an ecosystem tipping point. These interactions change pattern–process relationships across scales such that fine-scale processes can influence a broad spatial extent or a long time period, or broadscale drivers can interact with fine-scale processes to create surprising or unpredictable system dynamics (Peters et al. 2007).
Early-warning indicator	A system metric that can be monitored through time and is known to show predictable changes in advance of an event (i.e., tipping point) to provide warning of the event or clues suggesting increase in its probability of occurring.
Ecosystem state	A multidimensional description of an ecosystem, which may include metrics of composition, structure, functions, governing processes, and other emergent properties that distinguish the state from other possible states of interest.
External driver	A force of change that can affect the ecosystem but is unaffected by the ecosystem (as measured over the most relevant temporal scale). Drivers can be natural or anthropogenic processes, events, or activities that cause a change in an ecosystem process, component, function, property, or service. For example, sedimentation (e.g., from erosion caused by coastal development) is a driver of coral mortality. A stressor is a category of driver.
Feedback	An ecological process within an ecosystem that either reinforces or degrades resilience of a regime (Briske et al. 2006). Positive feedbacks are destabilizing (they amplify the amount of change the system will experience in response to a small perturbation), whereas negative feedbacks are stabilizing (they dampen effects of perturbations), counteracting change (Suding and Hobbs 2009, Nystrom et al. 2012).
Hysteresis	A pattern observed when the pathway of recovery of an ecosystem differs from its pathway of degradation (Suding and Hobbs 2009); path dependence. In other words, a different threshold must be crossed for recovery, often with time lags to recovery even when stressors are abated (Montefalcone et al. 2011). Factors such as random chance operating on which species colonize first and then exclude or facilitate coexistence of other species (priority effects) or the specific sequence of habitat alteration events in a successional process can cause path dependence.
Nonlinear	Nonlinear relationships have one or more curves or points of rapid change and are often used to graphically represent tipping points in driver–response relationships of ecosystems.
Regime shift	The rapid reorganization of a system from one relatively unchanging state over time to another (Carpenter and Folke 2006); synonym of tipping point. Distinct and relatively unchanging regimes are characterized by a set of governing processes, species compositions, and relationships among species and external drivers. Initial conditions can also shape an observed regime.
Resilience	The capacity of an ecosystem to tolerate disturbance without crossing a threshold into a different regime (Folke et al. 2004, Suding and Hobbs 2009). Speed of recovery following perturbation is a common empirical metric of resilience. Resilience imparts regime stability without precluding change, flexibility, and/or adaptation.
Stressor	A type of driver that is specifically linked directly or indirectly to human use(s) and/or actions that cause undesired change in an ecosystem.
Threshold	A relatively rapid change from one ecological condition to another. When a system is close to an ecological threshold, a large ecological response results from a relatively small change in a driver (Bennett and Radford 2003, Huggett 2005, Groffman et al. 2006, Suding and Hobbs 2009). Ecological thresholds exist at all levels of organization, including single populations and species, species interactions, ecosystem functions/processes, and whole ecosystems.
Trigger	An internal system behavior that initiates a regime shift, e.g., disease outbreak or mass coral bleaching. The behavior can be due to an external shock, e.g., cyclone, or culmination of a positive feedback loop (Suding and Hobbs 2009).

Note: The concept of ecosystem tipping points largely derives from theoretical ecology, with important contributions from subdisciplines focused on ecosystems, restoration and resilience, climatology, systems biology, neurobiology, mathematics, and engineering.

manuscript). Across 736 quantified stressor–response relationships involving a variety of climate, fishing, and food-web stressor types, over half were nonlinear. When nonlinearities occur, they are often strongly nonlinear, and thus may have detectable thresholds that can be quantified and incorporated into management decision-making (M. E. Hunsicker et al., *unpublished manuscript*).

Tipping points are perhaps less often documented and/or recognized at the ecosystem level than the species level. They occur as a consequence of changes in feedback processes that impart stability and resilience to the ecosystem's configuration. Ecosystems tend to resist major change until a "breaking point" is reached (Table 2). Commonly observed marine ecosystem tipping points include the sudden development of anoxic conditions in estuaries, transition of coral-dominated reefs to macroalgal-dominated reefs, and rapid loss of kelp cover after urchin population explosions (Samhouri et al. 2010, McClanahan et al. 2011, Rocha et al. 2015). A forthcoming synthesis of marine ecosystem shifts at 95 locations worldwide found that examples spanned a wide diver-

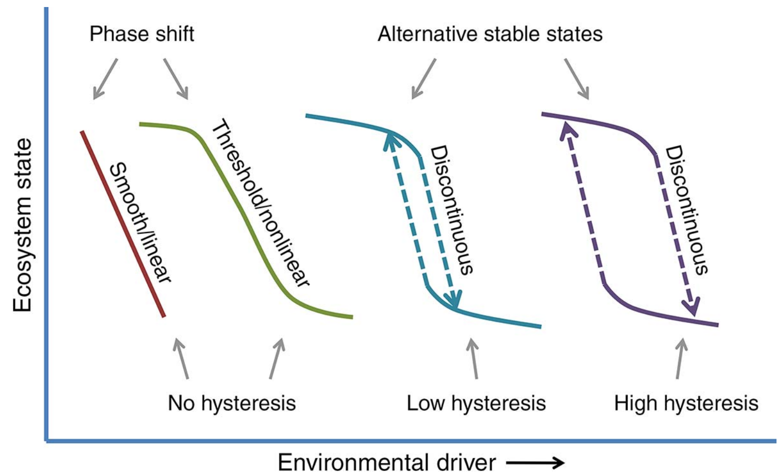


Fig. 1. Types of regime shifts. Phase shifts can be smooth or nonlinear, whereas alternative stable states show discontinuous change with some level of hysteresis. Modified from Dudgeon et al. (2010).

Table 2. A brief primer on the theory behind ecosystem tipping point.

Theory	Explanation
Ecosystems show alternative stable states, a.k.a. dynamic regimes.	Ecosystems may have alternative states with different structure and function, (a.k.a. regimes), under otherwise similar environmental conditions. Initial conditions (e.g., which species is colonized) and external conditions (e.g., the degree of resource extraction, pollution, habitat alteration, and inherent productivity) contribute to a regime's configuration. Stable states are not truly static: regular fluctuations and stochastic change occurs around an average state.
Changes to feedbacks cause tipping points.	A small number of feedback mechanisms maintain an ecosystem in a given state. When mounting stress disrupts one or more feedback mechanisms, the system can cross a tipping point and rapidly reorganize into another regime with new stabilizing feedback mechanisms. Thus, restoration may require triggering a new tipping point by disrupting feedback mechanisms.
Resilience mediates sensitivity to tipping points.	Resilience depends on factors like species diversity, functional redundancy (multiple species playing similar ecological roles), and complementarity among species (slight differences in how species carry out those roles; Chapin et al. 1997, Peterson et al. 1998, Luck et al. 2003, Laliberte et al. 2010, Karp et al. 2011, Thibaut et al. 2012, Mori et al. 2013). Because of diversity and redundancy in feedback processes, a combination of drivers is often needed to erode resilience to the point of breaking key stabilizing feedbacks (Scheffer and Carpenter 2003).
Characteristic changes in diversity and stability precede regime shifts.	Loss of resilience as a system approaches a tipping point may occur in distinct stages (Briske et al. 2006, McClanahan et al. 2011), resulting in a series of changes in ecosystem function that precede a system-level shift. Grassland and coral reef studies have identified consistent metrics that may indicate these stages. For instance, a dip in reef species richness occurs early on, whereas estimates of coral cover show a sudden drop just prior to a shift to algal dominance (McClanahan et al. 2011, Karr et al. 2015).
The trigger of a tipping point may be a small-scale event. Cross-scale interactions are key to regime shifts.	When stabilizing feedbacks have been altered and the system suffers a large loss of resilience, any further incremental change or shock to the system may be the final straw that produces a large response: a tipping point due to the collapse of stabilizing feedbacks. The spatial extent of a regime shift is often larger than the trigger event due to cascading effects. For example, a single lightning strike can ignite a fire that spreads nonlinearly across a vast range as the dominant processes controlling the fire move from the scale of individual trees to within patch variation in fuel load to among-patch connectivity (Peters et al. 2007). The accelerating spread of an invasive species, which gets a foothold in a new region by exploiting a local disturbance event, may show similar dynamics.
Connectivity encourages nonlinear/threshold responses.	Mechanisms of connectivity, such as larval dispersal, ocean currents, and migratory species, can facilitate the ripple effect of a localized regime shift by linking distant communities. However, connectivity can buffer impacts of stress when unimpacted areas serve as source populations. Thus, connectivity can enhance cross-scale interactions, which increases the likelihood of threshold responses and regime shifts (Nystrom et al. 2012).
Socioeconomic tipping points may accompany ecological tipping points.	When shifts give rise to new sets of dominant species and functions, associated ecosystem services often change in nature and extent (Graham et al. 2013). In some cases, these feedbacks lead to hysteresis, such that recreating the previous external conditions fails to produce the former regime or the system is very slow to return to its former state. Restoring an ecosystem that has crossed a tipping point and exhibits hysteresis may not be achieved by simply reversing or abating the causal drivers, and restoration thus will likely be more costly and unpredictable.

Table 3. Summary of principles for managing ecosystems prone to tipping points.

Social-ecological observation	Management principle
1. Tipping points are common.	1. In the absence of evidence to the contrary, assume nonlinearity.
2. Intense human use may cause a tipping point by radically altering ecological structure and function.	2. Address stressor intensity and interactive, cross-scale effects of human uses to avoid tipping points.
3. Early-warning indicators of tipping points enable proactive responses.	3. Work toward identifying and monitoring leading indicators of tipping points.
4. Crossing a tipping point may redistribute ecosystem benefits.	4. Work to make transparent the effects of tipping points on benefits, burdens, and preferences.
5. Tipping points change the balance between costs of action and inaction.	5. Tipping points warrant increased precaution.
6. Thresholds can guide target-setting for management.	6. Tie management targets to ecosystem thresholds.
7. Tiered management can reduce monitoring costs while managing risk.	7. Increase monitoring and intervention as risk of a tipping point increases.

sity of ecosystem types and geographic locations (C. Kappel, *unpublished manuscript*). Oceanographic connectivity may strengthen the nonlinearity of marine population- and ecosystem-level responses. Connectivity may facilitate spread of a regime shift across areas; conversely, connectivity can also impart stability and resilience when it allows replenishment from distant refuges (Allison et al. 1998, Olds et al. 2012). Importantly, even when ecological responses to stressors are relatively linear, such changes may trigger nonlinear responses in linked social-ecological systems, creating an ecosystem tipping point, such as when fishery productivity falls below a cost-effective level for fleet operation (Poe et al. 2014).

Management principle: in the absence of evidence to the contrary, assume potential for nonlinear relationships and tipping points

Clearly stating assumptions about linear vs. nonlinear ecosystem responses (such as within environmental impact assessments or fishery management plans), and examining consequences of assumptions, will help guide expectations and assessment strategies. Modifying assumptions, monitoring plans, and management actions to presume tipping points exist may reduce risk of adverse social, economic, and ecological outcomes and surprises associated with transitions to alternative ecosystem states, despite the apparent up-front cost of these modifications. Engaging experts to quantify relationships between ecosystem response variables and drivers of concern can reduce the need for assumptions. Even preliminary estimates of tipping points serve to document their presence and motivate increased monitoring and refinement of threshold estimates.

2. Intense human use, often involving multiple drivers, may cause a tipping point by radically altering ecological structure and function

Because complex systems absorb disturbance and resist change, great pressure is sometimes needed to cross a tipping point; in other cases, for systems that are already close to a tipping point or have lower resilience, smaller pressures suffice. There are several examples of systems that have crossed tipping points when local-scale anthropogenic stresses precede a period of large-scale climatic change, whether the climate change is anthropogenic or natural. In both the Baltic and Black Seas, overharvest of top predators and eutrophication from pollution produced significant alteration of trophic dynamics after a sudden change in climatic conditions (e.g., a switch from a predator guild dominated by fishes to jellyfish in the Black Sea [Daskalov 2002, Oguz and Gilbert 2007], and a switch from piscivore to planktivore domination in the Baltic Sea [Casini et al. 2009]). Effects of human exploitation can be exacerbated in ecosystems subject to large natural climatic oscillations (e.g., the Pacific decadal oscillation and Atlantic multidecadal oscillation; AMO), perhaps because loss of resilience from human impacts hampers the ability of key species and whole food webs to weather swings in temperature and productivity (Hsieh et al. 2008, Planque et al. 2010). The ecological effects of climate cycles become more complex and unpredictable when intense fishing or anthropogenic climatic stressors co-occur, making tipping points more likely (e.g., ocean acidification plus ocean warming; Griffith et al. 2011, Lindegren et al. 2013, Ohman et al. 2013).

In coastal systems, land- and ocean-based stressors can interact to cause marine tipping points. In many coral reef ecosystems, land-use changes have caused increased nearshore nutrient and sediment concentrations and, at the same time, overfishing of herbivorous fishes reduced grazer diversity (e.g., Caribbean [Hughes 1994], Seychelles [Graham et al. 2006]). In Discovery Bay, Jamaica, and elsewhere in the Caribbean, overfishing enabled the spiny sea urchin population to explode, which first maintained low algal cover in the absence of fish herbivory, but then succumbed to a disease epidemic. Ongoing nutrient enrichment combined with reduced grazer densities to produce algal overgrowth. A hurricane in 1989 then caused a significant die-off of the remaining coral. Historically, the system had recovered from hurricanes, but due to the loss of ecosystem resilience, this shock to the system shifted coral reefs to an algal-dominated regime with altered species interactions and feedbacks. Ocean acidification and temperature stress from climate change are expected to further reduce the resilience of reefs worldwide (Hoegh-Guldberg et al. 2007).

Tipping points have also been tied to single, intense stressors, most often intense harvest of a key predator (Estes et al. 1998, 2011, Myers et al. 2007, Baum and Worm 2009, Ferretti et al. 2010). Otter removal is the singular cause of rocky reef shifts from kelp forest to urchin barrens in the northeast Pacific (Estes and Palmisano 1974, Estes and Duggins 1995, Dean et al. 2000). Fishing is likely to be the singular cause of coral reef regime shifts in Fiji (Rasher et al. 2013) and the shift from cod- to lobster-dominated food webs in the Gulf of Maine (Steneck and Wahle 2013). These shifts occurred when a central node or compartment of the food web was removed, a potentially common cause of system-wide regime shifts and trophic cascades (Scheffer et al. 2001, Daskalov 2002, Frank et al. 2005, 2011, Estes et al. 2011, O'Gorman et al. 2011; C. Kappel et al., *unpublished manuscript*).

Management principle: address stressor intensity and interactive, cross-scale effects of human use to avoid tipping points

Understanding and tracking cross-scale interactions in both human and natural dimensions of a managed system is critical. Questions to consider include: How might global or regional drivers have the potential to override local management actions? And how might large-scale tipping points cascade up from local events, such as disease outbreaks, storm damage, and changes in fleet behavior? Tying management reference points to metrics of both human and natural dimensions may assist in reducing interactive effects (Large et al. 2013). For instance, during a warm AMO phase with higher total biomass available for landings, fisheries managers might consider less conservative harvest quotas for the northeastern United States shelf; in a cool AMO phase, more conservative harvest quotas may be more appropriate. In systems dominated by a keystone species that preserves a desired ecosystem state, managers could prioritize monitoring cumulative impacts to that species. In situations with many types of human uses and threats (e.g., most coastal zones), explicit decision rules can be adopted to address combinations of human uses. Caps on total allowable human use or total allowable harm (sensu Canadian species at risk; Vélez-Espino and Koops 2009) can provide a vehicle for this strategy. Such an approach requires cooperation and coordination across management sectors, which often operate on different time and geographic scales, adding to the potential for cross-scale social-ecological interactions. In some cases, substantive jurisdictional incompatibilities make such coordination extremely difficult to achieve.

3. Changes in early-warning indicators may precede ecosystem tipping points

Although it is difficult to predict the exact amount of stress that will trigger a tipping point, warning signs that precede the tipping point can be instrumental in avoiding collapse. Theory predicts that diversity and functional redundancy at multiple levels (e.g., within species, across species, and across trophic groups) affect a system's resilience to change (Table 2). As components of the ecosystem are compromised or lost, the system may lose resilience and become more prone to crossing a tipping point with the next shock or stressor (Briske et al. 2006, Brandl and Bellwood 2014). For example, a case study of Bristol Bay, Alaska, USA, sockeye salmon revealed how population-level diversity can maintain resilience of a heavily exploited species (Schindler et al. 2010). Diversity in genetic traits controlling behavior and environmental tolerance of individual spawning stocks creates a portfolio effect within and across watersheds: variation in timing of salmon returning from sea enhances the ability of the whole population to absorb environmental stresses, stabilizing ecosystem processes, ecosystem services, and the human economies that depend on them (Schindler et al. 2010).

New large-scale studies show that the particular sequence of change in measures of resilience and/or ecosystem state can be consistent at regional scales, suggesting these changes can be monitored to reveal early-warning indicators of a tipping point. System-specific metrics are beginning to emerge from syntheses of empirical data. For example, in South Pacific reef fishes, phylogenetic and functional diversity were found to be more sensitive indicators of human impacts than species richness (D'Agata et al. 2014). In separate studies of Indian Ocean and Caribbean coral reefs (McClanahan et al. 2011, Karr et al. 2015), increased spatial variance in macroalgal cover was identified as a leading indicator of decline in coral dominance while coral cover itself was a lagging indicator; the results held at local and regional scales. Both studies suggested a rule of thumb that preserving 50% of unfished biomass in the coral reef state should reduce the risk of a sudden change in state to macroalgal dominance while likely preserving high yields (Fig. 2; Hilborn 2010, Karr et al. 2015).

When high-quality time series chronicling historical ecosystem tipping points exist, they can be mined to identify species or system traits that changed in advance of the ecosystem shift and might serve as early-warning indicators of a future tipping point. Promising early-warning indicators include variance and autocorrelation of biomass, densities, and catch, and rate of recovery from perturbation, i.e., critical slowing down (Carpenter and Brock 2006, Scheffer 2009, Scheffer et al. 2009, Dakos

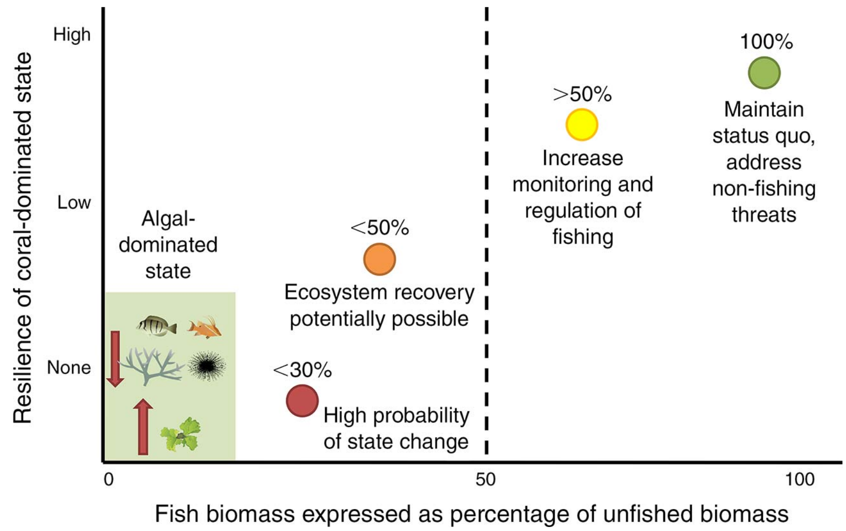


Fig. 2. Empirically derived rules of thumb can serve as management targets focused on avoiding levels of human use associated with tipping points or degraded states in fairly data-poor situations. Coral reef studies suggest that a number of coral reef system traits widely believed to relate to resilience (e.g., the proportion of herbivorous fishes, the number of fish species, and urchin density) show steep declines when fish biomass falls below 50% of unfished biomass. Unfished density can be estimated from established local no-take reserves. A tiered approach to risk might set response plans based on these targets (colored circles).

et al. 2011, 2012, Dai et al. 2012, 2013, Kefi et al. 2014). In a recent study, increased spatial variance in crustacean fishery catch was found to precede stock collapses by one to four years (Bering Sea and Gulf of Alaska; Litzow et al. 2013). Finding reliable leading indicators of tipping points is a promising and growing area of research (see review by Ditlevsen and Johnsen 2010, Boettiger and Hastings 2012*a*, *b*, Dakos et al. 2015), but still in the early stages and challenged by data needs (e.g., attempts to find early-warning indicators based on zooplankton in central Baltic Sea time series were equivocal, perhaps due to data quality; Lindegren et al. 2012).

Management principle: work toward identifying and monitoring leading indicators of tipping points

Though challenging to define and often data-intensive, early-warning indicators can enable managers to trigger rapid, adaptive management responses to pending ecosystem change (Fujita et al. 2013*b*). In the absence of system-specific indicator data, protecting functional diversity and redundancy may be a useful rule of thumb (Elmqvist et al. 2003). Understanding species' roles in the food web can further guide which components of diversity and redundancy are most critical. Partnering with scientists and on-the-water experts to investigate potential early-warning indicators of declining resilience (e.g., interannual variability in catch per unit effort; Litzow et al. 2008) can help managers develop indicators specific to vulnerabilities of the focal ecosystem and address priority stressors. When time-series data are unavailable, spatial data spanning a gradient of conditions may help characterize relationships between anthropogenic stressors and measurable ecosystem components and identify potential leading indicators of ecosystem shifts (Fig. 2; McClanahan et al. 2011, Karr et al. 2015).

Importantly, using early-warning indicators requires real-time data streams and management processes nimble enough to respond proactively and adaptively, ideally with strong localized control. A Pacific oyster aquaculture company in Washington State, USA, actively manages around a tipping point in ocean pH that leads to a precipitous decline in larval growth and viability. The operation has hourly pH measurements to enable use of an alternate water supply when acidity of nearshore waters reaches harmful levels (Barton et al. 2012, Washington Blue Ribbon Panel on Ocean Acidification 2012). Management frameworks can include decision rules that enable flexibility. For instance, in coral reef systems, plans focused on coral recovery could allow for imposing temporary, immediate bans on herbivore harvest at small scales when coral bleaching levels exceed a predetermined threshold.

4. Crossing a tipping point may redistribute benefits to stakeholders

When an ecosystem crosses a tipping point, its dominant species, food-web structure, diversity, and functions change. In some cases, tipping points cause severe loss of biodiversity and benefits (e.g., eutrophication and algal domination of coasts and reefs). However, the new regime may also provide new benefits (e.g., a switch from finfisheries to shellfisheries). For human economies to effectively capitalize on these new benefits, societal shifts are often required, including new capital investments, supply chains, and social dynamics. Thus, tipping points may be accompanied by a period of social and economic disruption. Importantly, once adaptation is underway, there can be a disincentive to support restoration of the older regime. Resource users can become entrenched in their preferences and investments over time in the existing regime. In the Gulf of Maine, for example, a high-value, cod-dominated ecosystem shifted to a more lucrative, lobster-dominated state as cod were overfished (Steneck et al. 2011). Many stakeholders (most obviously the lobster-fishing industry) consequently oppose efforts to restore cod dominance, which might compromise lobster productivity. Similarly, fierce debate continues over whether to avoid or support otter reestablishment in Southern California, USA, and elsewhere following decades of local extinction that allowed shellfisheries to flourish (see *Otters, urchins, and kelp forests: linking tipping points to target-setting and monitoring*). This entrenchment may be common in systems that exhibit tipping point behavior. The longer a regime has been stable (or the longer a user has interacted with the regime), the more managers might anticipate some resistance to restoration (Duarte et al. 2009).

Even when all stakeholders would eventually gain from a changing ecosystem state, it may be difficult to implement change if the immediate cost is disproportionate among stakeholders (Smith et al. 2010). In some cases, a less-desired state with fewer services may be preferred when the expense of restoring or avoiding degradation is too high or uncertain (e.g., removal of sewage input or removal of hardened shoreline and restoration of natural habitat; Kelly et al. 2014*a*). Compromises may be possible in which novel ecosystems are engineered (sensu Hobbs et al. 2006) to allow coexistence of otherwise mutually exclusive benefits through human or technological manipulations (e.g., mariculture, feed supplementation, hatcheries, and constructed habitats).

Management principle: work to make transparent the effects of tipping points on distributions of benefits, burdens, and preferences

Many management decisions are the result of decision makers trying to address underlying sets of (often contrasting) human values. Sudden and/or large shifts in ecosystem services associated with ecological tipping points highlight and possibly exacerbate potentially inequitable distribution of costs and benefits among stakeholders and sectors. For instance, recent modeling of the Baltic Sea food web estimated a lack of recovery of cod stocks following regime shift comes at an annual cost of EUR €120 million (Bleckner et al. 2015). Engaging user groups to explore the distribution of costs and benefits across stakeholders under possible tipping point scenarios can help foster dialogue about equity, which can inform decision-making about management alternatives. Stakeholder groups with the largest economic gains from the current regime are likely to have a louder voice (e.g., capacity to organize and fund lobbying and participatory management activities) than marginalized groups or industries. Management processes that enable all groups to have a seat at the table may help avoid inequitable outcomes of participatory management. Improving environmental equity among groups can also help produce “triple bottom line” solutions (i.e., social, environmental, and financial improvements), although a focus on equity can, under some circumstances, delay or lower probability of management success (Halpern et al. 2013).

5. Tipping points change the balance between costs of action and inaction

Crossing tipping points may come with a high cost if valuable ecosystem benefits are lost and time to recovery is long. In contrast, if ecosystems were to respond to stressors in a linear, additive manner and improve predictably with the removal of stress, risks and costs associated with ecosystem change would be lower and relatively constant. Risk is a function of both probability of occurrence and magnitude of effect; both will rapidly climb as a tipping point is approached. Probability of tipping points may be difficult to determine, with tipping points often only understood when inevitable and imminent, or even passed (Hughes et al. 2013), especially if the system is initially insensitive to mounting pressure. The impacts of crossing a tipping point are often difficult to predict but are exacerbated when hysteresis is strong, because recovery to the previous state is unlikely (Tables 1 and 2). The high cost and difficulty of restoration in the face of hysteresis can exceed the limits and/or budgets of human ecosystem engineering (Fig. 3). These various unknowns and barriers, and in particular, uncertainty in exactly where the tipping point lies, argue for increasing regulation of human uses and influences tied directly or indirectly to resilience and tipping points, especially when a system is thought to be moving toward a tipping point.

Precautionary regulation is often unpopular, financially costly, or impractical, partly due to economic discounting and underestimating future risks (Scheffer 2009). However, tipping points change the balance between the costs of action and inaction. The cost of inaction skyrockets in a system that exhibits tipping points as pressure on a system intensifies, compromising resilience and leaving little buffer for the system to absorb unforeseen shocks (Kelly et al. 2014*a*). Early action to preserve resilience of a desired state is more practical, affordable, and perhaps effective than late action to prevent a tipping point by taking extreme measures to halt stress (Kelly et al. 2014*a*). Note that if

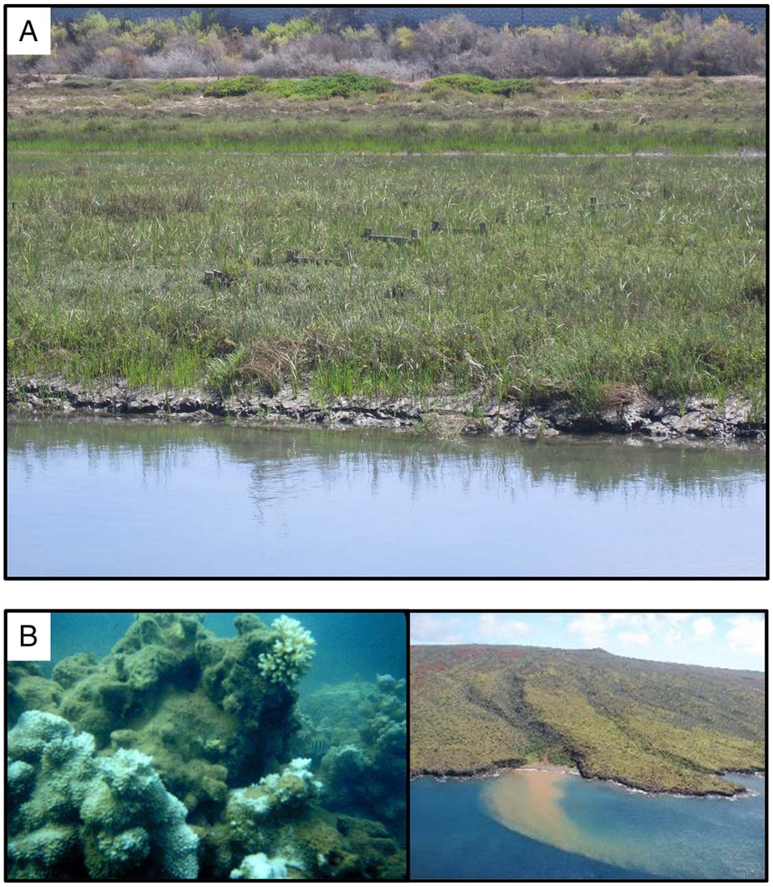


Fig. 3. Recovery stymied by hysteresis. (A) Following dredging of San Diego Bay, California, USA, attempts to restore tall salt marsh cordgrass (*Spartina foliosa*) for nesting by the endangered Light-footed Clapper Rail (*Rallus longirostris levipes*) were ineffective in sandy substrates (including dredge spoil deposits). Field experiments revealed that height was nitrogen-limited, but five years of annual fertilizer additions could not restore self-sustaining tall canopies (Lindig-Cisneros et al. 2003). Researchers and managers agreed that the mitigation site (shown here in its current state; photo by Joy Zedler) would never suit Clapper Rails. Fine clay soils of natural marshes could grow and sustain tall cordgrass, but importing clay and silt was not feasible. (B) Hysteresis plagues Hawaiian coral reefs within embayments downstream from erosion due to development, invasive ungulates, and native habitat removal. Very fine sediment remains trapped in protected embayments and is constantly resuspended but not flushed out by currents, blocking light and smothering corals for decades after the sedimentation event (Field et al. 2008, Storlazzi et al. 2009). There is no known method to safely and effectively remove such fine sediment (photos by Mike Field, USGS).

and when probing experiments to learn about thresholds become possible, new knowledge may reduce the level of precaution needed (Farrow 2004).

In some cases, the decision by fisheries managers to set harvest levels below maximum sustainable yield (MSY) has been motivated by boosting precaution in order to avoid severe economic consequences of crossing a tipping point (i.e., stock collapses; Punt et al. 2012). Australia has fully adopted risk-based measures throughout their fisheries management (Smith et al. 2009). Similarly, scientists are calling for managers to significantly reduce take of forage fish below MSY to avoid risk of adverse ecological effects for dependent predators (e.g., sea birds, mammals, and commercially valuable larger fish like halibut, salmon, and rockfish; Cury et al. 2011, Hunsicker et al. 2010, Smith et al. 2011, Pikitch 2012). Managers can proactively protect functional redundancy and diversity in the food web, e.g., by protecting species or populations that might have little economic value but boost food-web resilience (Link 2007).

Management principle: tipping points warrant increased precaution

Because the exact location of a tipping point is often unknown and difficult to quantify, greater precaution in setting management targets may be justified. Rigorous cost–benefit analysis can help to inform precautionary target-setting and reveal how costs and benefits are distributed among stakeholders to assess equity. Stakeholders will vary in their risk tolerance; the role of science is to uncover those tolerances and present them on economic, ecological, and cultural axes to inform policy development (Burgman 2005, Shelton et al. 2014). Increased information and tolerance for risk allow managers to approach a system's tipping point more closely, while lower tolerance and knowledge gaps justify greater precaution. Factors affecting risk tolerance for ecological tipping points include probability of crossing a tipping point, costs of precautionary actions, cost of restoration, probability of hysteresis or slow recovery, relative values of services lost and gained, costs of adapting to changes in resources and services, and the chance of triggering a socioeconomic collapse. Holding conversations among stakeholders and managers about the risks and costs associated with tipping points, and engaging stakeholders to clarify their tolerances for both, can yield important information for cost–benefit analysis. Communicating and quantifying the ancillary benefits of precautionary action is also important. For example, capping harvest levels below MSY tends to increase profits, improve sport fishing, and in some cases, improve dive tourism while reducing risk of stock collapse (Grafton et al. 2012). However, this approach requires strong regulatory control and access to plentiful data. Measures that make future benefits of precautionary action more salient, such as low-interest loan programs (e.g., the California Fisheries Fund), catch shares, and other incentive-based programs, may be helpful (Grimm et al. 2012, Fujita et al. 2013*a*).

6. Thresholds can inform target-setting for management

If threshold responses are strongly nonlinear, the thresholds themselves present logical limits that may simplify debate about how much use is acceptable (Rockstrom et al. 2009). For stressors that are not under management control, understanding thresholds can still guide management responses to change. Because ecosystem stability and predictability decrease as systems approach a threshold, using a precautionary buffer to set targets can help reduce risk of crossing a tipping point (Fig. 4). Risk tolerance, cost of precaution, and uncertainty in the threshold value all factor into size of the buffer (e.g., Samhouri et al. 2010, Cury et al. 2011, McClanahan et al. 2011, Large et al. 2013). Multiple examples of ecological threshold-based management standards exist within U.S. federal environmental laws, including MSY in the Magnuson Stevens Act, optimal sustainable production in the Marine Mammal Protection Act, and jeopardy determinations under the Endangered Species Act (see Kelly et al. 2014*a*).

Management principle: tie management targets to ecosystem thresholds

Identifying how and at what level activities and actions lead to ecosystem tipping points has high relevance to choosing effective management targets or limits. Exact targets will be influenced by societal risk tolerance, which is in turn related to the effort and expense required to mitigate risk. In restoration settings, management interventions that fall short of pushing a system past a recovery threshold may show no long-term progress. In other words, only a big investment is likely to pay off (i.e., "go big or go home"; Fig. 4; van der Heide et al. 2007, Martin and Kirkman 2009, Dixson et al. 2014). The unhelpful resilience of the undesired state dampens response to interventions (Standish et al. 2014). For instance, models of nutrient reduction strategies to significantly reduce the dead zone in the Gulf of Mexico recently revealed that the agreed-upon goals (widely considered ambitious) are unlikely to generate a detectable change in the size of the dead zone (Dale et al. 2010).

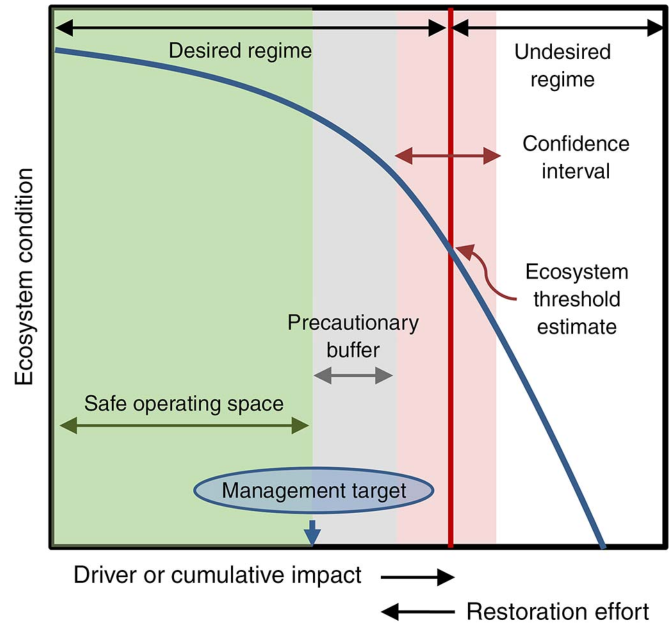
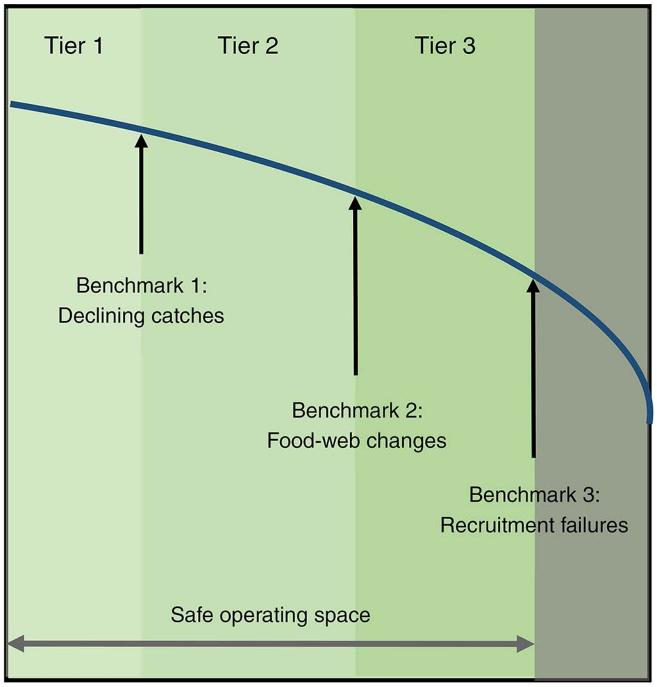


Fig. 4. A conceptual model of addressing tipping points with management targets. Maintaining or restoring a desired ecosystem regime may be aided by tying management targets to the threshold relationship(s) of top drivers to ecosystem condition. Assessments of cost, risk tolerance, and threshold confidence limits guide the width of a precautionary buffer that puts management targets within the safe operating space. To maintain a desired regime, the management target would be a maximum limit of a driver or cumulative impact to avoid a tipping point. To restore a desired regime, the management target would be a minimum restoration effort required to cause a tipping point. This conceptual example does not consider hysteresis, in which the threshold location differs depending on the direction of change across it (i.e., preservation vs. restoration of a desired state).

7. Tiered management can reduce monitoring costs while managing risk

Defining thresholds and setting precautionary buffers can be viewed as setting the boundaries of a system's "safe operating space," in which risk of unwanted regime shift is low and resilience is high (Fig. 4). Monitoring driver levels, ecosystem state indicators, and



Tier	Risk of tipping point	Threat reduction	Monitoring intensity
1	Low	None	Low
2	Moderate	Light	Moderate
3	High	Aggressive	High

Fig. 5. Defining a tiered management response to risk. The top panel expands the green-shaded portion of Fig. 4 with further heuristic detail on delineated tiers of risk based on hypothetical indicators of approach to a tipping point. The bottom panel shows a basic response plan structure used to respond to monitoring data on changes in risk.

metrics of resilience occurs with a tiered management system that boosts investments in intervention and monitoring in response to signs that the system is approaching the bounds of its safe operating space (Fig. 5). Multidimensional versions of Figs. 4 and 5 that acknowledge the many functions that make up an ecosystem, each with stressors that may contribute to ecosystem state change and require their own response plans, may be more effective when there are multiple interacting stressors and tipping points in a system (Rockstrom et al. 2009). Tiered management is a type of adaptive management that depends on routine monitoring that ramps up as a tipping point is approached. If a system is known to be far from the tipping point, i.e., in the center of the safe operating space, then fewer resources need to be applied toward monitoring and managers can be more liberal in allowing activities affecting the system (i.e., the low-risk tier). As the system begins to show signs of reduced resilience or proximity to a predicted tipping point, more resources can be invested in monitoring system indicators and assessing tipping point risk and management can switch to a more precautionary mode that initiates more aggressive threat abatement (i.e., the high-risk tier; Fig. 5). For instance, fisheries management in the USA now involves tiered decision-making based on proximity of a fishery to an overfishing threshold, risk tolerance, and amount and quality of information available (i.e., the NOAA-operated Allowable Catch Limits setting process and harvest control rules; Methot et al. 2014). Also, environmental monitoring of pollutants has addressed uncertainty and risk tolerance by using tiered sets of targets: a threshold-effect limit is set at a level of harm that is considered reversible and a probable-effect limit is set at a level of harm considered irreversible (MacDonald et al. 2000).

Kruger Park in South Africa uses a tiered management framework based on tipping point risk called "Thresholds of Potential Concern." When key indicators signal that one of these thresholds has been crossed, intense monitoring, more accurate estimation of key thresholds, detailed planning, and assessment of social preferences to inform management action are all triggered (Biggs and Rogers 2003). Importantly, before thresholds of potential concern are reached, monitoring and planning is relatively light, because intense preparation and measurement that occur too early may be of low value, given the shifting nature of threats and thresholds.

Management principle: increase monitoring and intervention as risk of a tipping point increases

Development of a tiered approach tailored to a specific system can help managers respond efficiently based on proximity to a tipping point. Investment in monitoring could be reduced when system indicators suggest risk of tipping is low. Intense monitoring and increased regulation is more valuable when risk of tipping is high. Benchmarks chosen based on changes in ecosystem condition can signal when managers should adjust management strategy to a new tier (Fig. 5). Cost–benefit analysis can make explicit the trade-offs between the cost of intense monitoring and the benefits derived from intense use when managers seek to operate close to a tipping point without crossing it. Moreover, if increased costs associated with managing close to a tipping point are acknowledged up front, these may influence decisions. Sequestering funds for management close to tipping points could further increase salience of these costs, similar to how a performance bond is designed to incentivize builders to avoid skimping to reduce costs in the short term in ways that may increase risk over the longer term (Little et al. 2014). Fundamental to effective application of this tiered approach are leading indicators that are easily measurable and can help managers set benchmarks, predict ecosystem shifts, and act in a timely fashion.

Otters, Urchins, and Kelp Forests: An Example of Linking Tipping Points to Target-setting and Monitoring

The 19th century extirpation and recent recovery of sea otters along the west coast of North America has triggered ecological, cultural, and socioeconomic transformations that continue to elicit complex trade-offs in values and priorities among coastal communities. These trade-offs emerge because of the different ecosystem regimes that arise in systems with and without sea otters. The sea otter is a keystone predator of urchin, abalone, and other shellfish in kelp forests. On high-latitude reefs, when otters are absent, urchins undergo population booms that wipe out kelp, denuding the bottom and creating "urchin barrens" (Steneck et al. 2002). Vast, old-growth kelp forests, and the diverse fish communities they support, are unable to reestablish once an urchin barren forms due to overgrazing of young plants. Long-term monitoring and experimental studies of sea otters and subtidal reefs in the Aleutian Islands (Alaska, USA), southeast Alaska, USA, and British Columbia, Canada, demonstrated that shifts between ecosystem states are rapid and absolute (Fig. 6). These data further reveal that the sea otter–kelp forest system is characterized by hysteresis, where forward and backward state switches occur under different levels of otter density (Fig. 7; Konar and Estes 2003).

The high biodiversity and productivity of a kelp forest support a number of societal benefits: enhanced commercial and recreational finfisheries, carbon storage, recreation, tourism, and coastal protection (Duggins 1980, Wilmers et al. 2012, Schmitz et al. 2014). In contrast, the urchin-dominated state provides lucrative urchin and shellfish fisheries, but its resilience is thought to be lower because biodiversity is low and the high density of shellfish increases risk of disease epidemics (Duggins et al. 1989, Lafferty 2004, Anthony et al. 2008). Furthermore, the singular focus of the urchin fishery enhances the tendency for overexploitation and fishery collapse. Nevertheless, fishing infrastructure and lifestyles have adapted to supporting the shellfishery, and the investments needed to switch to a diversified economy built around finfisheries and tourism are considerable. Thus, there may be strong preference for the lower-diversity, lower-resilience state because of socioeconomic entrenchment and, no less important, cultural legacies.

Through the lens of this well-studied example, we illustrate the relevance of each of the principles (Table 3) and the use of thresholds to set targets based on risk and uncertainty.

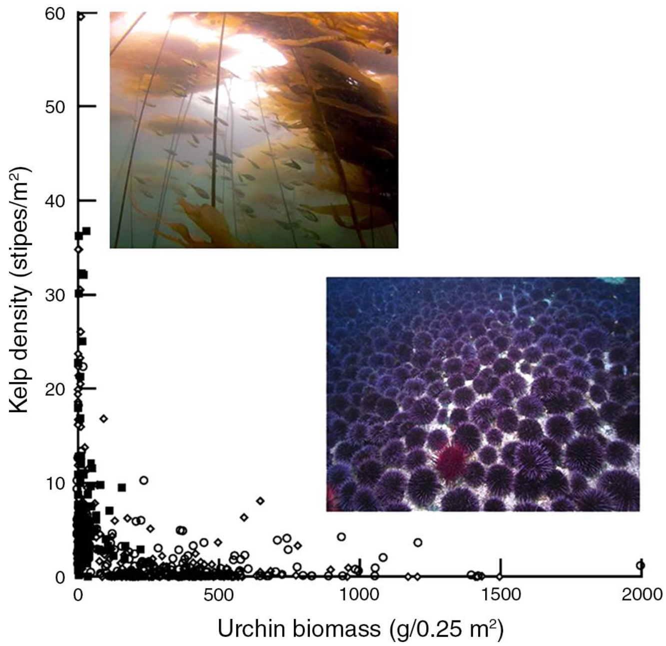


Fig. 6. Field estimates of kelp density and urchin biomass across 463 coastal sites in the Aleutian archipelago (Alaska, USA) between 1987 and 2006. Open circles are sites with <6 otters/km; solid squares are sites with >6 otters/km; diamonds are sites with no otter data available. These data demonstrate the nonlinear relationship with kelp cover and the lack of intermediate states, suggesting the transition between kelp- and urchin-dominated states is abrupt. Plot taken from Estes et al. (2010). Photographs by Jenn Burt and Lynn Lee.

1. *Tipping points are common*. Abrupt switches between kelp and urchin dominance have been shown around the world, with evidence for hysteresis (Fig. 6; Steneck et al. 2013, Filbee-Dexter and Scheibling 2014). Although kelp forest ecosystems may be more dynamic than other marine systems, they help highlight the need for management to acknowledge and address tipping point behavior.
2. *Intense human use is implicated*. The extirpation of otters due to hunting is a prime example of intense human use, in this case focused on a keystone species, driving an ecosystem past a tipping point.
3. *Early-warning indicators are possible*. Monitoring otter, urchin, and kelp densities and rates of population growth can indicate risk of tipping points. In particular, declining otter densities may offer a robust early-warning indicator of an imminent ecosystem shift to urchin barrens, although the threshold number of otters likely differs among regions.
4. *Ecosystem benefits shift with regimes.* Kelp forests support diverse finfisheries, recreation, and tourism, while urchin barrens support lucrative shellfisheries. Adapting infrastructure and industries to switch between these sets of services is costly, with clear trade-offs.
5. *Tipping points warrant increased precaution*. To maintain shellfisheries in the face of otter

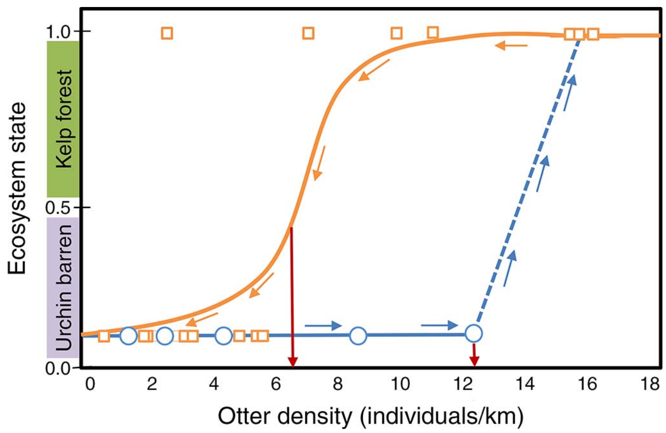


Fig. 7. Field studies of changing sea otter densities in the central and western Aleutian Islands show distinct thresholds of state change (red arrows) based on whether sites show increasing or decreasing otter densities, indicating hysteresis. Smoothed orange line is a logistic regression fit to raw data from systems with declining sea otter densities (squares; from Estes et al. [2010]), revealing a threshold of state change (ecosystem state of 0 indicates urchin dominance, ecosystem state of 1 indicates kelp dominance) when density falls below ~6.3 otters/km; solid blue line is a linear fit to raw data from systems with increasing sea otter densities (circles; J. A. Estes et al., *unpublished data*), demonstrating that an urchin-dominated state persists despite otter density reaching >12 otters/km. Dashed line estimates a potential shift to a kelp state above 12 otters/km; however, otter numbers at Attu Island, where these data were obtained, began to decline, reportedly from killer whale predation, and thus a shift to the kelp-dominated state never actually occurred (Estes et al. 1998). Arrows indicate the direction of change.

rebound, a risk-adverse strategy was implemented in southern California, USA, to relocate each otter that strayed into otter exclusion zones rather than wait until signs of otter population establishment or kelp regrowth to take action (Fig. 8).

6. *Thresholds aid target setting*. Robust estimates of otter densities tied to the kelp/urchin transition point can be used to set target otter densities depending on preferred regime (Fig. 7). Preferably, these threshold estimates derive from local data.
7. *Tiered management efficiently responds to monitoring data*. Response plans to either reduce or support otter and urchin population sizes (depending on desired regime) can be implemented with increasing intensity and monitoring as the tipping point is approached. To maintain kelp forests as otters declined, managers in Alaska, USA, implemented new regulations to protect critical otter habitat (Fig. 8).

Discussion

Policymakers and managers have the difficult task of protecting, managing, and restoring ecosystems to ensure sustainable delivery of ecosystem benefits (Lebel et al. 2006). New tools and concepts are required to manage with a tipping points perspective. The principles presented here may help managers evaluate and articulate strategies to incorporate tipping point knowledge into resource management frameworks (Table 3). The principles suggest priorities for applied research, such as identifying top drivers of regimes, estimating threshold levels of stressors (and confidence bounds around them), finding early-warning indicators, testing metrics of resilience and system stability, and improving assessments of risk and stakeholder preferences. As a whole, these principles support the need for formal stakeholder engagement in target-setting. Careful evaluation of stakeholder preferences and trade-offs may complicate management in the short term, but may yield more durable results. Where stakeholders are concerned about a new management strategy's costs and constraints, these principles can help articulate links between strong shifts in ecosystems and ripple effects on communities and economies, as well as the potential for cost savings.

Although the principles we outline are relevant to management of any type of ecosystem, they are especially important for marine systems. Coastal areas deliver critical services for the majority of the world's human population, and pelagic fisheries provide important food security for the globe. The coastal zone is associated with many overlapping uses and stressors, and fragmented and mismatched governance (Crowder et al. 2006). The pelagic zone is often subject to intense exploitation of species, such as herring, salmon, or tuna, whose abundances are also subject to natural and human-induced changes in climate with pervasive effects throughout the food web.

Incorporating these principles into existing management structures may not require major shifts from current practices and in some cases may create efficiency and cost savings. For instance, integrated ecosystem assessments, which are a general framework for implementing ecosystem-based management using explicit targets, can be geared toward preventing a tipping point or restoring a system that has crossed a tipping point (Levin and Möllmann 2014). In other cases, responding to tipping point behavior may require fundamentally different management structures, such as Kruger Park's Thresholds of Potential Concern, built within a safe operating space framework (Fig. 5). The appropriate management approach also depends on whether a tipping point is beyond local management control (e.g., climate change), or conversely, driven by local activities and effects subject to regulation or mitigation. In the former case, management can focus on building resilience in the social-ecological system to abrupt changes (Dawson et al. 2011). In the latter, managers might focus on preventing threshold levels of human stressors from being reached, alongside efforts to

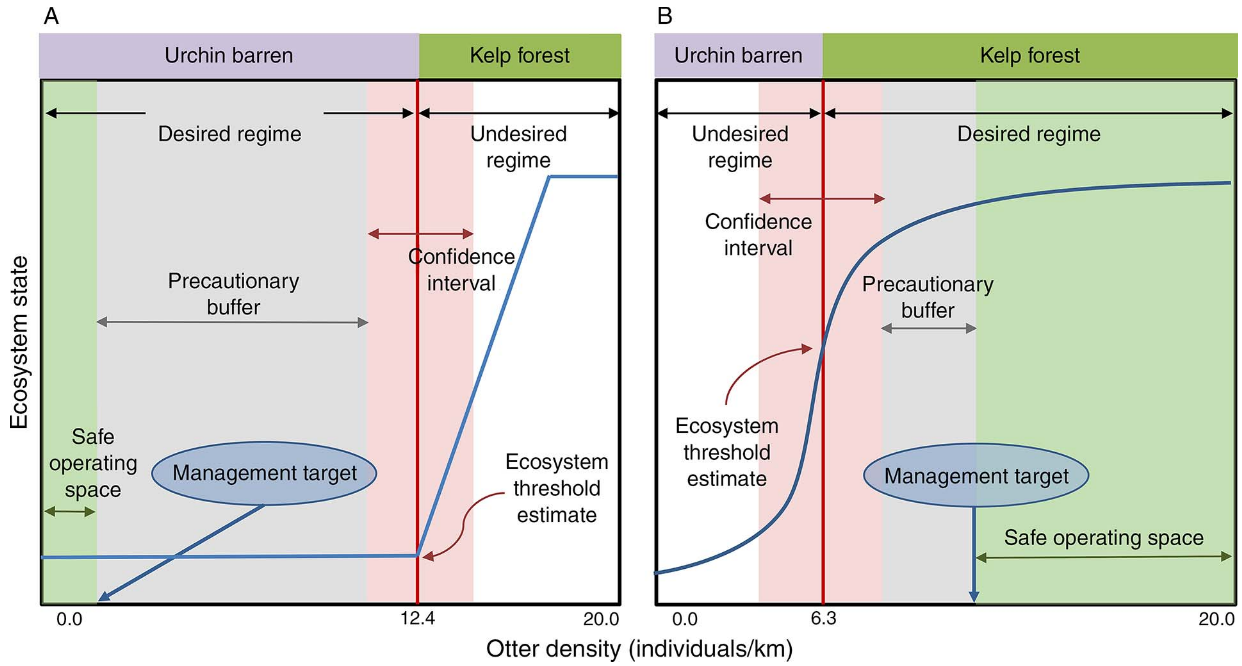


Fig. 8. Two applications of the conceptual model in Fig. 4 to the urchin/otter case study example. (A) The management goal is maintaining an otter-free zone. In response to strong preferences by shellfishermen to maintain urchin barrens and a low tolerance for risk, between 1989 and ca. 2001, the U.S. Fish and Wildlife Service (FWS) captured and moved every otter in Southern California, USA, that strayed beyond the designated sea otter zone around San Nicolas Island back to San Nicolas or central California. This objective creates a very wide precautionary buffer and a management target set close to zero otters. (B) Maintaining kelp forests through otter protection. In parts of Alaska, a sea otter recovery management plan seeks to maintain a minimum density of otters to support kelp forests and the tourism trade. Otters need habitat that offers protection from orcas, so in response to mounting orca predation, FWS designated critical habitat to protect areas where orca predation success is lowest. This strategy allows for a narrower precautionary buffer and a target minimum number of otters.

support a resilient state by protecting diversity and key feedback processes. In all cases, close examination of where cross-scale interactions across drivers, geography, and levels of government may add challenges and obstacles is important for proactive planning.

Ultimately, understanding shifts between ecosystem states, particularly given interacting and changing stressors, requires getting comfortable with estimation and prediction, and investing in good data. Ongoing research on effective system indicators, costs of management action or inaction, and societal preferences and trade-offs among management options will continue to generate new insights into how best to manage ecosystems prone to tipping points (Graham et al. 2014).

Acknowledgments

The coauthors thank our colleagues in the Ocean Tipping Points Scientific Working Group, All Hands Meeting, and Expert Management Advisory Group who provided insights and critique of our ideas and framing: Cindy Boyko, Malia Chow, William Douros, Ernie Gladstone, Elia Herman, Martha Kongsgaard, Frazer McGilvray, Will Stelle, John Weber, Steve Weisberg, Phil Williams, Joy Zedler, John Lynham, and Bruno Nkuiya. We also thank Terry Chapin, Steve Carpenter, and two anonymous reviewers for critical feedback on this manuscript. Primary funding was provided by the Gordon and Betty Moore Foundation, with additional support to K. A. Selkoe from National Science Foundation (BioOCE Award 1260169).

Literature Cited

Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology and Evolution 15:337–341.

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8:S79–S92.

Anthony, R. G., J. A. Estes, M. A. Ricca, A. K. Miles, and E. D. Forsman. 2008. Bald Eagles and sea otters in in the Aleutian archipelago: indirect effects of trophic cascades. Ecology 89:2725–2735.

Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio dependence. Journal of Theoretical Biology 139:311–326.

Barton, A., B. Hales, G. G. Waldbusser, C. Langdon, and R. A. Feely. 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: implications for near-term ocean acidification effects. Limnology and Oceanography 57:698–710.

Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78:699–714.

Bennett, A., and J. Radford. 2003. Know your ecological thresholds. Thinking Bush 2:1–3.

Biggs, H., and K. H. Rogers. 2003. An adaptive system to link science, monitoring and management in practice. Pages 59–80 *in* J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA.

Biggs, R., M., et al. 2012. Toward principles for enhancing the resilience of ecosystem services. Annual Review of Environment and Resources 37:421–448.

Bleckner, T., M. Llope, C. Möllmann, R. Voss, M. F. Quaas, M. Casini, M. Lindegren, C. Folke, and N. C. Stenseth. 2015. Climate and fishing steer ecosystem regeneration to uncertain economic futures. Proceedings of the Royal Society B 282:20142809.

Boettiger, C., and A. Hastings. 2012*a*. Early warning signals and the prosecutor's fallacy. Proceedings of the Royal Society B 279:4734–4739.

Boettiger, C., and A. Hastings. 2012*b*. Quantifying limits to detection of early warning for critical transitions. Journal of the Royal Society Interface 9:2527–2539.

Brandl, S. J., and D. R. Bellwood. 2014. Individual-based analyses reveal limited functional overlap in a coral reef fish community. Journal of Animal Ecology 83:661–670.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecology and Management 59:225–236.

Burgman, M. 2005. Risks and decisions for conservation and environmental management. Cambridge University, Cambridge, UK.

Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. Ecology Letters 9:308–315.

Carpenter, S. R., and C. Folke. 2006. Ecology for transformation. Trends in Ecology and Evolution 21:309–315.

Casini, M., J. Hjelm, J. C. Molinero, J. Lovgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences USA 106:197–202.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.

Crowder, L. B., et al. 2006. Resolving mismatches in US ocean governance. Science 313:617–618.

Cury, P. M., et al. 2011. Global seabird response to forage fish depletion—one-third for the birds. Science 334:1703–1706.

D'Agata, S., D. Mouillot, M. Kulbicki, S. Andrefouet, D. R. Bellwood, J. E. Cinner, P. F. Cowman, M. Kronen, S. Pinca, and L. Vigliola. 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. Current Biology 24:555–560.

Dai, L., K. S. Korolev, and J. Gore. 2013. Slower recovery in space before collapse of connected populations. Nature 496:355–358.

Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. Science 336:1175–1177.

Dakos, V., S. R. Carpenter, E. H. van Nes, and M. Scheffer. 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. Philosophical Transactions of the Royal Society B 370:20130263.

Dakos, V., S. Kefi, M. Rietkerk, E. H. van Nes, and M. Scheffer. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. American Naturalist 177:E153–E166.

Dakos, V., E. H. van Nes, P. D'Odorico, and M. Scheffer. 2012. Robustness of variance and autocorrelation as indicators of critical slowing down. Ecology 93:264–271.

Dale, V. H., et al. 2010. Hypoxia in the northern Gulf of Mexico. Springer series on environmental management. Springer, New York, New York, USA.

Daskalov, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. Marine Ecology Progress Series 225:53–63.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.

Dean, T. A., J. L. Bodkin, S. C. Jewett, D. H. Monson, and D. Jung. 2000. Changes in sea urchins and kelp following a reduction in sea otter density as a result of the Exxon Valdez oil spill. Marine Ecology Progress Series 199:281–291.

Ditlevsen, P. D., and S. J. Johnsen. 2010. Tipping points: early warning and wishful thinking. Geophysical Research Letters 37:L19703.

Dixson, D. L., D. Abrego, and M. E. Hay. 2014. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897.

Doak, D. F., et al. 2008. Understanding and predicting ecological dynamics: are major surprises inevitable? Ecology 89:952–961.

Duarte, C. M., D. J. Conley, J. Carstensen, and M. Sanchez-Camacho. 2009. Return to Neverland: shifting baselines affect eutrophication restoration targets. Estuaries and Coasts 32:29–36.

Dudgeon, S. R., R. B. Aronson, J. F. Bruno, and W. F. Precht. 2010. Phase shifts and stable states on coral reefs. Marine Ecology Progress Series 413:201–216.

Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology 61:447–453.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25–64.

Edmondson, W., and J. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnology and Oceanography 26:1–29.

Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs 65:75–100.

Estes, J. A., and J. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Estes, J. A., M. T. Tinker, and J. L. Bodkin. 2010. Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian Archipelago. Conservation Biology 24:852–860.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

Fairchild, J. F., T. W. Lapoint, J. L. Zajicek, M. K. Nelson, F. J. Dwyer, and P. A. Lovely. 1992. Population-level, community-level and ecosystem-level responses of aquatic mesocosms to pulsed doses of a pyrethroid insecticide. Environmental Toxicology and Chemistry 11:115–129.

Farrow, S. 2004. Using risk assessment, benefit-cost analysis, and real options to implement a precautionary principle. Risk Analysis 24:727–735.

Ferretti, F., B. Worm, G. L. Britten, M. R. Heithaus, and H. K. Lotze. 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecology Letters 13:1055–1071.

Field, M. E., S. A. Cochran, J. B. Logan, and C. D. Storlazzi. 2008. The coral reef of south Moloka'i, Hawai'i; portrait of a sediment-threatened reef. U.S. Geological Survey Scientific

Investigations Report 2007-5101. USGS Information Services, Denver, Colorado, USA.

Filbee-Dexter, K., and R. E. Scheibling. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Marine Ecology Progress Series 495:1–25.

Foley, M. M., et al. 2010. Guiding ecological principles for marine spatial planning. Marine Policy 34:955–966.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 35:557–581.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623.

Frank, K. T., B. Petrie, J. A. D. Fisher, and W. C. Leggett. 2011. Transient dynamics of an altered large marine ecosystem. Nature 477:86–U98.

Fujita, R., J. Lynham, F. Micheli, P. G. Feinberg, L. Bourillón, A. Sáenz-Arroyo, and A. C. Markham. 2013*a*. Ecomarkets for conservation and sustainable development in the coastal zone. Biological Reviews 88:273–286.

Fujita, R., J. H. Moxley, H. DeBey, T. Van Leuvan, A. Leumer, K. Honey, S. Aguilera, and M. Foley. 2013*b*. Managing for a resilient ocean. Marine Policy 38:538–544.

Grafton, Q. R., T. Kompas, T. N. Che, L. Chu, and R. Hilborn. 2012. BMEY as a fisheries management target. Fish and Fisheries 13:303–312.

Graham, N. A. J., D. R. Bellwood, J. E. Cinner, T. P. Hughes, A. V. Norstrom, and M. Nystrom. 2013. Managing resilience to reverse phase shifts in coral reefs. Frontiers in Ecology and the Environment 11:541–548.

Graham, N. A. J., J. E. Cinner, A. V. Norstrom, and M. Nystrom. 2014. Coral reefs as novel ecosystems: embracing new futures. Current Opinion in Environmental Sustainability 7:9–14.

Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. P. Bijoux, and J. Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Sciences USA 103:8425–8429.

Greening, H., and A. Janicki. 2006. Toward reversal of eutrophic conditions in a subtropical estuary: water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. Environmental Management 38:163–178.

Griffith, G. P., E. A. Fulton, and A. J. Richardson. 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. Global Change Biology 17:3058–3074.

Grimm, D., I. Barkhorna, D. Festab, K. Bonzonb, J. Boomhowerb, V. Hovlanda, and J. Blau. 2012. Assessing the key players in a food web can help guide management strategies to address tipping points. Marine Policy 36:644–657.

Groffman, P. M., et al. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13.

Halpern, B. S., et al. 2013. Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. Proceedings of the National Academy of Sciences USA 110:6229–6234.

Hilborn, R. 2010. Pretty Good Yield and exploited fishes. Marine Policy 34:193–196.

Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomology 91:293–320.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hsieh, C. H., C. S. Reiss, R. P. Hewitt, and G. Sugihara. 2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 65:947–961.

Hugget, A. J. 2005. The concept and utility of ecological thresholds in biodiversity conservation. Biological Conservation 124:301–310.

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

Hughes, T. P., C. Linares, V. Dakos, I. A. van de Leemput, and E. H. van Nes. 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends in Ecology and Evolution 28:149–155.

Hunsicker, M. E., et al. 2010. The contribution of cephalopods to global marine fisheries: Can we have our squid and eat them too? Fish and Fisheries 11(4):421–438.

Johannessen, O. M., and M. W. Miles. 2011. Critical vulnerabilities of marine and sea ice-based ecosystems in the high Arctic. Regional Environmental Change 11:S239–S248.

Karnosky, D. F., K. S. Pregitzer, D. R. Zak, M. E. Kubiske, G. R. Hendrey, D. Weinstein, M. Nosal, and K. E. Percy. 2005. Scaling ozone responses of forest trees to the ecosystem level in a changing climate. Plant Cell and Environment 28:965–981.

Karp, D. S., G. Ziv, J. Zook, P. R. Ehrlich, and G. C. Daily. 2011. Resilience and stability in bird guilds across tropical countryside. Proceedings of the National Academy of Sciences USA 108:21134–21139.

Karr, K., R. Fujita, B. S. Halpern, C. V. Kappel, L. B. Crowder, K. A. Selkoe, P. M. Alcolado, and D. Rader. 2015. Thresholds in Caribbean coral reefs: implications for ecosystem-based fishery management. Journal of Applied Ecology 52(2):402–412.

Kefi, S., V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and V. Dakos. 2014. Early warning signals of ecological transitions: methods for spatial patterns. PLoS ONE 9:e92097.

Kelly, R. P., A. L. Erickson, and L. A. Mease. 2014*a*. How not to fall off a cliff, or using tipping points to improve environmental management. Ecology Law Quarterly 41:843–886.

Kelly, R. P., A. L. Erickson, L. A. Mease, W. Battista, J. N. Kittinger, and R. Fujita. 2014*b*. Embracing thresholds for better environmental management. Philosophical Transactions of the Royal Society B 370:20130276.

Konar, B., and J. A. Estes. 2003. The stability of boundary regions between kelp beds and deforested areas. Ecology 84:174–185.

Lafferty, K. D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. Ecological Applications 14:1566–1573.

Laliberte, E., et al. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13:76–86.

Large, S. I., G. Fay, K. D. Friedland, and J. S. Link. 2013. Defining trends and thresholds in responses of ecological indicators to fishing and environmental pressures. ICES Journal of Marine Science 70:755–767.

Lebel, L., J. M. Anderies, B. Campbell, C. Folke, S. Hatfield-Dodds, T. P. Hughes, and J. Wilson. 2006. Governance and the capacity to manage resilience in regional social-ecological systems. Ecology and Society 11:19.

Leslie, H. M., and K. L. McLeod. 2007. Confronting the challenges of implementing marine ecosystem-based management. Frontiers in Ecology and the Environment 5:540–548.

Levin, P., and C. Möllmann. 2014. Marine ecosystem regime shifts: challenges and opportunities for ecosystem-based management. Philosophical Transactions of the Royal Society B 370:20130275.

Lewontin, R. C. 1969. The meaning of stability. Brookhaven Symposia in Biology 22:13–24.

Lindegren, M., D. M. Checkley, Jr., T. Rouyer, A. D. MacCall, and N. C. Stenseth. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. Proceedings of the National Academy of Sciences USA 110:13672–13677.

Lindegren, M., V. Dakos, J. P. Groeger, A. Gardmark, G. Kornilovs, S. A. Otto, and C. Moellmann. 2012. Early detection of ecosystem regime shifts: a multiple method evaluation for management application. PLoS ONE 7:e38410.

Lindig-Cisneros, R., J. Desmond, K. E. Boyer, and J. B. Zedler. 2003. Wetland restoration thresholds: can a degradation transition be reversed with increased effort? Ecological Applications 13:193–205.

Link, J. S. 2007. Underappreciated species in ecology: "ugly fish" in the northwest Atlantic Ocean. Ecological Applications 17:2037–2060.

Little, R. L., J. Parslow, G. Fay, R. Q. Grafton, A. D. M. Smith, A. E. Punt, and G. N. Tuck. 2014. Environmental derivatives, risk analysis, and conservation management. Conservation Letters 7:196–207.

Litzow, M. A., F. J. Mueter, and J. D. Urban. 2013. Rising catch variability preceded historical fisheries collapses in Alaska. Ecological Applications 23:1475–1487.

Litzow, M. A., J. D. Urban, and B. J. Laurel. 2008. Increased spatial variance accompanies reorganization of two continental shelf ecosystems. Ecological Applications 18:1331–1337.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20:223–228.

Luck, G. W., G. C. Daily, and P. R. Ehrlich. 2003. Population diversity and ecosystem services. Trends in Ecology and Evolution 18:331–336.

MacDonald, Donald D., C. G. Ingersoll, and T. A. Berger. 2000. Development and evaluation of consensus-based sediment quality guidelines for freshwater ecosystems. Archives of Environmental Contamination and Toxicology 39:20–31.

Martin, K. L., and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology 46:906–914.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences USA 108:17230–17233.

Meador, J. P., T. K. Collier, and J. E. Stein. 2002. Determination of a tissue and sediment threshold for tributyltin to protect prey species of juvenile salmonids listed under the US Endangered Species Act. Aquatic Conservation: Marine and Freshwater Ecosystems 12:539–551.

Methot, R. D., G. R. Tromble, D. M. Lambert, and K. E. Greene. 2014. Implementing a science-based system for preventing overfishing and guiding sustainable fisheries in the United States. ICES Journal of Marine Science 71:183–194.

Michalak, A. M., et al. 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. Proceedings of the National Academy of Sciences USA 110:6448–6452.

Montefalcone, M., V. Parravicini, and C. N. Bianchi. 2011. Quantification of coastal ecosystem resilience. Treatise on Estuarine and Coastal Science 10:49–70.

Mori, A. S., T. Furukawa, and T. Sasaki. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88:349–364.

Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850.

Nystrom, M., A. V. Norstrom, T. Blenckner, M. de la Torre-Castro, J. S. Eklof, C. Folke, H. Osterblom, R. S. Steneck, M. Thyresson, and M. Troell. 2012. Confronting feedbacks of degraded marine ecosystems. Ecosystems 15:695–710.

O'Gorman, E. J., J. M. Yearsley, T. P. Crowe, M. C. Emmerson, U. Jacob, and O. L. Petchey. 2011. Loss of functionally unique species may gradually undermine ecosystems. Proceedings of the Royal Society B 278:1886–1893.

Oguz, T., and D. Gilbert. 2007. Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep Sea Research Part I: Oceanographic Research Papers 54:220–242.

Ohman, M. D., K. Barbeau, P. J. S. Franks, R. Goericke, M. R. Landry, and A. J. Miller. 2013. Ecological transitions in a coastal upwelling ecosystem. Oceanography 26:210–219.

Olds, A. D., K. A. Pitt, P. S. Maxwell, and R. M. Connolly. 2012. Synergistic effects of reserves and connectivity on ecological resilience. Journal of Applied Ecology 49:1195–1203.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems 10:790–796.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Petraitis, P. S., E. T. Methratta, E. C. Rhile, N. A. Vidargas, and S. R. Dudgeon. 2009. Experimental confirmation of multiple community states in a marine ecosystem. Oecologia 161:139–148.

Pikitch, E. K. 2012. The risks of overfishing. Science 338:474–475.

Planque, B., J. M. Fromentin, P. Cury, K. F. Drinkwater, S. Jennings, R. I. Perry, and S. Kifani. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems 79:403–417.

Poe, M. R., K. C. Norman, and P. S. Levin. 2014. Cultural dimensions of socioecological systems: key connections and guiding principles for conservation in coastal environments. Conservation Letters 7:166–175.

Punt, A. E., M. S. M. Siddeek, B. Garber-Yonts, M. Dalton, L. Rugolo, D. Stram, B. J. Turnock, and J. Zheng. 2012. Evaluating the impact of buffers to account for scientific uncertainty when setting TACs: application to red king crab in Bristol Bay, Alaska. ICES Journal of Marine Science 69:624–634.

Rabalais, N. N., R. J. Diaz, L. A. Levin, R. E. Turner, D. Gilbert, and J. Zhang. 2010. Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences 7:585–619.

Rasher, D. B., A. S. Hoey, and M. E. Hay. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94:1347–1358.

Rocha, J., J. Yletyinen, R. Biggs, T. Blenckner, and G. Peterson. 2015. Marine regime shifts: drivers and impacts on marine systems. Philosophical Transactions of the Royal Society B 370:20130273.

Rockstrom, J., et al. 2009. A safe operating space for humanity. Nature 461:472–475.

Salazar, M. H., and S. M. Salazar. 1991. Mussels as bioindicators: a case study of tributyltin effects in San Diego Bay, California USA. Canadian Technical Report of Fisheries and Aquatic Sciences 1774:47–75.

Samhouri, J. F., P. S. Levin, and C. H. Ainsworth. 2010. Identifying thresholds for ecosystem-based management. PLoS ONE 5:e8907.

Scheffer, M. 2009. Critical transitions in nature and society. Princeton University, Princeton, New Jersey, USA.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker.

2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648–656.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Schmitz, O. J., et al. 2014. Animating the carbon cycle. Ecosystems 17:344–359.

Shelton, A. O., J. F. Samhouri, A. C. Stier, and P. S. Levin. 2014. Assessing trade-offs to inform ecosystem-based fisheries management of forage fish. Scientific Reports 4:7110.

Smith, A. D. M., et al. 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science 333:1147–1150.

Smith, D., A. Punt, N. Dowling, A. Smith, G. Tuck, and I. Knuckey. 2009. Reconciling approaches to the assessment and management of data-poor species and fisheries with Australia's harvest strategy policy. Marine and Coastal Fisheries 1:244–254.

Smith, M. D., J. Lynham, J. N. Sanchirico, and J. A. Wilson. 2010. Political economy of marine reserves: understanding the role of opportunity costs. Proceedings of the National Academy of Sciences USA 107:18300–18305.

Standish, R. J., et al. 2014. Resilience in ecology: abstraction, distraction, or where the action is? Biological Conservation 177:43–51.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436–459.

Steneck, R. S., et al. 2011. Creation of a gilded trap by the high economic value of the Maine lobster fishery. Conservation Biology 25:904–912.

Steneck, R. S., A. Leland, D. C. McNaught, and J. Vavrinec. 2013. Ecosystem flips, locks and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. Bulletin of Marine Science 89:31–55.

Steneck, R. S., and R. A. Wahle. 2013. American lobster dynamics in a brave new ocean. Canadian Journal of Fisheries and Aquatic Sciences 70:1612–1624.

Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? Oikos 87:185–190.

Storlazzi, C. D., M. E. Field, M. H. Bothner, M. K. Presto, and A. E. Draut. 2009. Sedimentation processes in a coral reef embayment: Hanalei Bay, Kauai. Marine Geology 264:140–151.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology and Evolution 24:271–279.

Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859–873.

Thibaut, L. M., S. R. Connolly, and H. P. A. Sweatman. 2012. Diversity and stability of herbivorous fishes on coral reefs. Ecology 93:891–901.

Travis, J., F. C. Coleman, P. J. Auster, P. M. Cury, J. A. Estes, J. Orensanz, C. H. Peterson, M. E. Power, R. S. Steneck, and J. T. Wootton. 2014. Integrating the invisible fabric of nature into fisheries management. Proceedings of the National Academy of Sciences USA 111:581–584.

van der Heide, T., E. H. van Nes, G. W. Geerling, A. J. P. Smolders, T. J. Bouma, and M. M. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. Ecosystems 10:1311–1322.

Vélez-Espino, L. A., and M. A. Koops. 2009. Quantifying allowable harm in species at risk: application to the Laurentian black redhorse (*Moxostoma duquesnei*). Aquatic Conservation: Marine Freshwater Ecosystems 19:676–688.

Walker, B., and D. Salt. 2012. Resilience practice: building capacity to absorb disturbance and maintain function. Island Press, Washington, D.C., USA.

Washington State Blue Ribbon Panel on Ocean Acidification. 2012. Ocean acidification: from knowledge to action, Washington State's strategic response. H. Adelsman and L. Whitely Binder, editors. Publication no. 12-01-015. Washington Department of Ecology, Olympia, Washington, USA.

Wilmers, C. C., J. A. Estes, M. Edwards, K. L. Laidre, and B. Konar. 2012. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. Frontiers in Ecology and the Environment 10:409–415.