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Threshold Effects in Semi-Enclosed Marine Systems

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Introduction

The natural history of the twentieth century documents dramatic changes in many ecological systems, mostly due to the influence of the expansion of human civilization. Semi-enclosed marine systems (SEMSs) are no exception to this. Here is an example, from Jansson and Dahlberg (1999):

In the 1940s, the Baltic Sea was a nutrient-poor sea with low biological production, clear water, and rocky shores with dense growths of the brown seaweed bladderwrack, providing food and shelter for many species, including spawning and nursery grounds for many fish. There was sufficient oxygen in the bottom water for cod to spawn in the deep areas of the Baltic Proper, except for periods of oxygen depletion in the Gotland Deep. Top consumers like seal and sea eagle were common and people living around the Baltic Sea could eat fish without risking their health. The Baltic Sea of today is different. Eutrophication and toxic substances now affect the entire Baltic Sea ecosystem, even the offshore areas. Filamentous green and brown algae shade the bladderwrack and may even totally replace it. Increased plankton blooms and organic particle production [have] lowered light penetration by 3 m and oxygen depletion and hydrogen sulfide formation sometimes dominate as much as one third of the total bottom area. To reduce the nutrient load to the levels of the 1940s, a reduction by 65% for phosphorus and 80% for nitrogen is needed.

Box 3-1. Glossary

Threshold: A particular level of some internal or external condition at which a large change in ecosystem state is observed

Stable state: A state at which a system will persist unless perturbed, and to which it will return after a disturbance

Regime: The dynamic conditions that characterize an ecosystem state

Pressures: Human activities causing environmental problems

Impact: The effects of human pressures on an ecosystem state

Hysteresis: The condition in which the trajectory a system goes through when pressure levels are increased differs from the trajectory when pressure levels are reduced (see Figure 3-1B)

The authors describe an apparent large change in the state of the Baltic Sea as a consequence of eutrophication and the release of toxic substances into the water. They suggest that humans should aim to decrease these perturbing inputs in order to return the sea to the original condition. However, despite a significant reduction in the extent of those disturbances, little recovery has been witnessed in the Baltic Sea. It appears that a threshold has been passed and that a return from the new degraded state to the old state is very difficult, posing significant problems to management.

A large body of ecological theory has developed to explain dramatic changes in ecosystems that are hard to reverse. We mainly draw on work by Scheffer and colleagues (1998, 2001) from temperate lakes, arid ecosystems, and coral reefs (see glossary in Box 3-1 for terminology). This theory proposes that, in general terms, two types of threshold responses can be recognized (Figure 3-1). The first type refers to a continuous response of an ecosystem to an increase in external pressure, which starts or is most apparent at a specific threshold level of the external condition (Figure 3-1A). With changing pressure levels, as conditions change, the system gradually moves from an original state or regime, through an affected and altered state, to a state or regime that humans consider degraded because of deterioration in the services that the ecosystem can provide us. Upon reduction of the pressure, the system returns to its original state, tracing the same path backward. We refer to this as a nonhysteretic threshold response (vs. hysteretic; see explanation below). The gradual nature of the change implies that managers can infer from a slowly deteriorating system that there is eminent danger of reaching a critical state and can take measures to prevent this from occurring.

The second type of threshold response is characterized by a dramatic change when external forcing exceeds a particular threshold. As a consequence, the system jumps

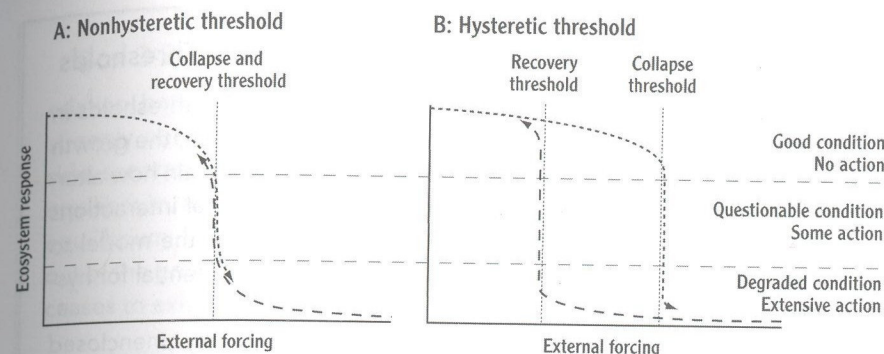


Figure 3-1. Graphical representation of two types of threshold responses of ecosystems to changing conditions. Horizontal dashed lines represent change trajectories, and vertical dotted lines represent threshold levels. Panel A represents a nonhysteretic response to changing conditions, where the dotted line is where a threshold effect is experienced. This threshold, however, is reversible. Moreover, a continuous change is experienced from a more or less pristine to a critical, highly degraded state. This change can easily be reversed. Panel B represents a hysteretic threshold, where the switch from a pristine condition to a degraded condition (short-dashed line) occurs at a different threshold level than the switch back from the degraded to the pristine condition (long-dashed line). Hence, ecosystem conditions can be reversed only by a dramatic change in the external forcing.

abruptly (in relative terms, because it may still take years in large systems) from an original regime to a degraded one with little warning. The change in ecosystem state cannot be easily reversed with a change in external forcing. External pressure has to be reduced below a second threshold at a very different level (recovery threshold in Figure 3-1B) before the ecosystem regains the old regime. Thus, we refer to this second threshold as a *hysteretic threshold*.

A hysteretic threshold may result from a self-enforcing positive feedback relation between biotic or abiotic components of a system. In Box 3-2, we explain the background behind this type of threshold, using a simplified model of algal blooms in a SEMS. In this model, positive feedback processes cause the system to have two stable states, one state in which grazers control algal growth, and another in which grazing effects on high algal stocks are minor. These two states only co-occur for a limited set of parameter values (the gray area), and hence dramatic shifts may occur when the system is pushed outside of this zone. The model presented in Box 3-2 shows that both a hysteretic and a nonhysteretic response can be found, depending on parameter values. Thus, in nature, the two responses are extremes of a continuum, and in-between situations can exist, for instance, where the hysteresis range along the external forcing axis in Figure 3-1 is very small. Nevertheless, the distinction is likely to be important for managers.

Theory on hysteretic thresholds and the associated alternative regimes has been

Box 3-2. Alternative Stable States and Hysteretic Thresholds

The emergence of alternative stable states and hysteretic thresholds in SEMSs can be explained by a simple model of, for instance, the growth of algae. We analyze an example model in this box to explain how alternative stable states are generated by nonlinear ecological interactions and how hysteresis can follow from this. Finally, we use the model to illustrate the effect of the openness of a SEMS on the potential for hysteretic thresholds.

Consider a population of algae within a SEMS (or any unenclosed water body) that is controlled by grazing by pelagic herbivores and exchange with the outside marine world. A possible description of the dynamics of such a population is given by

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K} \right) - c \frac{B^2}{B^2 + d^2} - f(B - B_0),$$

where B defines the algal biomass per unit volume, r is the intrinsic growth rate determined by nutrient availability, K is the carrying capacity set by light availability, c is the potential grazing rate, d is the half-saturation value for grazing, f is the exchange rate with the outside marine world (expressed as a fraction of the volume of the water body), and B_0 is the algal biomass concentration in the outside waters. Note that we assume, for simplicity, that population dynamics of the grazers are not controlled by algal densities but, for instance, by fisheries and that the algal concentration in the outside waters is constant. For a more detailed description in a specific setting, see Oguz (2007).

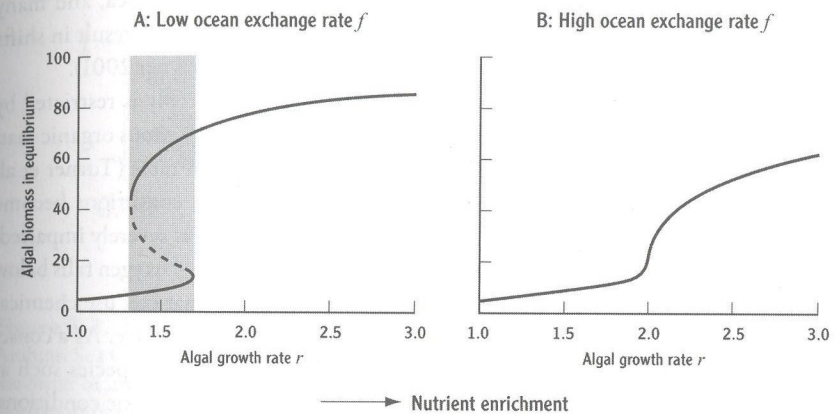
We can use the model to study the implication of increased nutrient availability, leading to an increased algal growth rate r , on the dynamics of the algae by analyzing for changes in equilibrium algal biomass. Figure A below reveals that, for low ocean exchange conditions, the

(continued)

applied extensively to enclosed systems such as small and shallow lakes as typically found in northern temperate regions (Scheffer 1998). Whether the concept can be used to explain threshold responses in large-scale systems such as SEMSs is an important topic that we will discuss in this chapter. First, we will briefly discuss two example studies in SEMSs and address whether there is evidence to categorize the thresholds as nonhysteretic or hysteretic. Then, we will discuss whether there is evidence in SEMSs for alternative regimes and associated dynamics, given their semi-open nature. The questions we address are the following:

Box 3-2 (continued)

relation between the equilibrium biomass and algal growth rates is strongly nonlinear. In the gray zone, two equilibria can occur side by side, separated by an unstable equilibrium (the dashed line). In the lower equilibrium, algal densities are controlled by grazing, while in the upper equilibrium, high algal growth prevents grazing control. When we move out of the gray area, a sudden shift may occur when one of the equilibria ceases to exist.



The hysteretic nature of the relation between equilibrium algal biomass and algal growth rate, as in Figure A, depends on the partially enclosed nature of the system. If we increase exchange with the open ocean, algal densities are depressed by outflow, and grazing intensity is always sufficient to control algal biomass (as in Figure B). In this instance, we find a nonhysteretic threshold. This implies that sufficient exchange with the open ocean may prevent the occurrence of hysteretic thresholds in SEMSs.

- Does the disturbing effect of, for instance, increased nutrient input increase gradually with the amount added, or is there a threshold amount beyond which a dramatic shift to a new state is observed?
- How easy is it to reverse the impact of pollution or eutrophication—does it suffice simply to reduce the load below the threshold, after which recovery will follow the same reverse trajectory?

Finally, we will discuss the implications of our findings in light of the management of coastal zones.

Nonhysteretic Thresholds—Oxygen Depletion in Arabian Sea

One of the most vivid and clear examples of a dramatic, but reversible, nonhysteretic threshold is the response of both pelagic and benthic ecosystems to declining oxygen concentrations. Low oxygen concentrations can result from natural causes, as documented for the unpolluted Scottish fjord Loch Etive during the 1970s (Edwards and Grantham 1986). However, there are many studies that report on severe hypoxia or even anoxia as a consequence of organic pollution or eutrophication from human activities. Example studies come from the western Indian shelf (Naqvi et al. 2000), Gulf of Mexico (Turner and Rabalais 1994, 2003), Black Sea, Baltic Sea, East China Sea, and many more. Oxygen depletion not only adversely affects fisheries, but also can result in shifts in ecosystem structure and biogeochemical cycling (Rabalais and Turner 2001).

Oxygen depletion occurs in subsurface layers when physical supply is restricted by stratification/stagnation, often in combination with availability of copious organic matter associated with eutrophication, which drives higher respiration rates (Turner et al. 1998). Below an O_2 threshold concentration of around $60 \mu M$, conditions become hypoxic, under which the mobility/behavior of aerobic organisms is severely impaired, although this threshold varies from system to system. When dissolved oxygen falls below about $1 \mu M$ ($\sim 0.02 \text{ mL L}^{-1}$ in Figure 3-2), only those organisms that can use chemical species other than O_2 for respiration, mostly microorganisms, can survive. As a consequence, microbial activity leads to a sequential reduction of chemical species such as NO_3^- and SO_4^{2-} that occurs at well-defined thresholds. Under the suboxic conditions, dramatic changes in the community structure (e.g., proliferation of bacteria) and chemical cycling (e.g., recycling of Mn at the interface, rapid turnover of N_2O) will occur.

Under even more-severe conditions when NO_3^- gets completely removed, a transition to fully anoxic conditions involving SO_4^{2-} reduction takes place. The only known area where this phenomenon occurs on a regular (seasonal) basis along an open coast is the western Indian shelf. Here low-oxygen subsurface water upwells during summer. Strong stratification and high respiration rates drive serial shifts to suboxic and anoxic conditions before a change in coastal circulation associated with the monsoon reversal restores the oxic environment. However, this essentially natural oxygen deficiency seems to have intensified in recent years, presumably due to enhanced fertilizer runoff from agriculture (Naqvi et al. 2000). This is consistent with trends observed in other coastal areas.

In SEMs having estuarine circulation, such as the Black and Baltic seas, all three types of conditions—oxic, suboxic, and anoxic—can be found. Of these, the Baltic Sea experiences somewhat larger variability due to the inflow of saline water from the North Sea that occurs approximately at decadal scales, causing intermittent reoxygenation below the pycnocline (Walter et al. 2006). The switchovers from oxic to suboxic and anoxic conditions in both directions observed on a seasonal scale over the Indian shelf and on a decadal scale in the Baltic are indicators of reversibility of ecosystem response

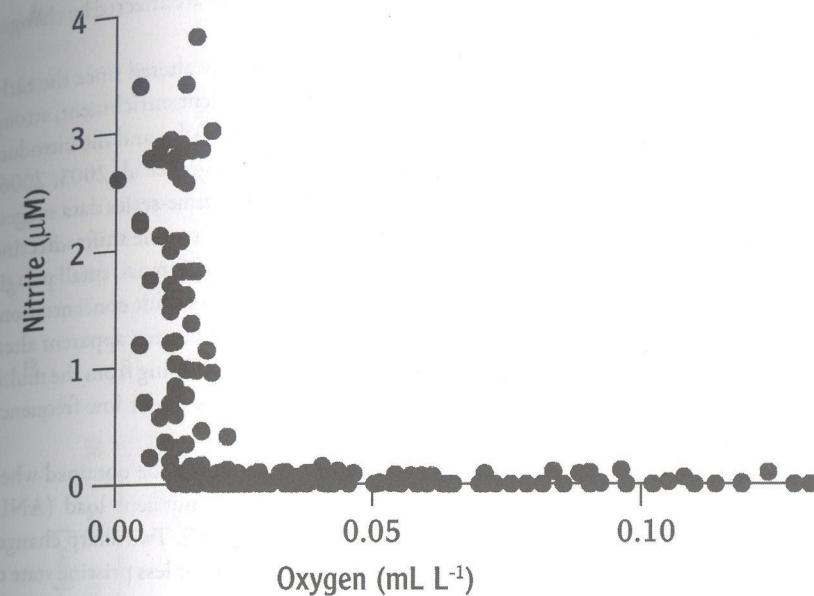


Figure 3-2. Plot of NO_2^- (an intermediate of denitrification) versus O_2 within the Arabian Sea O_2 -deficient zone. Note the abrupt threshold at O_2 equal to about $1 \mu M$ for the onset of microbial NO_3^- reduction. The data were generated by S.W.A. Naqvi and L. Codispoti in October 1994 on the TN039 cruise of the USJGOFS Arabian Sea Process Study, on which O_2 was measured using the colorimetric procedure suitable for low O_2 concentrations. Figure adapted from Naqvi et al. 2003; used with permission from Blackwell Publishing/CRC Press.

to biogeochemical/physical forcing even though the system may not immediately attain exactly the same state after each cycle.

Hysteretic thresholds

Regime Shifts in the Black Sea

A number of good examples can be found of nonhysteretic thresholds, as was described in the above section. The number of case studies pointing to hysteretic thresholds with strong hysteresis effects is much more limited. Moreover, they are often prone to intense debate on the validity of the claim of hysteresis. Below, we discuss the changes observed in the Black Sea ecosystem as a potential example of a hysteretic threshold, but we also discuss alternative explanations for the observed changes. This case study highlights the

difficulty in identifying potential hysteresis effects in systems that are affected by changes in multiple forcing factors.

The structure of the Black Sea ecosystem has been profoundly altered since the early 1970s, most likely resulting from the combined effects of nutrient enrichment, strong changes in temperature regime, overexploitation of pelagic fish stocks, and the introduction of gelatinous zooplankton carnivores (Daskalov 2003; Oguz et al. 2003, 2006; Oguz 2005; Oguz and Gilbert 2007). Long-term (1960–2000) time-series data suggest that the Black Sea ecosystem has reorganized through successive regime shifts affecting many ecosystem state variables (Daskalov 2003). Phytoplankton biomass, small pelagic fish stocks, Secchi disk depth, and dissolved oxygen and hydrogen sulfide concentrations close to the oxic–anoxic interface all exhibit abrupt transitions between apparent alternate regimes. These Black Sea regime shifts were abrupt events, differing from the multi-decadal-scale cyclic events observed in pelagic ocean ecosystems under low-frequency climatic forcing.

Some insight into the possible drivers of this abrupt change can be obtained when phytoplankton biomass is plotted against the anthropogenic nutrient load (ANL) through the Danube River (Figure 3-3A; Oguz and Gilbert 2007). Two sharp changes can be seen that took phytoplankton from a “low biomass,” more or less pristine state of the early 1970s (mean of about 3.0 g m^{-2}) to the “high biomass” state in the early 1980s (mean of about 17.5 g m^{-2}), occurring at apparent ANL thresholds of 300 and 600 kilotonnes y^{-1} . While the transition to a higher-biomass state appeared to have occurred rather abruptly, the transition back to the lower-biomass state was more gradual and followed a different trajectory. The observation that the return trajectory follows a different route from the initial trajectory indicates hysteresis, pointing to the presence of a hysteretic threshold. Hence, the data suggest the presence of two stable states: a near-pristine state characterized by a low phytoplankton density, and a second state characterized by high phytoplankton density and a drastically altered community structure.

Increase in anthropogenic nutrient load is not the only potential driver of ecosystem change in the Black Sea. There has been significant variation in the sea surface temperature (SST) during the observation period that is likely related to changes in wind regimes. When phytoplankton biomass is plotted against ANL and SST in a three-dimensional graph (Figure 3-3B), the additional likely role of climatic variations in promoting sharp changes in the phytoplankton biomass becomes evident. The high- and low-biomass states are linked to two different sea surface temperature regimes (lower than 7.8°C and greater than 8.4°C , respectively). The system preserved its poorly productive state for the entire range of ANL up to 600 kilotonnes y^{-1} even though it had accumulated appreciable nutrients in subsurface waters. These nutrients, however, were not made available by physical mechanisms into the surface layer for biological production. The Black Sea switched to a highly productive state (denoted by RS1) only after the SST became lower than 7.8°C , possibly reflecting increased mixing. Thus, it would appear that two conditions must be met before the system moves to the new high-biomass

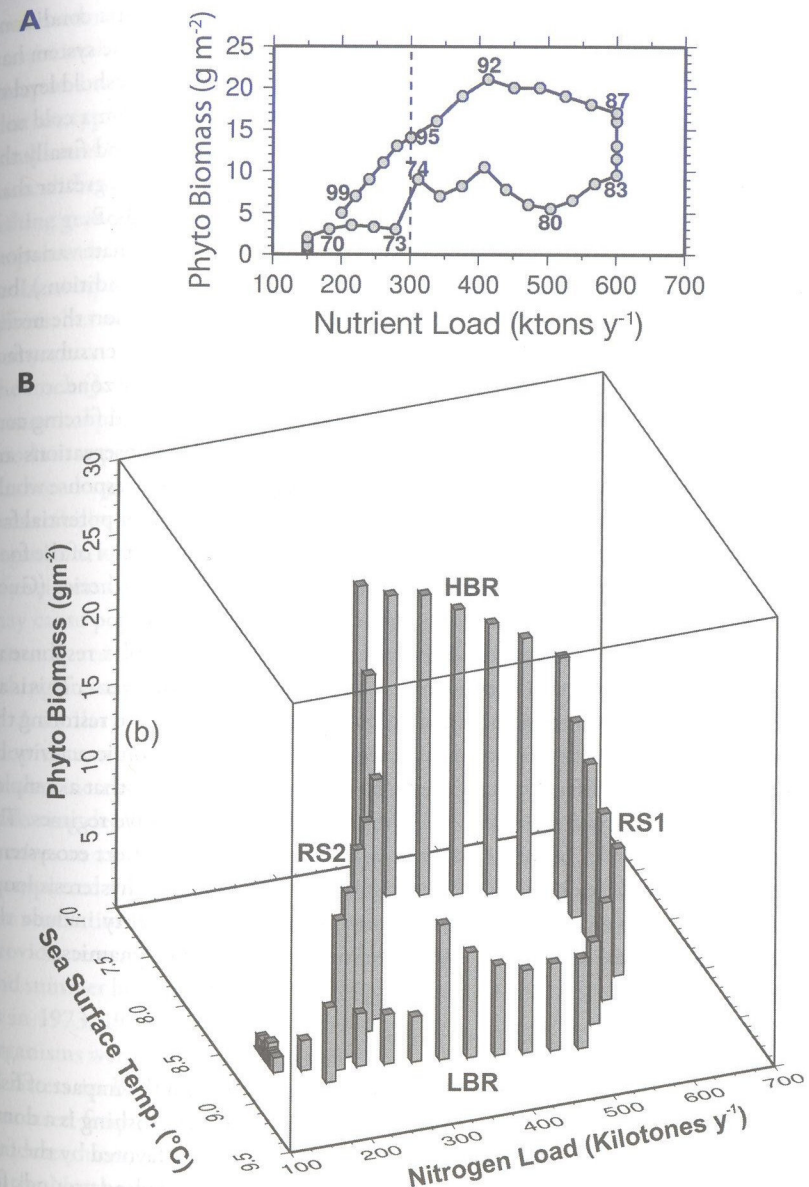


Figure 3-3. (A) Phytoplankton biomass distribution in relation to the anthropogenic nutrient load (in kilotonnes y^{-1}) showing trajectories from a low-biomass regime (LBR) to a high-biomass regime (HBR), with apparent abrupt transitions between them during 1973–1974 and 1984–1985, and a gradual recovery to the low-biomass regime. (B) Phytoplankton biomass (in g m^{-2}) as a function of both nitrogen load and sea surface temperature. Figure from Oguz and Gilbert 2007, copyright 2007; used with permission from Elsevier.

state: a sufficient annual nutrient load and a persistent change in climatic conditions leading to greater mixing between surface and subsurface waters. Once the system had moved to a new regime, it appeared resistant to decreasing ANL, to a threshold level of 300 kilotonnes y^{-1} and SST lower than 7.8°C. As the system shifted from a cold to a warm regime, the biological production declined at an increasing rate, and finally the system reverted gradually to its less productive, low-biomass state for SSTs greater than 8.4°C during the second half of the 1990s, as denoted by RS2 in Figure 3-3B.

Figure 3-3B points to an important interaction between ANL and climate variation. The ANL appears to introduce the necessary nutrients (i.e., external conditions), but these remain locked in the subsurface layers. Climate change sets in motion the necessary physical mechanisms for an abrupt change by increasing mixing between subsurface and surface layers, resulting in a flux of subsurface NO_3^- to the productive zone.

Abrupt changes may also be caused by slight changes in the monitored forcing coupled with unpredicted and frequently unmonitored forcing. More observations are needed to address the issue of whether and at what ANL level a threshold response would be observed if sea surface temperature remains unaltered. Moreover, other potential factors could also be present, such as concomitant changes in top-down control of the food web due to alterations in the top predator, resulting from excessive fisheries (Gucu 2002).

The Black Sea case shows clearly that ecosystems can display a complex response to human-induced changes and that these changes can take a long time to reverse. This is an important message for the management of SEMs, as the costs involved in restoring the degraded ecosystem may outweigh the gains from the restored economic activity by orders of magnitude. The Black Sea case study, however, also emphasizes that a complex response trajectory does not necessarily imply the presence of alternative regimes. The multitude of ways in which both natural and anthropogenic changes affect ecosystems can generate complex developmental trajectories, which may appear as hysteresis loops when projected in a two-dimensional effect–response plot but in reality include the effects of multiple natural and anthropogenic pressures on ecosystem dynamics.

Threshold Effects Induced by Overfishing

Some classical examples of apparent hysteretic thresholds come from the impact of fishing on marine ecosystems, mostly from studies from the open ocean. Fishing is a dominant human activity in many open and semi-enclosed seas, and it is favored by the fact that continental shelves and associated coastal zones are optimal breeding grounds for many edible species, including top predators such as bluefin tuna but also for other trophic groups. A good example is the northern Atlantic cod, where following a swift collapse of the cod stocks, subsequent recovery has been limited (Hutchings 2000). Examples of stock collapse originate from both continental shelf and open-ocean fisheries. Studies on the recovery of marine stocks, however, indicate that populations that are

harvested using bottom-deployed seines and trawls, typically used in SEMs and on continental shelves on shallow benthic environments, show a more limited recovery compared with populations that are harvested using purse seines and mid-water trawls that are typically used in open-ocean fisheries (Hutchings 2000). This limited recovery results mostly from losses due to bycatches and destruction of bottom habitats, which are more difficult to avoid in bottom-deployed seines and trawls compared with midwater fishing gear. Hence, fish stocks in SEMs may be particularly vulnerable to collapse in response to increased fishing pressure.

In many instances, fish stock collapses are not solely triggered by increased fishing efforts, but are related to recruitment failure. Recruitment fluctuates significantly from one year to another for many species, with only a few years producing a large renewal of the stock (Jennings et al. 2001). This suggests that variability in abiotic and biotic environmental processes can have a strong impact on maintenance of the stock. The need for good correspondence between environmental conditions and fish reproductive periods has been long understood (Lasker 1975, 1978; Cushing 1982). A mismatch causes higher vulnerability and larger fluctuations in recruitment, as compared with other groups of organisms, which in turn implies that the overlap of high fishing pressure, deterioration of environmental conditions due to human activities, and unfavorable recruitment years may cause population collapse. This rarely provokes extirpation of the population but generally results in long times for the recovery of the stocks, complicated by continuing fishing pressure (Hutchings 2000).

A similar collapse has been observed in the Adriatic Sea, where data on fish landings show that an abrupt change in recruitment occurred between 1977 and 1979, while the catches increased in 1980. This led to a drastic decrease of the anchovy stock over the following decade (Cingolani et al. 1996). The Northern Adriatic Sea (depth < 50 m) receives an average freshwater discharge of 3,000 $m^3 s^{-1}$ (Hopkins et al. 1999), which is transported southward by the Western Adriatic Current. Dry and cold winds facilitate the ventilation of the winter water column. During summer a weak cyclonic circulation provides renewal of the bottom layer. Increase in the residence time of low-salinity water and summer heating, coupled with sluggish circulation, cause widespread anoxic events, as in 1973, 1984, and 1988 (Stachowitsch 1991). In 1984, 90% of the sessile benthic organisms were killed, and after three years the recovery for some species was only 11%.

Stress on bivalve mollusk populations and intense dredging could be the cause of increased frequency of mucilaginous events (i.e., an anomalous accumulation of algal exudates, mostly polysaccharides, on the sea bottom and, afterward, along the coastline) in the Northern Adriatic Sea, through reduction of phytoplankton removal from the water column and accumulation of excess photosynthesized carbon in the low-nutrient summer conditions (F. Boero, Università Degli Studi Di Lecce, personal communication), thus producing a shift in ecosystem functioning. Even persistent anoxia may produce abrupt changes in recruitment. Eggs are vulnerable to low oxygen levels, and unfavorable coupling of physical dispersal with sinking into anoxic bottom waters may

severely hamper recruitment (Voss 2007). These losses have profound consequences for bottom-feeding fish.

Regime Shifts in Other SEMSs

The case studies discussed above are not isolated incidents but provide some well-described examples of threshold effects that have been found in a wide range of SEMSs. There is an extensive body of literature reporting on threshold effects in other marine systems. Strong effects of eutrophication are found in the Gulf of Mexico. An increase in nutrient release to the Mississippi River and its tributaries resulted in enhanced surface-water primary production, and an increased accumulation in continental shelf sediments of marine organic carbon, adjacent to the Mississippi River discharge (Turner and Rabalais 1994; Rabalais et al. 2001, 2002, 2007). Seasonal development of hypoxic conditions was first noticed in the 1970s, followed by an abrupt increase in the early 1980s in the size and severity of the hypoxia (verified by changes in paleoindicators, hydrologic data, and modeled hindcasts of oxygen conditions; Scavia et al. 2003; Justic et al. 2005; Turner et al. 2006; Rabalais et al. 2007). Whether these abrupt changes in the Gulf of Mexico are reversible is not known because there is no concerted effort to reduce nutrient loads in these coastal waters.

A potential regime shift, resulting from the combined effects of eutrophication and increased fisheries, seems eminent in the SEMS to the east of China. The observed symptoms of eutrophication in this system (Li et al. 2007) lead to the diagnosis that this ecosystem is approaching a crisis. Inputs of inorganic nitrogen from large rivers have increased continuously during the last fifty years, while the supply of light-absorbing sediments has been decreased due to the construction of dams (cf. Zhang et al. 1999; Yang et al. 2006). These changes in inputs have led to eutrophication in coastal waters of the East China Sea (Zhang 2002). The phytoplankton are changing, with more frequent algal blooms and a higher ratio of dinoflagellates to diatoms in these blooms (Zhou et al. 2001).

Overfishing has removed the large fish that eat small fish, and so these smaller fish have become more abundant in commercial catches. Although this should allow a more efficient transfer of production into the fishery, the overall fish catch per unit of effort has dropped. According to our best understanding of ecosystem theory, increase in small fish abundance results in a decrease in the abundance of grazing planktonic invertebrates and hence makes more likely a switch to an ecosystem dominated by harmful algae and jellyfish, with increasing episodes of bottom-water hypoxia killing benthic animals. The outcome of the crisis will be a collapsed ecosystem—collapsed in its ability to provide the services needed to support human life in the adjacent land, as will be discussed in Chapter 12. What we do not know is how well or quickly the system will recover from such a collapse and what the regime will look like when recovery is final. Our mathematical analysis in Box 3-2 suggests that the openness of the sea may be important in the ability

of a system to recover; the more rapid the exchange of water with an undisturbed ocean, the greater the reversibility (in speed and extent) of change.

In most of these studies, data series are insufficiently long to distinguish between continuous versus discontinuous change. Moreover, in many systems, the return trajectory is unknown, as the drivers of the observed regime shift have not been reversed (e.g., the northern Gulf of Mexico). Finally, in many systems, human activity has combined with climate variability to yield multiple pressures upon ecosystems, and it is unknown which one is most important in explaining the observed change. Hence, although evidence for threshold effects has been found in many rocky intertidal systems (Petraitis and Dudgeon 2004; but see Bertness et al. 2002 for a counterview) and benthic communities (van Nes et al. 2007), we are forced to conclude that for large-scale SEMSs, there is only limited and often indecisive evidence for hysteretic thresholds, and there is little understanding of the functioning of internal feedbacks in many marine ecosystems. Yet, the evidence that dramatic shifts occur is real for many SEMSs, emphasizing that the potential for nonlinear responses of marine ecosystems is of clear importance to both scientists and managers of these vulnerable ecosystems.

Management Implications

The issues raised in this chapter are of clear importance to managers, as they deal with abrupt and unexpected changes in ecosystems that can occur when a threshold is exceeded. We have attempted to distinguish two types of threshold. One kind of threshold is like a warning of a banana skin on a footpath: If you ignore the warning, you may slip and fall. However, with a bit of luck, you will be able to pick yourself up and return to the path. This *nonhysteretic* threshold is a warning that an ecosystem is about to experience a disturbance due to human activities, from which, however, it will recover as soon as the human pressure is decreased. The second kind of threshold is like a warning of a cliff ahead. If you ignore the warning, you will fall over the cliff and experience a severe change of state, likely a very permanent one, or otherwise spend a long time and much effort to get back to the top of the cliff. This is the *hysteretic* threshold.

Of course, the cliff is a metaphor. It is not always easy to see that ecological dysfunction is imminent. Thus, managing the environment is not like walking along a footpath. It is more akin to wandering on rough ground in a fog, and therefore scientists need to provide managers with *indicators* to warn when a cliff is near. Some indicators were reviewed by Tett and colleagues (2007). As an example, we will consider the measurement of dissolved oxygen. This is especially useful in the case of ecosystems that are sensitive to the undesirable disturbance associated with eutrophication, which corresponds to a catastrophic collapse in ecosystem health. Tett and colleagues (2007) pointed out that some ecosystems are more sensitive than others to nutrient enrichment (as defined by Cloern 2001). Clear examples are coastal systems that (1) become layered due to warming or freshwater supply to the surface, and (2) exchange their waters only weakly with

those in the nearby ocean (see Chapter 6, this volume). As discussed in this chapter, the Baltic Sea, the Black Sea, and the Gulf of Mexico are examples of such sensitive systems. In each case, increased nutrient input (together with changed nutrient element ratios) has led to increased primary production and hence to increased sinking of organic matter. The decay of that organic matter consumes oxygen in deep water. The annual minimum of the concentration of oxygen in these waters provides a good indicator of the impact of nutrients on the ecosystem. Environmental management agencies in many countries have already set minimum allowable levels between 2 and 4 mg L⁻¹ dissolved oxygen, because seabed animals begin to die when concentrations fall below this level. In some cases, this is a nonhysteretic threshold: When dissolved oxygen concentrations are restored, the benthic community recovers quickly. In other cases, such as that documented for the Baltic Sea by Laine and colleagues (1997), the extent of benthic community destruction is so widespread that recovery is a slow process, suggesting a possible hysteretic threshold. In these systems, it is wise to closely monitor dissolved oxygen. If the threshold is approached, it is a warning that there is a risk of a benthic catastrophe—that the edge of the cliff is approaching—and hence that remedial action is necessary.

As we will discuss in the final section, the ideas about nonhysteretic and hysteretic threshold changes that have been presented in this chapter are hypotheses. We have tried to explore these hypotheses with recent observations, and we conclude that mechanisms other than hysteretic thresholds might explain the changes observed in many SEMSs with equal likelihood. Nevertheless, the data themselves show that there can be abrupt changes in the state of ecosystems in SEMSs, even if we cannot fully explain these changes. Taking account of the precautionary principle, managers should act now to protect SEMSs against threshold changes. They should do this by reducing human pressures such as those of nutrient enrichment and overfishing. We urge this especially for systems that appear, from already documented changes or because of low flushing, to be sensitive to possible hysteretic threshold changes. It will also be necessary to keep in mind the effect of global warming as an uncontrollable pressure on these ecosystems.

Scientific Conclusions

We have presented observational evidence that SEMSs can change abruptly to a new regime that provides fewer ecosystem services to humans. We have attempted to interpret these changes as being nonhysteretic, and thus reversible, or hysteretic and hard to reverse. Some changes, such as those associated with hypoxia in deep waters, appear to be reversible, although restoration of an original micro-biogeochemical regime is faster than restoration of macrobenthic communities. In other cases, time series of data are not long enough to distinguish between a reversible versus irreversible change. Even in the case of the Black Sea, our best example, a complex trajectory in the driver-response phase plane (Figure 3-3) may indicate hysteresis and the presence of alternative regimes, but it may also be a two-dimensional projection of a multidimensional trajectory involving

several forcing factors. The theory of alternate stable states (or regimes) that has been offered to explain hysteretic threshold dynamics has its origins in the study of relatively small and enclosed temperate lakes. SEMSs are, however, typically larger, more energetic, and more heterogeneous than such lake systems and, in addition, more likely to be subject to multiple external pressures. Hence, their response to pressure will possibly be even more nonlinear than that observed in shallow lakes.

These considerations imply that the concepts presented in Figure 3-1 provide an overly simplified picture of the complex relations between external pressures and ecosystem response. We therefore need better conceptual and mathematical models of ecosystem change in SEMSs to take account of food web complexity, exchange with the ocean, and replacement of locally damaged populations. The second research need is for sustained study of those SEMSs in which humans are, somewhat blindly, carrying out perturbation experiments. A third research need is one that we have already mentioned: the need for indicators to monitor against hysteretic threshold change in SEMSs. We need indicators of the impact of pressures on ecosystems that will provide reliable warning of the closeness of a threshold. In addition, we need indicators of the sensitivity of ecosystems, including for SEMSs, to pressures that might cause irreversible shifts. Finding these indicators will require a deep understanding of the structure and function of marine coastal ecosystems.

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