

A W O R K S H O P R E P O R T

Thresholds in the Recovery of Eutrophic Coastal Ecosystems



Chesapeake Bay Program



Thresholds in the Recovery of Eutrophic Coastal Ecosystems

A Synthesis of Research
and Implications for Management

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Cover photo: Aerial view of Kent Island with the Chesapeake Bay beyond, photo by Jack Greer

This report synthesizes the results of a workshop, Thresholds in the Recovery of Eutrophic Coastal Ecosystems, held at the Belmont Center near Baltimore, Maryland in February 2007. The workshop brought together members of the scientific community in the Bay region and beyond, along with selected policy leaders and resource managers, to discuss how the concept of thresholds might inform restoration efforts in the Chesapeake Bay.

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EXECUTIVE SUMMARY

Despite thirty years of significant public investment, an ambitious management effort in the Chesapeake Bay has not reached its goals for nutrient reduction or ecological recovery. As restoration efforts continue to push nutrient concentrations toward target levels, scientists and managers will need to anticipate a range of possible ecological responses. They will need to be prepared to modify management approaches to direct change towards desirable outcomes.

Predicting ecological pathways for the Bay's recovery will not be a trivial matter. The Bay's response to nutrient reduction may be nonlinear or time delayed. It may experience threshold-type behaviors, where once a certain level of a controlling variable (like water clarity) is reached, recovery will occur in a sudden burst as key ecological processes (like benthic photosynthesis) are rejuvenated. An understanding of the Bay's likely responses in the context of such nonlinear or threshold events will help managers better monitor recovery, manage public expectations, and maintain a clear and confident approach to the restoration of Bay ecosystems.

Recent history provides some insight on the spectrum of possible responses of the Bay to decreased nutrient loads. Despite reports that nutrient loading from the Susquehanna River has leveled or declined slightly, the mainstem Bay has not seen substantial improvement in the distribution of underwater grasses or in bottom water oxygen condition. In some Bay tributaries, like the Potomac and Patuxent River estuaries, however, nitrogen and phosphorus loads have decreased significantly and parts of their respective ecosystems have shown clear signs of improvement — albeit sometimes following surprisingly nonlinear trajectories. Other places, such as the Potomac's Gunston Cove tributary, show indications of ecological “stubbornness,” where nutrient loads have decreased but the system remains slow to respond. In many Bay regions, nutrient loads simply have not decreased — in the Choptank River, for example, nitrogen loads have remained unchanged from 1985 to 2006, while phosphorus loads actually experienced a significant increase in this time period.

European examples of ecosystem responses to decreased nutrient loading offer some clues for what might lie in store for the Chesapeake if nutrient load reductions succeed. Since 1987, Denmark has reduced nitrogen and phosphorus loading to all water bodies as part of a major national commitment. Streams and lakes nationwide have exhibited significant decreases in nutrient concentrations accompanied by decreases in phytoplankton biomass, increases in water clarity, and cascading improvements in fish community structure. But while Danish coastal waters have experienced similar decreases in nutrient loading, responses of bay, fjord, and estuarine ecosystem properties have lagged behind streams and lakes. Thus far only small improvements in water quality have occurred in these coastal systems.

For many estuaries, including the Chesapeake Bay, current simulation models may prove inadequate to predict observed complex ecological responses to nutrient management. We simply do not have a clear understanding of important mechanisms that control threshold responses. To make matters worse, variable and changing climatic conditions may interact synergistically or antagonistically with management efforts, making responses to management particularly difficult to discern, much less to forecast.

EXECUTIVE SUMMARY, Continued

Identifying clear intermediate management targets for the Bay — such as decreasing winter nutrient levels, restoring habitat in shallow water systems (areas that may prove more sensitive to nutrient reduction efforts), or reducing the spring phytoplankton bloom — could help steer restoration strategies to enhance the ecosystem's ability to catalyze its own recovery. To answer the complex interdisciplinary questions necessary for meeting these targets, ecological researchers and resource managers must synthesize historical data, test existing models, conduct effective natural experiments, and devise adaptive management protocols.

Major report findings include:

- To develop an early warning system to predict future threshold responses, we must improve our understanding of past threshold events in the Chesapeake Bay through rigorous analysis of historical data sets. Time-series of ecological and biogeochemical indices derived from dated sediment cores represent the kind of long-term historical record that could help reconstruct nonlinear trends in recent decades and centuries. Relatively long-term data sets for water clarity and benthic invertebrate abundance, which include series of observations over the past several decades, may also be useful in this regard.
- Key factors such as water depth, water clarity, salinity, climate, food web dynamics, and fisheries removals may play significant roles in determining where and when time delays and thresholds might occur in the recovery of the Chesapeake Bay ecosystem.
- Current modeling approaches may not be sufficient to capture some response patterns that are nonlinear or that exhibit threshold-type changes that can move the ecosystem into a new state. Separate, but linked, forecasting models might be necessary to capture relevant ecological dynamics (including threshold trajectories) for shallow (near-shore) and deeper parts of Chesapeake Bay.
- Adaptive management experiments (such as manipulating freshwater flow), combined with intense nutrient reduction efforts in shallow regions of the Bay, especially in oligohaline and tidal-fresh areas, could prove strategic. Recent studies in shallow lakes and coastal lagoons suggest that these areas are likely to respond more quickly to reductions in nutrient loads. Such approaches, if paired with efforts to restore habitat (e.g., underwater grasses) and key food web components (e.g., various filter-feeding species) could help move the system toward a threshold where positive feedback processes help sustain and build on recovery efforts.
- Significant effort should be directed towards managing public expectations with regard to the ecosystem's response to restoration efforts, making the concepts of thresholds and nonlinear responses more comprehensible to a broad audience.

INTRODUCTION

Nature adapts to changing environmental conditions in complex, sometimes nonlinear, ways. In the Chesapeake Bay and other aquatic systems worldwide, ecological responses to nutrient reduction have followed different trajectories under different environmental conditions. Rarely do environmental variables such as water quality, habitat condition, and living resource abundance improve in parallel with decreased nutrient loading. Responses may be slower than expected or, following extended lag periods, may appear as abrupt changes (so-called threshold responses). The ability to forecast ecological response trajectories is critical, though difficult in situations where nonlinearity is the norm. To develop publicly supported, cost-effective strategies for nutrient control, managers need to anticipate the kinds of ecological changes one might expect from varying scenarios.

In mid-February of 2007, scientists from the Bay community and abroad came together to share information and identify knowledge gaps about potential pathways forward for the Chesapeake in response to nutrient reduction. The goal of this workshop, held at the Belmont Center near Baltimore, Maryland was to improve interpretation and forecasting of trajectories by which the Chesapeake Bay might respond to decreased nutrient loads.

This two-day workshop brought a mix of researchers, modelers, and managers. It drew on the expertise of scientists who have studied aquatic ecosystems where ecological state changes have occurred, and on those with experience in implementing novel management solutions. The workshop featured a series of formal presentations by invited speakers, and workshop participants were charged to address the following questions:

1. Describe documented examples of aquatic ecosystem responses to nutrient load reduction. What are the shapes of those response functions (i.e., linear, nonlinear, threshold)?
2. What causes time lags and nonlinear responses to management efforts? What approaches could minimize these lags? What information is needed to better predict nonlinear threshold responses?
3. How might strategies for habitat rehabilitation (e.g., seagrass and wetland re-vegetation and oyster reef restoration) enhance ecological feedbacks that may promote rapid improvements in environmental conditions?
4. How might climate variability and long-term climate change modulate ecological feedbacks and responses to reductions in nutrient inputs?
5. How might analyses of historical monitoring data be improved to identify incipient “early warnings” that are precursor indices of abrupt ecological changes (thresholds)?

6. To what extent are existing numerical and analytical models — now used in estuarine science and management — capable of simulating (1) thresholds in response to nutrient loading changes and (2) recovery trajectories that might not parallel the decline path (hysteresis)?

This report provides background on threshold responses and synthesizes the major concepts put forth by the invited presentations and by the workshop's breakout groups. In addition, the report provides brief summaries of formal presentations (Appendix I), the workshop agenda (Appendix II), and a list of workshop participants (Appendix III).

BACKGROUND

What Is a Threshold?

The word threshold describes a breakpoint between two different states of a system at physiological or ecological scales. When a threshold is crossed, change may be either abrupt or gradual, on temporal scales that range from seconds to years. What unifies threshold responses, irrespective of scale, is the behavior observed when that threshold is crossed. With the crossing of a threshold, the internal processes of a system change so that the state of the system moves in a different direction, towards a different so-called attractor or structural state.¹

Thresholds on Physiological Scales

In biological science, the concept of thresholds commonly describes physiological responses to environmental conditions, where cellular to organism-level functions appear constrained by a minimum concentration of an essential substrate (such as oxygen), or by a maximum value of a toxic or stressful condition (such as a contaminant). Such thresholds are identified experimentally as the minimum or maximum values at which a negative or positive change can be initially observed for a key physiological function or process. Controlled laboratory experiments have been used to define, for instance, minimum threshold requirements for levels of dissolved oxygen that are needed to support growth and survival of specific aquatic animals. Conversely, maximum values have been established experimentally for levels of anthropogenic contaminants (e.g., methyl mercury) or natural metabolites (e.g., hydrogen sulfide) that can be tolerated by particular organisms.

The issue of scale can prove tricky. For example, even trace concentrations of toxic contaminants may elicit biological responses in an organism at molecular scales. Because of compensatory biochemical and behavioral processes, however, those same trace concentrations may not cause significant impairment of physiological functions observed in the environment.

Thresholds on Ecosystem Scales

Ecological thresholds can be characterized by a controlling variable that drives a change in state and in internal processes such as rates of birth, mortality, growth, consumption, or decomposition (Figure 1). When an environmental threshold is breached, the response can be dramatic. Biological and ecological reactions to a particular controlling variable or driver can lead to virtually irreversible shifts in system structure and function (e.g., Folke et al. 2004). In such cases, the switch between two or more different ecosystem states may be characterized by high or low abundance of specific organism groups. For example, shallow lakes have been shown to switch often between two radically different states depending on initial conditions and exter-

¹ Adapted from the Resilience Alliance (<http://www.resalliance.org/183.php>).

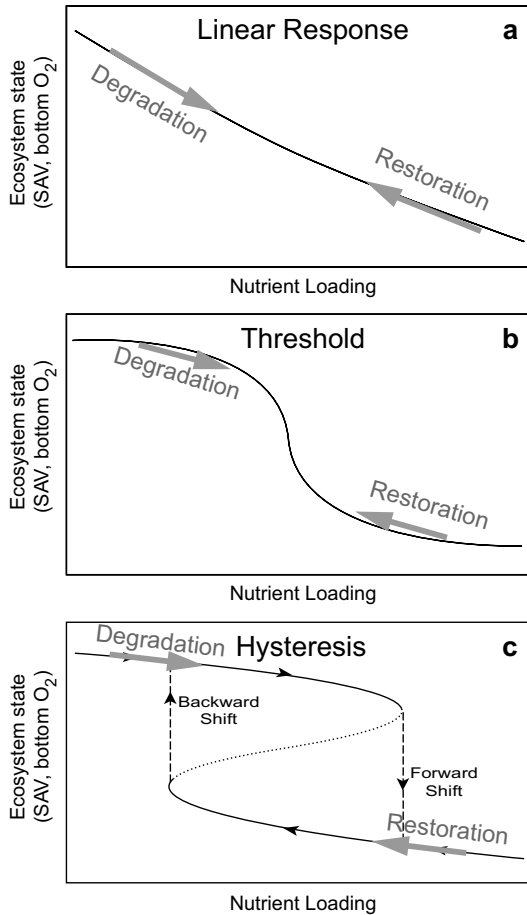


Figure 1. Ecosystems respond to nutrient loads in different ways. Pathways can be *linear* (a), where the degradation and restoration follow the same proportional course with increasing and decreasing nutrient loads; *threshold* (b), where responses show an S-shape (sigmoidal), appearing as a sudden jump in ecosystem state over a narrow range of nutrient loading; or *hysteretic* (c), where degradation and recovery follow separate trajectories that reflect different system states (e.g., with or without SAV) and the system may shift abruptly between states at different nutrient loading rates, depending on whether it is degrading or restoring (adapted from Scheffer et al. 2001).

This enhances the survival of SAV beds.

nal forces. One state is characterized by relatively clear water with high abundance of submerged aquatic vegetation (SAV) and many large fish; the second state is characterized by turbid waters, high abundance of phytoplankton, few SAV, and few large fish.

In these systems, shifts between two alternative stable states often occur at different levels of the controlling variable (such as nutrient loading) through distinct pathways, depending on whether that external driver is increasing or decreasing (e.g., Zhang et al. 2003). In some cases, two different states can exist under the same levels of the controlling variable. In ecological (and other) systems this “hysteresis” often arises from positive feedback mechanisms that reinforce the current state of the system (Figure 1c).

These threshold responses may differ depending on spatial scales. For example, as water clarity begins to deteriorate in a coastal bay ecosystem, loss of SAV may occur rapidly (over weeks) at the spatial scale of a single small plant bed, but may take several years to occur in larger beds and throughout the entire Bay, despite the fact that both responses arise from the same change in environmental conditions. This scale-dependent difference appears to result from complex ecological feedback processes — whereby SAV stands enhance particle trapping and water clarity and are more effective when plant beds exceed a minimum size (e.g., Fonseca and Bell 1998).

Aquatic systems offer several well-documented examples of positive feedback control that can induce threshold behavior. Two cases associated with eutrophication involve hypoxia and SAV (Figure 2). In the first instance, excess nutrients stimulate algal growth, which sinks to the bottom to fuel oxygen depletion, which in turn enhances nutrient recycling, which then stimulates more algal growth. Positive feedback in this case reinforces the state of eutrophication. In the second instance, beds of underwater grasses (SAV) can slow currents and foster the sinking of suspended particles and assimilation of nutrients, which in turn increases light available for SAV photosynthesis and growth.

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Other examples of regime shifts in aquatic ecosystems like the Chesapeake Bay include changes in top-down control. In the Patuxent River, for example, the sea nettle (*Chrysaora quinquecirrha*) has followed a downward trajectory that closely mirrors the downward spiral of the native oyster, *Crassostrea virginica*. The oyster began its unabated freefall in the early 1980s as a result of the cumulative effects of overfishing and the diseases MSX and Dermo. Like oysters, sea nettle densities in the Patuxent River are now more than an order of magnitude lower than in the mid-1980s (Breitburg and Fulford 2006).

The fate of oysters and sea nettles seems closely linked. Oyster shells provide a hard surface for sea nettle polyps, the sedentary, bottom-dwelling stage of the jellyfish's life cycle, to settle upon. Without enough hard surfaces available, sea nettles cannot complete their reproductive cycle. The Patuxent River reached a threshold level of hard surface availability in 1985, beyond which the nettle population could not sustain a constant level. The decline of nettles has also led to a rise in the population of comb jellies and, since comb jellies eat free-swimming oyster larvae, oyster larvae face higher and higher predation rates. The sea nettle-oyster link in the Bay's food web is reinforced by

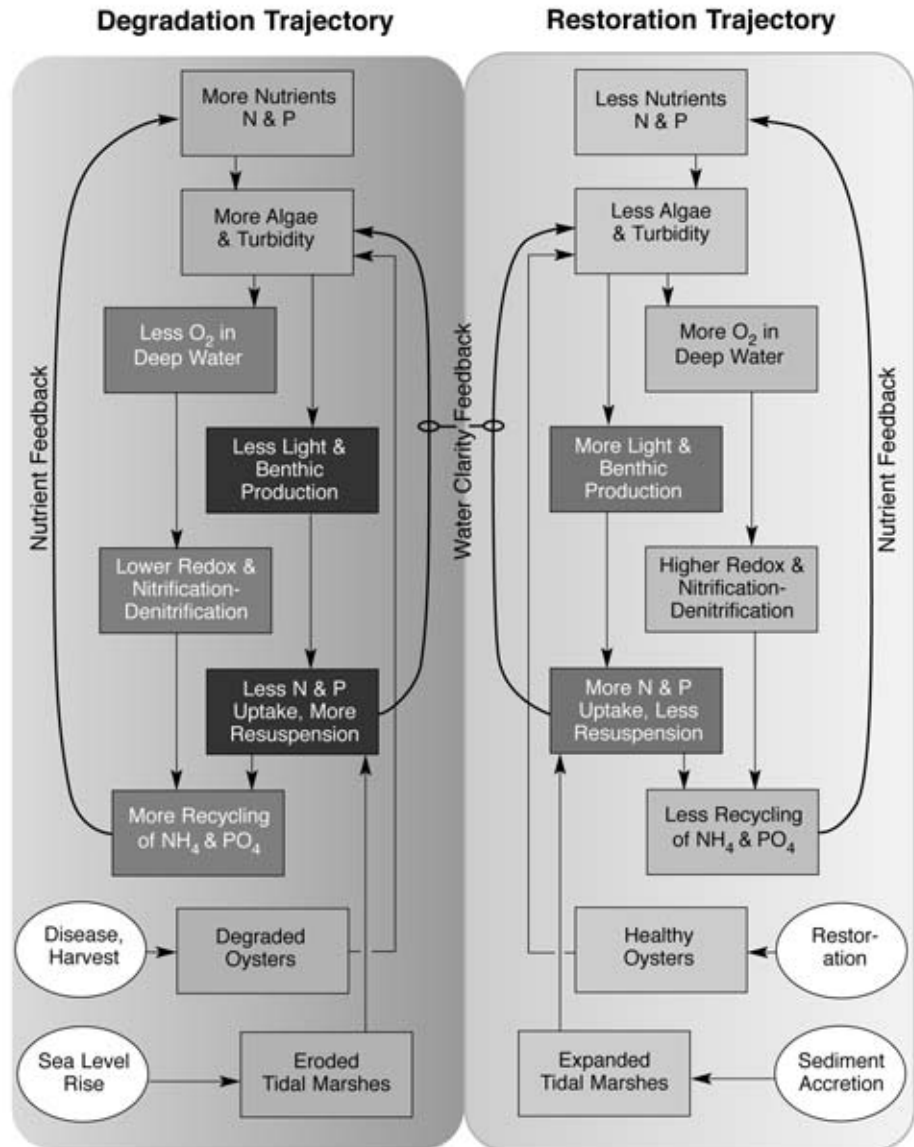


Figure 2. Restoration efforts could jump start catalytic pathways for the Bay that help recovery, just as external stressors such as oyster diseases, intense fishing pressure, and sea level rise can reinforce a feedback loop in which additions of nitrogen and phosphorus lead to eutrophic conditions. In this diagram, added nutrients affect algal biomass (light gray boxes) directly, and these in turn influence bottom-water oxygen and nutrient recycling (medium gray boxes) as well as water clarity and benthic primary production (dark gray boxes). Positive feedback exerts inverse effects on ecological conditions along the two trajectories of degradation and restoration, in both cases reinforcing trends once they are underway (adapted from Kemp et al. 2005).

trophic interactions that are effectively stuck in a rut — fewer oysters mean fewer nettles, fewer nettles mean many comb jellies, many comb jellies mean fewer oyster larvae, fewer oyster larvae mean fewer oysters (Breitburg and Fulford 2006).

Although reports of abrupt regime shifts and multiple stable states are growing in number (e.g., Walker and Meyers 2004, Schroder et al. 2005), the underlying mechanisms that initiate and maintain these large changes are often poorly described. Now theoretical ecology is providing a mathematical basis for state changes. Simple deterministic models produce unexpected (non-deterministic) behavior that, depending on initial conditions, moves between alternative stable states driven by so-called “strange attractors” (e.g., May 1977). Numerous examples suggest that these simple models can simulate important types of observed ecological dynamics (e.g., Holling 1973, Scheffer et al. 2001). Recent studies have demonstrated that more conventional and complex aquatic ecosystem models are also capable of generating relatively abrupt threshold responses to small changes in external drivers such as nutrient loading (e.g., Janse 1997, Kemp et al. 2001).

Technical Background

MODELING THRESHOLD BEHAVIOR

Models can be constructed to describe threshold relationships at the larger scales of interest (e.g., populations and ecosystems) using simple mathematical expressions. For example, logistic functions (e.g., $Y = \alpha X^2 [\beta + X^2]^{-1}$) depict lagged responses of a particular process (Y) to changes in some environmental condition (X) with smooth, but rapid, transitions from zero response at large values of X to large responses at smaller X, where α describes the maximum value of Y and β describes the “quasi-threshold” value of X.

More abrupt thresholds can be generated using subtraction functions (e.g., $Y = \alpha(X - x_t) [\beta + (X - x_t)]^{-1}$), where x_t is a step-function threshold and X, Y, α and β are defined as above. To work properly, such functions must be constrained numerically to non-negative values. In this case, the process, Y, is zero until X increases beyond x_t , and the equation describes a hyperbolic relationship with a positive intercept of the X-axis at the threshold value (x_t).

Logistic equations and simple hyperbolic ($Y = \alpha X [\beta + X]^{-1}$) functions will also exhibit threshold behavior where Y approaches α at values of X exceeding β . When values of X are reduced from $>\beta$ to $<\beta$, Y will initially exhibit no response until $X < \beta$, at which point $Y \sim \alpha X$. In contrast, models dominated by first-order linear functions (e.g., $Y = \alpha X + \beta$) will generally exhibit no threshold behavior.

In typical aquatic ecosystem simulation models, ecological processes are assembled using arrays of hyperbolic and first- and second-order functions. The ensemble behavior of these models often resembles first-order linear responses to changes in external drivers. As a consequence of complex interactions among sets of equations, however, these models can also produce apparent thresholds and other nonlinear responses over ranges of external conditions. In reality, very few of these models have been carefully examined to test for evidence of thresholds. Computational tools to predict threshold responses in aquatic systems are largely lacking.

A range of simple equations can be used to produce linear and nonlinear dynamics (see Modeling Threshold Behavior, p. 6). A better understanding of the mechanisms that control threshold responses, including an array of positive feedbacks, will be necessary to develop ecosystem models capable of simulating these behaviors.

CASE STUDIES

Aquatic ecosystems may respond to increases or decreases in nutrient loading in a variety of ways. While the number of case studies of aquatic ecosystem responses to changing nutrient inputs is growing, relatively few of these studies have clearly documented the mechanistic controls on these responses. Our recent workshop explored case studies from coastal, estuarine, and freshwater systems, where significant changes in nutrient loading elicited a spectrum of responses that ranged from linear, to abrupt threshold changes, to parallel but separate pathways of degradation and recovery (hysteresis). These examples include changes that may have resulted from other factors that interact with nutrient loading, such as alterations in food web structure and climatic conditions. Presentations and discussions emphasized that responses to reduced nutrient loading tend to be modulated by key physical characteristics, including average water depth, water column stratification, water residence time, and the presence of salt.

Lake Ecosystems

Freshwater aquatic ecosystems, especially ponds and lakes, are generally well studied, with long-term records (decades to centuries) available that illustrate the eutrophication and subsequent recovery of lakes worldwide. The workshop presentation by Erik Jeppesen from the National Environmental Research Institute of the University of Aarhus, Denmark compared data from 23 Danish lakes (Jeppesen et al. 2002) and 35 European and North American lakes (Jeppesen et al. 2005), showing that a decrease in phosphorus input generally led to a decrease in total phytoplankton biomass and an increase in water clarity. Because phosphorus (P) tends to be the nutrient most limiting to algal growth in lakes (e.g., Schindler 1978), P reduction in these systems also led to increases in relative abundance of fish-eating fish, decreases in biomass and abundance of zooplankton-eating fish, and increases in the relative abundance of the efficient algal-grazing zooplankton (especially *Daphnia* spp.) (see Pelagic Food Webs in Lakes Compared to Estuaries, p. 10). In the few lakes where data were available, submersed vascular plants generally increased with phosphorus removal; for some lakes, however, there was no change in SAV abundance despite improved water clarity.

Shallow and deep lakes responded differently to phosphorus reduction (Jeppesen 2003). In shallow lakes, diatoms assumed a greater role within the phytoplankton community structure as nutrient loading decreased, while in deep lakes nitrogen-fixing blue-green algae tended to be more prominent. Additionally, the effect of phosphorus reduction on *Daphnia* abundance was generally more pronounced in shallow lakes.

All lakes studied showed signs of recovery in response to decreases in nutrient loading within 10-15 years. Observed time lags resulted from internal recycling of phosphorus pools that had accumulated in the sediments. Lakes with longer water residence times recovered more slowly. Adding or removing plants or animals to/from the system (biomanipulation) also affected the rate of recovery. For example, the direct removal of plankton-eating fish (planktivorous) or the addition of fish-eating fish (piscivorous) tended to accelerate recovery trends. Furthermore, transplanting submersed macrophytes (SAV) to the lakes also tended to stimulate plant rebound.

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Estuarine Ecosystems

In contrast to the long (> 80 year) history of eutrophication studies in freshwater systems, eutrophication research in estuaries and coastal systems dates back barely three decades (e.g., Kemp et al. 2005). As a result, there are fewer case studies of responses to nutrient reductions available for estuaries than for lake systems (Smith 2003).

Danish water bodies offer one solid model for comparison between freshwater and estuarine systems. Since 1987 Denmark has reduced nitrogen and phosphorus loading to all water bodies as part of a major national commitment. In most cases, the results have been relatively clear for streams and lakes, which have generally exhibited significant decreases in nutrient concentrations and attendant decreases in phytoplankton biomass, increases in water clarity, and cascading improvements in fish community structure (Carstensen et al. 2006, Kronvang et al. 2005). Danish coastal waters have experienced similar decreases in nutrient loading, but responses of bay, fjord, and estuarine ecosystem properties have lagged behind streams and lakes. Significant signs of ecological recovery have been evident thus far only in terms of water clarity (Conley et al. 2002, Kronvang et al. 2005). A recent dry period has helped further trigger marked reductions in coastal nutrient concentrations, and other improvements in ecosystem properties are expected to follow soon (Kronvang et al. 2005). The systematic nature of these nutrient loading reductions, accompanied by an extensive monitoring program to track ecological changes in coastal waters throughout Denmark, should provide a basis for improved understanding of responses of coastal ecosystems to reduced nutrient loading.

A few other case studies in estuarine or brackish systems describe clear ecosystem responses to nutrient reduction. For example, the shallow subtropical waters of Tampa Bay and nearby areas experienced a steady decline in nitrogen and phosphorus loading starting in the late 1970s. Within 5 years, annual mean levels of nutrient concentrations, phytoplankton biomass, and turbidity declined rapidly. Seagrass rebounded, although its recovery lagged behind water quality improvements by nearly a decade (e.g., Johansson 2002).

Delays in phytoplankton response and associated eutrophication recovery following reductions in nutrient loading have also been reported for the Seto Inland Sea of Japan, particularly for red tide outbreaks which persisted for years undiminished (Yamamoto 2003). Shallow water ecosystems of the Dutch Wadden Sea responded to nutrient reductions with shifts in phytoplankton community structure (diatoms down, flagellates up) that altered food web structure and abundance of functional groups of benthic macrofauna and water birds (Philippart et al. 2007). Persistently high phytoplankton biomass in downstream estuarine regions following reduced watershed nutrient loading have been attributed to tidal inputs of nutrients from seaward sources for both the Dutch Wadden Sea, which is connected to the North Sea (de Jonge 1997), and the lower Patuxent River estuary, connected to the mainstem Chesapeake Bay (Testa 2006).

In general, the substantial biogeochemical gradients in estuaries associated with mixing of river and ocean water, along with strong tidal mixing, make it particularly difficult to predict how ecological responses to reductions in nitrogen and phosphorus from watershed sources will vary along estuarine salinity gradients (e.g., Paerl et al. 2004). Daniel Conley's workshop presentation suggested that reductions in nutrient loading to brackish coastal waters of the Baltic Sea and other smaller estuaries could reduce recycling of large deep-water pools of phosphorus, and thereby reverse large-scale eutrophication trends (e.g., Conley et al. 2002).

Technical Background

PELAGIC FOOD WEBS IN LAKES COMPARED TO ESTUARIES

A key difference in pelagic food web structure between lake and estuarine ecosystems derives from the presence and absence (respectively) of large-bodied Cladoceran zooplankton, which are both efficient grazers on phytoplankton and favored food for plankton-eating fish. These Cladocerans are typically dominated by *Daphnia* spp., which have little tolerance of salinity. Although the smaller Calanoid copepods that tend to dominate estuarine and marine zooplankton are also an important food source for many pelagic fish, these herbivores are far less capable of controlling phytoplankton abundance than their larger freshwater cousins. Consequently, the so-called “top-down control” that cascades from fish-eating fish to planktivorous fish to herbivorous zooplankton to phytoplankton tends to be much stronger in fresh versus marine environments.

Conversely, freshwater systems tend to respond less readily to changes in nutrient loading and associated “bottom-up control” on phytoplankton and fish. Although these animals are sensitive to feeding by planktivorous fish, they often find dependable refuge from predation by hiding in shallow SAV stands. When SAV beds are abundant, *Daphnia* can regulate phytoplankton biomass and associated shading effects, which in turn helps sustain SAV survival, even under conditions of relatively high nutrient loading. When SAV beds are stressed by physical disturbance or hyper-eutrophic conditions (where algal growth overwhelms *Daphnia* grazing control) rapid declines in SAV abundance allow planktivorous fish to decimate *Daphnia*. Under such conditions the lake will undergo an abrupt, and difficult-to-reverse, shift to a turbid water regime with low abundance of SAV and *Daphnia*. Even in deeper lakes, *Daphnia* grazing can retard phytoplankton growth under modestly high nutrient loading, unless *Daphnia* are preyed down by expanded numbers of planktivorous fish — caused, for example, by increased fishing harvest of their predators. Thus, many lakes have strongly interacting responses to nutrient loading and predation pressures.

For estuaries, the absence of *Daphnia* and its powerful phytoplankton-grazing potential makes these systems less prone to such abrupt shifts in phytoplankton and SAV abundance in response to changes in nutrient loading. In some shallow coastal ecosystems, herbivorous grazing by benthic bivalve filtration is sufficient to exert strong top-down control on phytoplankton abundance. In northern San Francisco Bay, for example, top-down control by the invasive clam *Corbula amurensis* dramatically altered the spring bloom dynamics and the organization of the food web (Cloern 1983). Under such circumstances, benthic grazing control may affect ecosystem responses to changes in nutrient loading that are more like those described for many lakes.

Chesapeake Bay

Nutrient loading to the Chesapeake Bay has generally increased during the last 50-100 years (e.g., Hagy et al. 2004). Although the volume of the mainstem Bay’s hypoxic bottom water in summer varies directly with inter-annual fluctuations in climate and associated spring river flow (Hagy et al. 2004), long-term increases

in hypoxia generally track with increased nitrogen loading. However, it appears that the hypoxic volume per nitrogen load to the Bay increased significantly after 1980. This is especially surprising because recent analyses indicate that nutrient loading rates have been stable or declining since 1988 (e.g., Langland et al. 2007). Thus, the dramatic shift in hypoxia versus nitrogen loading may reflect an unexplained change in ecosystem structure (Hagy et al. 2004, Kemp et al. 2005). On the other hand, although SAV distribution declined dramatically with nutrient enrichment between 1960 and 1990, SAV abundance in the upper and middle Bay has actually increased slightly since 1990 (Orth et al., in prep).

Despite overall increases in nutrient loading, a few of the estuary's tributaries have undergone major reductions in the past two decades (e.g., Kemp et al. 2005). The workshop presentation of Michael Kemp et al. reviewed four relatively well-studied examples for Bay tributaries that may help guide expectations on recovery trajectory and timing: the Patuxent River, the upper Potomac River (near Washington, DC), Gunston Cove (a secondary tributary of the Potomac), and Back River (near Baltimore).

Patuxent Tributary. Watershed nitrogen and phosphorus inputs to the Patuxent River estuary increased steadily from 1950 through the mid to late 1980s, after which nutrient loading declined markedly through the early 2000s, primarily due to improved wastewater treatment. The initial increase in nutrient loading resulted in immediate increases in phytoplankton biomass and turbidity followed by a dramatic loss of submersed aquatic vegetation (SAV) in the mesohaline region starting in the mid 1960s. With the recent nutrient input reductions, the middle region of the estuary experienced significant declines in phytoplankton biomass and improvements in water clarity. Underwater grasses have recovered in portions of the oligohaline and tidal fresh Patuxent, but not in the lower mesohaline regions (e.g., Kemp et al. 2005). Overall, ecological responses to nutrient reductions have been significant with little delay in the upper estuary but more muted in the middle estuary. There has been little SAV recovery in the middle or lower Patuxent (see Figure 3). In fact, there has been no indication that levels of phytoplankton or bottom water oxygen have returned to former states in the lower estuary. This is likely due to the influence of nutrient-rich tidal waters entering the river mouth from the mainstem Bay (Breitburg et al., in review).

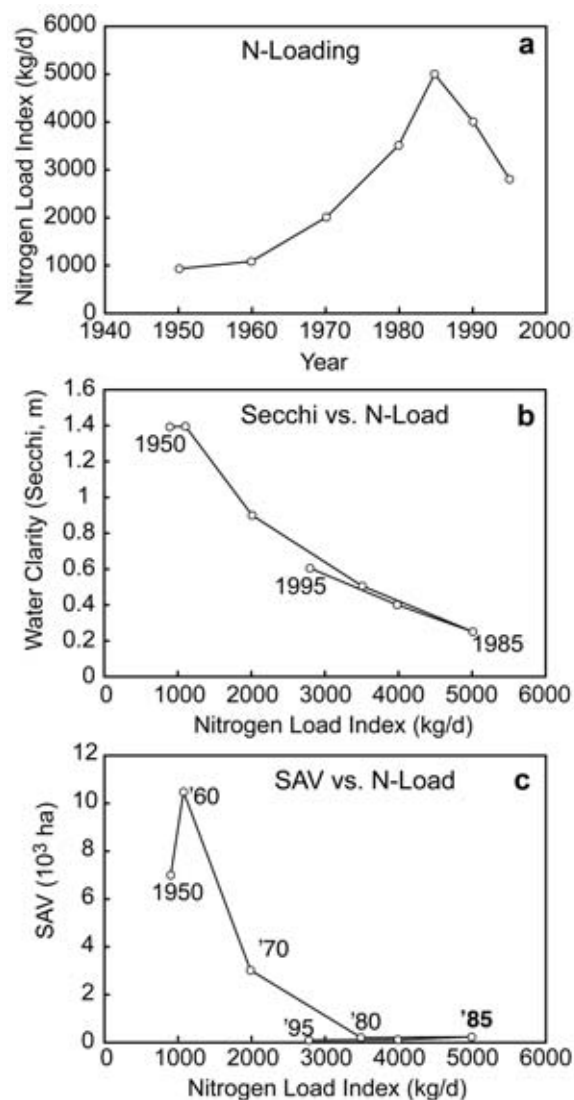


Figure 3. As nitrogen loads (a) began to decrease in the Patuxent River in 1985, water clarity (b) followed a linear pathway of improvement. But (c) underwater grasses (SAV) showed little response, likely remaining under a water quality threshold for recovery (Kemp et al. 2005).

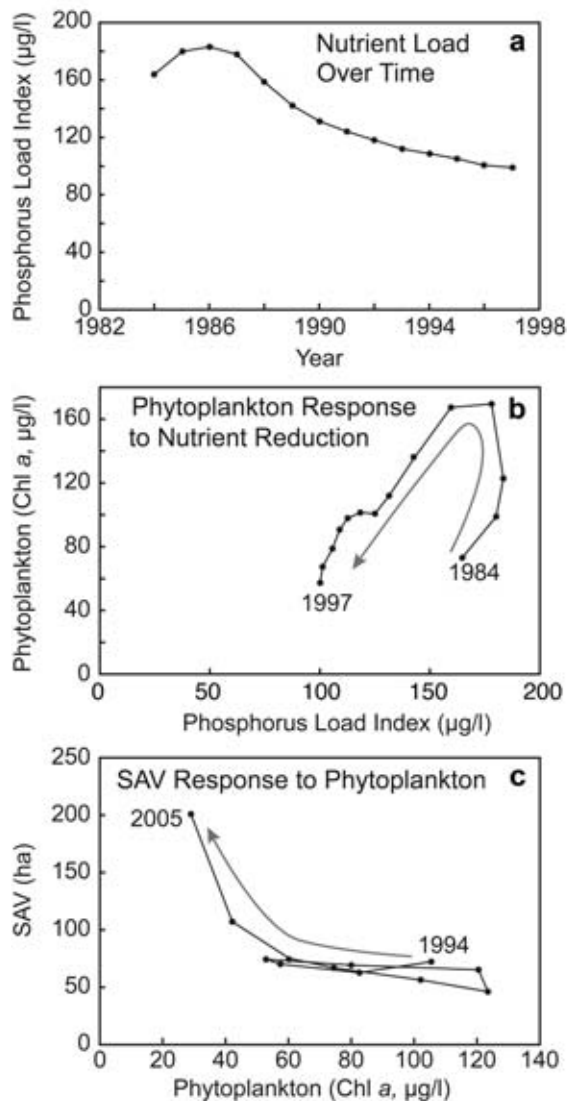


Figure 4. Although phosphorus loads (a) have declined steadily since 1986 in Gunston Cove, a tidal fresh tributary of the Potomac River, phytoplankton abundance (b) did not respond in a linear manner. Despite lower phosphorus loads (by 50 percent) in 1997 than in 1984, phytoplankton biomass was roughly the same in the two years. This is a classic pattern of hysteresis, indicating that the recovery trajectory will follow a separate path. Underwater grasses (c) showed signs of abrupt rebound when phytoplankton biomass dropped below 40 $\mu\text{g/l}$, perhaps unmasking a water clarity threshold for growth (Jones 2000, unpublished).

Potomac Tributary. Similar to the Patuxent, the Potomac River has experienced decreases in nitrogen and phosphorus loading due to reduction in sewage effluent discharge. In the low salinity (oligohaline) portion of the estuary, phytoplankton biomass and water column dissolved oxygen both showed immediate response to nutrient reduction. Recovery of SAV in this estuarine region, which was generally delayed by a decade or more, was preceded by an outbreak of invasive filter-feeding clams (*Corbicula fluminea*) that caused further decreases in phytoplankton and turbidity (Cohen et al. 1984), and may have contributed to the rebound of diverse SAV species (Phelps 1984). As with the Patuxent, little to no recovery has been evident yet in the lower Potomac, which is more closely connected to the mainstem Bay (Kemp et al. 2005).

Gunston Cove Tributary. In this smaller freshwater tidal tributary of the upper Potomac, monitoring has linked recent reductions in nutrient loading to responses of both phytoplankton and SAV abundance. Phosphorus decreased in the late 1980s due to upgrades at the Blue Plains Waste Water Treatment Plant. Between 1984 and 1995 phosphorus concentrations in Gunston Cove decreased by almost 50 percent. Phytoplankton abundance first increased, perhaps showing evidence of a response time lag, and then began to decrease. By 1995, algal biomass measured the same as in 1984, but at a significantly lower level of nutrient loading — an apparent hysteresis trend (see Figure 4). In contrast, SAV exhibited a threshold-type response to decreasing nutrient loads, with no sign of hysteresis. When algae biomass decreased to $\sim 40 \mu\text{g/l}$ in response to nutrient reduction efforts, SAV abundance increased abruptly (Jones 2000, and unpublished). This threshold may be related to algae-induced effects on water clarity that set minimum light requirements (~ 20 percent of surface light reaching the sediments) for plant growth (e.g., Carter et al. 1994, Kemp et al. 2004).

Back River Tributary. The Back River is a small Chesapeake tributary near Baltimore, Maryland with a highly urbanized watershed. This estuary experienced a 50 percent reduction in nitrogen and phosphorus loading from

1985-2005 in the hyper-eutrophic tidal fresh portion of the river. However, the reduction in nutrient loading was accompanied by only a marginal decline in phytoplankton abundance. Even after this large reduction in loading, nutrient concentrations remained above saturation thresholds (i.e., levels above which algal growth is not limited by nutrient supplies), meaning that the phytoplankton production was probably limited by availability of light rather than nutrients. Further reduction in nutrient loading and/or increases in nutrient assimilation within the estuary will be required to lower nutrient concentrations below saturation levels. Only then will further reductions begin to decrease algal growth and improve associated eutrophication conditions.

FACTORS CONTROLLING THRESHOLD RESPONSES

Threshold responses in aquatic systems arise from a complex interplay of variables. Workshop discussions identified several factors that appear to exert strong influences on responses to changes in nutrient loading. These include: physical characteristics of the water body, salinity, food web interactions, fisheries removals, time delays, and climate.

Physical Factors: Depth, Stratification, and Circulation

Since deeper aquatic systems have a larger volume of water per unit of primary production, they tend to respond more slowly to increases or decreases in nutrient loading. Water, nutrients, and other materials entering deeper systems tend to have longer residence times, allowing the assimilation, transformation, and recycling of inputs many times before permanent burial in sediments or export to the sea or atmosphere.

Water in deeper aquatic systems also has greater potential to form vertical layers, where warmer and less saline upper layers are separated from colder, saltier bottom layers, and mixing between layers is limited. In estuaries, this layering is also controlled by the relative input of freshwater, which strengthens stratification by adding buoyancy to the upper layer, and by tidal energy, which generates vertical mixing that destroys the layering (e.g., Dyer 1997). Bottom layers of stratified systems are prone to depletion of dissolved oxygen because stratification retards replenishment of oxygen removed from lower layers by respiration (e.g., of bacteria). With eutrophication and larger inputs of organic matter from nutrient-stimulated algal blooms, the need for bottom layers to be re-oxygenated becomes more acute (Hagy et al. 2004). All else equal, these factors tend to make deeper systems with larger volumes of bottom water slower to respond to changes in nutrient loading (Kemp et al. 2005).

Shallower systems may respond more quickly than deep systems to decreases in nutrient loading, at least initially, because small improvements in water clarity can make a big difference in the shallows. When adequate light reaches the sediment surface, benthic photosynthesis of algae and SAV becomes more important than phytoplankton photosynthesis.² Benthic-dominated ecosystems generally regulate nutrient flows within sediments and plant biomass more efficiently than plankton-dominated systems, and once benthic photosynthesis can be re-established, other feedback mechanisms (e.g., reduced nutrient recycling across the sediment-water interface and reduced resuspension of sediments) are likely to exert significant effects (e.g., Kemp et al. 2004). Benthic systems trap and bind suspended particles, thereby maintaining clearer water and better conditions for their own growth. Shallow coastal ecosystems may also have rich communities of filter-feeding benthic bivalves that enhance water clarity by removing phytoplankton and other suspended particles that block light. Once repopulated by benthic plants and filter-feeding animals, shallow systems can become

² Benthic algae can survive and grow when the fraction of incident light reaching the sediment surface (L_s) exceeds 1%, whereas SAV survival requires L_s to exceed 20%.

resilient, sustaining healthy communities across relatively wide ranges of nutrient loading (e.g., Kemp et al. 2005).

Salinity

A growing body of evidence suggests that coastal marine ecosystems differ markedly from lakes in their response to reduced nutrient loading. This is likely because marine ecosystems are regulated by different nutrients, different biogeochemical processes, and different food web structures. The tidal waters of estuaries like Chesapeake Bay are characterized by large salinity gradients ranging from freshwater at the headwater end to nearly full-strength seawater at the ocean end. Given these differences in ecological and biogeochemical processes, regional differences are likely in ecosystem responses to decreased nutrient loading. Establishing regional nutrient management strategies for Chesapeake Bay will require careful consideration of salinity effects.

While primary production is generally limited more by phosphorus (P) availability in lakes, marine systems are generally limited by nitrogen (N) availability, with estuaries tending to exhibit a blend of N- and P-limited production that follows the salinity gradient (e.g., Fisher et al. 1999). The tendency of marine productivity to be N-limited can be attributed to the characteristic chemistry and turbulence of saline tidal waters (Howarth and Marino 2006). As a consequence, harmful blooms of nitrogen-fixing blue-green algae tend to be relatively less frequent in estuarine and marine ecosystems (Paerl 1988). Management of phosphorus (but not nitrogen) loading to tidal fresh waters may improve water quality in the upper estuary, but this will tend to remove the algal nitrogen-filter in this region, thereby promoting more algal blooms in the saltier nitrogen-limited downstream waters (Paerl et al. 2004). In addition, the lower ionic strength of freshwater (compared to saltier marine water) results in relatively higher rates of denitrification and lower nitrogen recycling (Seitzinger et al. 1991), as well as stronger binding to particles and lower recycling of phosphorus (e.g., Froelich 1988). These characteristic differences in nutrient recycling in fresh and saline systems would therefore tend to produce very different ecological trajectories in response to reduced nutrient loading, where nutrient levels would decline more rapidly in freshwater systems as nutrient inputs from watersheds are decreased. Physical-chemical processes can also exert direct effects on estuarine organisms. Nutrient enrichment may create a layer of fluffy particulate matter (flocculation) that can contribute to high turbidity that limits SAV growth (Kemp et al. 2004, Gallegos et al. 2005). In low salinity regions, however, this increased turbidity and flocculation enhances fish recruitment (North and Houde 2003).

In addition, planktonic food webs differ widely between marine systems and lakes, and they will likely respond differently to changes in nutrient loading. The presence of large-bodied zooplankton makes freshwater systems relatively brittle in their responsiveness to nutrient loading changes — with little response over a broad range of nutrient inputs, followed by abrupt changes under extreme conditions (Jeppesen 2003). In contrast, the absence of this powerful phytoplankton grazing potential makes estuaries and coastal ecosystems less prone to such abrupt shifts in phytoplankton and SAV abundance with changes in nutrient loading (see *Pelagic Food Webs in Lakes Compared to Estuaries*, p. 10). Under certain conditions, however, benthic filter-feeding bivalves in more saline systems can play a similar role in regulating phytoplankton. Understanding salinity tolerances for keystone taxa can help determine differences between these ecosystems in terms of the speed and trajectory of their responses to changes in nutrient loading.

Food Web Interactions

Aquatic organisms simultaneously affect and respond to changes in nutrient loading through complex trophic interactions. A number of examples from the Chesapeake Bay and other aquatic ecosystems link changes in nutrient levels to changes in interactions among invertebrate and fish consumers. Various studies have suggested that eutrophication exerts both direct and indirect effects on food webs and fisheries (e.g., Caddy 1993). For example, at low-to-modest levels, nutrient increases tend to enhance secondary production and fisheries harvest. At higher nutrient levels, however, changes in habitat conditions and food web configuration may lead to local declines in production and local changes in the structure of fish communities with increased nutrient loading. The confounding effects of increased prey production and decreased habitat quantity and quality can add spatial complexity to patterns of production and predator-prey interactions (Breitburg 2002).

As with phytoplankton dynamics, responses to nutrient increases at higher trophic levels also appear to differ between freshwater and marine systems. For example, fish biomass increases across a wide range of increasing nutrient levels in shallow freshwater systems, but begins to decline at nutrient concentrations beyond an intermediate threshold in shallow saline systems (Jeppesen et al. 1994). This difference may be largely attributable to the efficient filtration and nutritious food value characteristic of large-bodied zooplankton found in freshwater. Because bottom water hypoxia is a common response to nutrient enrichment in both deep lakes and estuaries, the associated loss of animal habitat will likely exert a negative effect on secondary production in both aquatic systems. In addition to benthic hypoxia, increased turbidity from eutrophication also tends to reduce benthic primary production and interfere with the associated food webs. As discussed previously, nutrient enrichment in both freshwater and coastal ecosystems can cause a shift from predominantly benthic (demersal) food webs to predominantly pelagic (e.g., de Leiva-Moreno et al. 2002, Vadeboncoeur et al. 2003).

As noted, benthic filter feeding in estuaries can suppress effects of nutrient enrichment (e.g., Mohlenberg 1995) and facilitate recovery of water clarity and SAV in tidal waters with declining rates of nutrient loading. Although restoration of oysters has been touted as a means to accelerate Chesapeake Bay recovery from eutrophication (e.g., Newell 1988), numerous practical obstacles and issues of scale complicate this effort (e.g., Newell et al. 2007).

Many other large benthic macrofaunal invertebrates can also have an impact on nutrient responses in estuarine ecosystems. Some — through burrowing and other behaviors — are capable of stimulating sediment biogeochemical processes that retard rates of nutrient recycling that would otherwise stimulate phytoplankton growth and sustain eutrophic conditions (e.g., Peligri et al. 1994, Mayer et al. 1995). Some animals add oxygen to sediment by forming and ventilating tubes and burrows several centimeters into sediment that would otherwise be anoxic. This tends to stimulate coupled nitrification-denitrification processes that remove bioavailable nitrogen from the system. Other animals tend to vertically mix sediment particles at scales of tens of centimeters, thereby burying phosphorus fixed to these particles and rendering it less available for recycling from sediment to overlying waters. Shifts in food web interactions, caused by overfishing or introductions of non-native predators, can reduce the abundance of these keystone benthic fauna. In addition, when eutrophication causes bottom waters to experience prolonged anoxic conditions, these animals cannot survive, and

the fraction of nitrogen and phosphorus inputs that are recycled from sediments to the overlying water column tends to increase. This can shift in ecosystem structure and biogeochemical cycling tends to impede recovery from eutrophic conditions, even with reduced nutrient loading (e.g., Kemp et al. 2005).

Multiple Stressors and Fisheries Removals

Virtually all ecosystems experience multiple stresses resulting from human activities, many of which interact in non-additive ways (Folt et al. 1999). Individual stressors alter the playing field upon which additional stressors act in various ways: (1) by selecting for tolerant species; (2) by changing the distribution of structural species (organisms such as oysters, kelps, and corals that create physical structure upon which other species depend); and (3) by changing the abundance, distribution, or interactions of predators, prey, parasites, and hosts (reviewed in Breitburg and Riedel 2005). These interactions can occur by either simultaneous or sequential exposure to stressors. Multiple stressor interactions not only alter the magnitude of stressor effects, but also alter the patterns of variability and predictability on which management strategies often rely.

Fisheries removals represent a special case of the problem of multiple stressor interactions because fishing can strongly alter food web structure and the ability of the food web to process nutrients. Most estuaries that receive high levels of nutrient loadings also experience (past or current) high levels of fisheries removals that alter food web structure (e.g., Lotze et al. 2006).

Fishing harvests that reduce populations of herbivorous grazers and suspension feeders tend to increase the deleterious effects of anthropogenic nutrient loading (Szmant 2002). This pattern has been seen in diverse coastal systems from estuaries to coral reefs. For example, the decline of the Eastern oyster (*Crassostrea virginica*) due to overfishing and disease has reduced top-down control of phytoplankton in Chesapeake Bay, thereby increasing phytoplankton, decreasing water clarity, and adding organic inputs that tend to support depletion of bottom water dissolved oxygen (Newell and Ott 1999). On the other hand, removal of herbivorous fishes, combined with a disease that greatly reduced the population of an herbivorous sea urchin, resulted in increased algal biomass that inhibited coral recruitment in Caribbean reefs (Hughes 1994).

Time Delays

Aquatic systems may exhibit relatively slow responses to nutrient loading reductions, resulting in time delays between management action and ecosystem reaction. The delay in response may arise in part from mechanisms associated with large nutrient pools lying at various land-sea interfaces. For example, nitrogen in streams that drain into the Bay comes from both surface runoff and groundwater discharge. While surface water delivery correlates closely with freshwater flow, groundwater moves slowly. The average age of groundwater in the Bay's tributaries is 10 years, with a range from less than 1 year to more than 50 years. The slow movement of groundwater into the Bay will cause a lag time, generating a delay between the implementation of nutrient-reduction practices and the improvement of water quality (Lindsey et al. 2003). In addition, large pools of available phosphorus in Bay sediments may continue to be recycled back into the water column to support phytoplankton production for 5-10 years after reducing inputs from the watershed (e.g., Jeppesen et al. 2002), although there is still considerable uncertainty with regard to this hypothesis (Boynton et al. 1990).

Time delays can also arise from time required for aquatic ecosystems to restructure themselves and to restore natural feedback processes. Beds of underwater grasses, for example, take time to re-establish to the densities and aerial coverage needed to self-regulate water clarity via particle trapping and nutrient assimilation. For benthic fauna to become re-established and for certain biogeochemical processes to be reconstituted, the intensity, extent, and duration of hypoxia must diminish for an adequate period of time. Benthic processes can then further increase nutrient retention in sediments and reduce nutrient bioavailability associated with recycling. Management actions can help shorten time lags between nutrient reduction and ecosystem recovery by helping to reduce fishing pressure and by targeting the restoration and protection of key habitats and species, such as marshes, SAV beds, and reefs of filter-feeding benthos that can improve water clarity by absorbing nutrients and trapping sediment particles.

Climate

Both climate variability and long-term trends of climate change may modulate how the Chesapeake Bay and other estuaries respond to nutrient reduction efforts. Under a climate-warming scenario, the Bay may experience increases in temperature, resulting in more intense storms, more freshwater flow (especially in winter-spring) and more runoff. There may also be increased periods of drought. An increase in water volume due to sea level rise may further increase salinity levels and gradients, each of which could affect distribution and abundance of key organisms that cannot tolerate extremes in salinity (Pyke et. al 2008, in press). Rising sea level could also introduce shelf/oceanic species into the system, including toxic harmful algae such as *Dinophysis*, responsible for oyster harvest closures in 2002 (Marshall et al. 2004), and *Alexandrium*, responsible for whelk kills in the York River in 2007 (W. Vogelbein, unpubl. obs.). With increased oceanic input along with prolonged resting stages in life cycles of some taxa, these events could become frequent and could threaten human health and the living resources of the tidal system.

Each of these potential effects of climate warming could cause a shift in ecosystem structure that alters the Bay's response to reduced nutrient loading. A rise in temperature will tend to exacerbate bottom water hypoxia by increasing respiration rates and decreasing oxygen solubility (amount of O₂ that the water can hold). An increase in temperature would likely alter the structure of Bay plant and animal communities and associated food webs. Species of northern affinity, such as eelgrass, are already at their southern limit. Eelgrass, a dominant SAV species in the saltier parts of the Bay, has already exhibited die-off events during recent exceptionally warm summers (Orth et al. 2008), and this species may be lost from the Bay as water temperatures increase. More temperature-tolerant SAV species, such as *Ruppia maritima*, may replace eelgrass; however, such species have generally shorter growing seasons and may provide inferior habitat for fish and invertebrates. Warmer winter temperatures might also make the Bay susceptible to invasive species transported in ballast waters from warmer climes, species that might otherwise die off in winter if accidentally introduced. Invasive species certainly have the potential to cause threshold-type responses, resulting, for example from dramatic changes in trophic structure.

Increasing streamflow, rising temperatures, and increasing depths due to sea level rise would likely reduce the exchange between warmer surface waters and cooler deeper waters, leading to enhanced stratification. This could change the onset, duration, and extent of seasonal hypoxia. If this comes to pass, managers may need

to reexamine current nutrient reduction goals to account for the need to offset consequences of rising temperatures and increased runoff.

One potentially positive result of climate change could be more efficient terrestrial processing of nitrogen from airborne sources. For example, in winter, when atmospheric nitrogen deposits on the snow pack, it accumulates and then enters the estuary in a pulse as the snow pack melts. But as the size of the snow pack shrinks, more atmospheric nitrogen will deposit on soil, which is more retentive than snow. Additionally, since the landscape will not remain frozen as long, the microbial community should remain more active and may enhance nutrient removal processes like denitrification.

Many of these proposed impacts of climate change on the Bay ecosystem may shift baseline conditions we can expect to achieve with reduced nutrient loading (Duarte and Conley, 2007). Workshop discussions emphasized the critical role for models in creating scenarios for exploring consequences of climate change. Researchers and managers will likely need to modify existing models if they are to capture key mechanisms that might drive ecosystem responses to climate change.

THRESHOLD RESPONSES AND IMPLICATIONS FOR MANAGEMENT

Evidence from case studies suggests that decreased nutrient loading in the Chesapeake Bay will likely elicit a range of ecological responses, which could include nonlinear patterns and trends. For example, the recovery trajectory that the Bay follows could exhibit abrupt ecological changes when certain environmental variables reach threshold levels. Some of these changes could boost recovery efforts. Others could hinder them.

Case studies described in the previous section of this report offer some guidance, with clues for when to expect thresholds or signs of hysteresis. They also suggest strategies, such as restoration of key habitats (e.g., wetlands, SAV beds, oyster reefs), which might shorten delays in response to reduced nutrient loading. Other kinds of biomanipulation that enhance top-down controls on algae may also be useful. These examples underscore the importance of carefully tailoring management approaches to specific physical characteristics of the environment — such as shallow versus deep or fresh versus saline. Preceding discussions also raise questions about how variable and changing climatic conditions may alter the effectiveness of specific management actions intended to induce ecosystem recovery.

Predictive tools currently available to forecast incipient thresholds are limited. Similarly, methods for collection and analysis of Bay monitoring data are not organized to recognize early signs of forthcoming shifts in ecosystem structure. So how can managers best prepare for and steer the trajectory of the estuary's response to changes in nutrient loading?

Managing Expectations

One overarching theme that emerged from workshop discussions was the need to manage public expectations with respect to the Bay ecosystem's response to restoration activities. Concepts such as thresholds, time lags, and hysteresis are not part of the public lexicon. Communicating the idea that water quality in Chesapeake Bay is not likely to improve linearly with decreases in nutrient loading presents a clear challenge. The message would be one that is hard for the public to accept — especially in the context of more than three decades of restoration effort.

Issues surrounding the restoration of the Chesapeake Bay have held the political spotlight for years. Citizens of the region are concerned about its murky waters and the status of underwater grasses, oysters, blue crabs, and striped bass. In 2003, the high-level Chesapeake Bay Watershed Blue Ribbon Finance Panel was charged with developing innovative solutions for financing the multi-billion dollar Bay restoration effort. The Panel called on the Bay states and the federal government to make a six-year, \$15 billion investment in the creation of a regional Finance Authority to be charged with prioritizing and distributing restoration funds throughout the watershed. The Panel made the argument that we know how to restore the Bay, but we simply lack the resources to do it. This view may have oversimplified our understanding of precisely how and when the

ecosystem will respond to decreases in nutrient loads. While increased funding is unquestionably needed to address nutrient inputs from farms, stormwater, waste treatment, and air deposition, providing the public with firm predictions for observable results remains a difficult challenge for scientists and policy makers.

Effective management approaches must recognize the values of (1) focusing on restoring the Bay's "self-healing" capacity (e.g., nutrient assimilation, sediment trapping, and water clarification) and (2) exploiting favorable variations in climatic conditions (e.g., drought periods).

Aligning popular expectations of nutrient management results with observed ecological responses will pose a continuing challenge for environmental managers (e.g., Schwartz 1996). Workshop participants discussed the utility of approaches that highlight the process of decision-making in the face of scientific uncertainty. Scenario analysis, where choices between alternate futures for the Chesapeake Bay can be elaborated and evaluated, might be particularly helpful. *Chesapeake Futures*, a collaborative effort undertaken by the Scientific and Technical Advisory Committee of the Chesapeake Bay Program, offers an example of such an alternate outcome-based approach that takes into consideration different policy choices for the Chesapeake region.

Closing Knowledge Gaps

Although the Chesapeake Bay is among the best-studied estuaries on earth, important knowledge gaps remain, particularly in relation to understanding and predicting ecosystem responses to reduced nutrient loading. Some deficiencies identified include:

- Use of historical data sets and sediment core chronologies to infer long-term trends.
- Ability to relate observed trends to underlying ecological mechanisms.
- Modeling approaches that can incorporate nonlinear and threshold-type behaviors into both forecasting and hindcasting.
- Use of adaptive management to improve restoration success in the Chesapeake Bay.

Rich and robust data sets from more than 30 years of monitoring in the Chesapeake watershed offer long-term records on water quality, benthic faunal diversity and health, phytoplankton abundance, SAV bed area and cover, juvenile fish abundance, fisheries harvest, and more. But with a few notable exceptions, these relatively long-term data sets remain largely untapped. Workshop participants noted that all previous efforts to locate and critically evaluate historical data have resulted in a better understanding of how the Bay functions. These data records also tend to point to periods of change, often demonstrating a threshold response. Unfortunately, however, it appears that most of these data sets were initiated well after the historical periods during which the most dramatic changes in environmental conditions occurred. For example, it appears that the temporal and spatial scales of seasonal hypoxia expanded dramatically during the two decades from 1950-1970 (e.g., Zimmerman and Canuel 2002, Hagy et al. 2004), prior to the establishment of routine monitoring efforts. By combining historical data sets with information recorded in sediment cores (e.g.,

stable isotopes, organic biomarkers, and microfossils), it may be possible to extend these data sets well beyond the past 30-50 years.

Historical Data Sets

Which long-term data sets could prove most useful for managers in helping to shape the trajectory of the Bay's recovery? Although these existing databases are generally well known, they have not been fully exploited in relation to the concept of ecological thresholds (see *Detecting and Predicting Thresholds*, p. 23). Historical data sets for benthic faunal communities, water clarity, and sediment cores might be particularly relevant.

Benthic Communities. Historical data sets of benthic animal community composition and abundance over time might provide important information about threshold-type responses. Many organisms in this part of the Bay food web are especially sensitive to environmental stressors, and this community is one that is likely to respond abruptly to reductions in nutrient and sediment loading. Virtually all benthic animals are sensitive to bottom water oxygen conditions, and seasonally low oxygen levels may preclude survival of many species. Burrowing and feeding activities of key benthic faunal groups can radically alter the fate of nutrients and organic matter reaching the Bay bottom, where many large long-lived organisms tend to enhance removal of nitrogen and phosphorus from the water column (thereby limiting algal production peaks). Loss of these species from bottom habitats may have increased the efficiency by which nutrients are recycled and retained in the Bay, leading to sharp increases in phytoplankton growth per unit nutrient loading. Routine surveys of benthic macrofauna in the mesohaline Bay were initiated in the 1970s and 1980s and continue to the present.

Water Clarity. Long-term data records exist to provide information on the depth of light penetration using the simple and dependable Secchi depth method (the depth where a white disk being lowered into the water first disappears from sight of a shipboard observer). While Secchi disk data offer a reliable indicator of light penetration in the Bay from the early 1900s to the present, these data are scattered in unpublished notebooks and data logs in institutions around the region. In general, Secchi depth data can be conveniently converted to estimate light attenuation coefficients so that light levels at any water depth can be estimated. Limited analysis of these data (e.g., Stankelis et al. 2003) has revealed useful information on trends of historical increases in Bay turbidity. These data can be used to compute shifts in the relative importance of benthic versus planktonic productivity over time and may allow identification of abrupt changes in the importance of benthic photosynthesis associated with both SAV and algae (e.g., Kemp et al. 2005). Workshop participants suggested that rapid loss of benthic photosynthesis may account for many historical changes in structure of the Bay ecosystem, but little is known about what environmental conditions would be needed to re-establish those shallow Bay regions where benthic photosynthesis once dominated.

Sediment Cores. While most historical data for the Bay ecosystem come from time-series samples collected in the environment, the oldest and longest records have been preserved in Bay sediments, chronologic sequences that reflect natural geological and biological processes (e.g., Cooper and Brush 1991, 1993; Cronin and Vann 2003). Vertical strata of sediments at the bottom of the Bay contain chemical and biological markers. These markers index temporal trends in biological communities, as well as biogeochemical processes related to long-term environmental changes like eutrophication (Zimmerman and Canuel 2000,

DETECTING AND PREDICTING THRESHOLDS

Although theoretical evidence predicts the existence of thresholds in an ecosystem's response to external forces, objective empirical evidence will be needed to support these ideas (e.g., Scheffer and Carpenter 2003). Improved understanding of the mechanisms that shape observed ecological trajectories may emerge from analysis of long-term historical data, including nutrient loading, climatic variations, fisheries harvests, and key ecological properties and processes. Although few such analyses have been applied to Chesapeake Bay data, various statistical methods might prove useful in detecting significant thresholds in temporal data records (e.g., Schroder et al. 2005). Such approaches could provide a basis for predicting future threshold events.

Change-point Detection. Change-points are points along an ordered environmental gradient (time series) where the data separate into two groups (above and below the point) with statistically distinct characteristics (e.g., different means, variances, slopes). Limited examples for Chesapeake Bay data include change-point analysis to relate variations in ecological properties (e.g., benthic macrofauna and SAV) in small sub-estuaries to differences in broad categories of watershed development (e.g., King et al. 2005, Brooks et al. 2006, Li et al. 2007). Change-point detection methods that have been applied to coastal data sets (e.g., Qian et al. 2003) include (a) nonparametric techniques for reducing the summed deviation among data points, (b) Bayesian analysis of randomly distributed response variables along environmental gradients, and (c) classification and regression tree (CART) analysis.

Composite Time-series Analysis of Field Data. Methods applied for composite time-series analysis include (a) principal components analysis, (b) composite average standard deviates, (c) autoregressive modeling, and (d) Fisher information analysis (e.g., Mantua 2004). These approaches are used to analyze parallel time-series data for oceanographic, fisheries, and climatic variables in various coastal regions, detecting thresholds, regime shifts, and hysteretic responses of phytoplankton, water clarity, oxygen, and fish to changes in climate and fishing (e.g., Weijerman et al. 2005, Oguz and Gilbert 2007).

Simulation Modeling. By exploring how a system interacts as a whole, simulation modeling could play an important role in understanding mechanisms underlying thresholds and identifying precursor indicators that foreshadow them. These insights would be derived through hindcasting experiments, while forecasting simulations could be used to test and validate derived concepts (Scheffer et al. 2003). At present, it is unclear whether existing simulation models are equipped to capture these threshold behaviors, particularly with respect to changes in biotic resources. Indeed, understanding of complex threshold behavior associated with changes in nutrient loading, fishing pressure, and food web structure can sometimes only be resolved using combinations of statistical and numerical simulation models (e.g., Yamamoto 2003, Oguz and Gilbert 2007).

2002). Analysis of such sediment cores has provided quantitative data streams for important indices of water clarity and seasonal hypoxia (for review see Kemp et al. 2005). Sediments in lakes and ponds within the Bay watershed contain similar markers that could be used to infer changes in land use and climate. Similarly, rings laid-down in the trunks of ancient trees record annual variations in environmental conditions that reflect changes in climatic and anthropogenic drivers. Could these natural data records be further analyzed to detect nonlinear temporal responses to changes in nutrient loading from the watershed? How well do the trends of these longer data records correspond to more recent trends developed from monitored samples collected over recent decades?

Fisheries. Both top-down (e.g., fisheries removals) and bottom-up (e.g., nutrient loadings) forces contribute to change in the Chesapeake ecosystem (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006). Unsustainable fishing practices, for example, have caused declines in fisheries landings and abundance of mid- to upper-trophic level consumers. Analysis of fisheries landing data, available for most commercial species from 1950 to the present, can provide indices of changes in food web structure (e.g., ratio of pelagic- to benthic-feeding fish, Kemp et al. 2005) caused by fisheries removals and other environmental factors. These long-term Bay data sets that quantify parallel trends in food webs, fishery landings, nutrient loading, and climate, especially when partitioned by region (e.g., data compiled by the Potomac River Fisheries Commission), could prove useful in signaling trophic structures that reflect recovering and/or degrading trajectories. Such analyses could help managers devise effective strategies for integrated ecosystem management of water quality, habitats, and fisheries.

Setting Attainable Benchmarks

Moving restoration efforts forward with an expectation that ecosystem responses could be nonlinear poses a challenge for managers. It will be important to set achievable benchmarks to give structure to this process. Although the Clean Water Act's water quality criteria for Total Maximum Daily Loads, or TMDLs (e.g., oxygen, chlorophyll, water clarity) offer reasonable targets for Bay restoration, other more integrative benchmarks — such as the reduction of the spring phytoplankton bloom and increase in SAV cover in shallow waters — may also be useful in this process.

In Chesapeake Bay, the basic pattern of size and timing of the spring bloom is fairly consistent, but the details can vary substantially from year to year with changes in river flow and temperature (e.g., Harding et al. 2002). The extent of this spring bloom and associated organic deposition rates have been causally linked to the rate of oxygen decline in spring and the timing of incipient summer hypoxia (e.g., Boynton and Kemp 2000). There is evidence that seasonal cycles of phytoplankton biomass and productivity have changed with eutrophication of certain Bay tributaries (e.g., Boynton et al. 1982) and that inter-annual variations in the spring algal bloom appear related to both hypoxia and water clarity (e.g., Hagy et al. 2004, Kemp et al. 2005).

While current efforts are generally intended to reduce the spring bloom and increase SAV cover, restoration benchmarks would establish much more precise measurements in space and time and would index these measurements to specific increments of progress.

Experimenting with Adaptive Management

Based on experiences of researchers working in other aquatic systems (see Erik Jeppesen's talk for examples), approaches involving manipulations of parameters, both biological (e.g., adding fish, bivalves, and/or SAV) and physical (e.g., varying stream flow, adding breakwaters), could be used in conjunction with nutrient load reductions to move systems at the tributary scale closer to desired restoration goals. For adaptive management efforts to be most effective they need to focus strategically in Bay regions that are most likely to demonstrate clear and significant responses. Research results may offer important clues for where to begin this process.

For example, shallow lakes respond more strongly to nutrient loading changes and biomanipulation than do deeper lakes (e.g., Jeppesen et al. 2003). In general, ecological processes are concentrated in smaller volumes in shallow water systems, and associated benthic processes will generally have greater impact on water quality and plankton dynamics in shallower systems. Benthic dominated communities tend to be characterized by relatively efficient photosynthetic, nutrient cycling, and grazing processes. Although there are many important shallow water regions in the mainstem of Chesapeake Bay (e.g., Susquehanna Flats) and there is an on-going shallow water-monitoring program in all tidal waters of the system, an adaptive management effort focusing on tributaries would generally include extensive shallow water areas and have a relatively high probability of success. An adaptive management initiative that takes a tributary-by-tributary approach would resonate with the goals of the Chesapeake Bay Program Tributary Strategies. Specific suggestions for adaptive management experiments in the Chesapeake watershed include (1) manipulation of the magnitude and variability of water flow through the Conowingo Dam and (2) the restoration of shallow benthic communities dominated by marshes/wetlands, SAV, benthic microalgae, and/or benthic bivalves in selected tributary areas.

The Susquehanna River Basin Commission is in the process of establishing criteria for minimum flow regimes based on needs of Bay ecosystems, in addition to human water uses. This may offer a unique opportunity to develop adaptive management approaches for examining ecological effects of varied river flow. For example, many SAV species tend to be highly responsive to inter-annual variations in stream flow and associated water clarity. Although high salinity stresses some SAV species during periods of low flow, improved water clarity that generally accompanies lower river flow tends to favor better SAV growth and survival. Large-scale SAV restoration efforts during low flow years might help to establish large dense SAV beds capable of assimilating nutrients and trapping suspended sediments to further improve growth conditions. This might allow the beds to cross a stability threshold that enables them to survive wetter, more turbid conditions in subsequent years.

Benthic communities tend to exert dominant controls on ecosystem processes in shallow water environments. Benthic filter-feeding bivalves can effectively regulate growth of phytoplankton in shallow water columns (e.g., Cloern et al. 1983). Ongoing discussions regarding restoration of native and/or non-native oysters or other bivalve species in the Bay should note that impacts on improving water quality would be most effective in shallow water areas. By combining strategies to reduce inputs of nutrients and suspended sediment, along with efforts to boost benthic communities, adaptive management efforts may be able to enhance growth of SAV beds and benthic microalgal mats, both of which tend to retain and recycle nutri-

ents as well as trap and bind suspended sediments. These autocatalytic mechanisms enable benthic plants to enhance their own growth conditions.

Obviously, any adaptive management initiative should be designed to maximize cost-effectiveness and positive outcome. Ensemble forecasts and scenario experiments using a suite of existing models could be used to help identify candidate projects, especially in the early stages of such a program. Where possible the management action should include combinations of reductions in nutrient inputs from the watershed and restoration of habitats that are likely to enhance water quality or related growth conditions for keystone organisms (see Linking Land to Water, below). Inputs from watershed sources need to be carefully monitored and modeled during the management experiment, including estimates of the physical transport of nutrients and organic matter between adjacent regions. Responses of water quality, habitat conditions, food webs, and fish-

Technical Background

LINKING LAND TO WATER

Reaching thresholds for recovery in the Chesapeake Bay will require synergistic management efforts both on land and in the water. Although this report focuses predominantly on open water portions of Chesapeake Bay, the linkages between water and land, as the primary source of nutrient pollution, sediments, and toxics, should not be ignored.

Recent efforts to link activities on land to the condition of aquatic ecosystems have produced a key set of ecological indicators for ecosystem condition. The Atlantic Slope Consortium (<http://ccrm.vims.edu/projects/final_ASC_report.pdf>), which brought together more than 40 scientists from six different institutions, developed over 30 indicators for shallow water coastal ecosystems across three major drainage basins that extend from the Appalachian Mountains to the Atlantic Ocean: the Delaware, the Susquehanna-Chesapeake, and the Albemarle-Pamlico.

These indicators connect the amount of development, proximity of streams, and patterns of land use to ecological metrics such as marsh bird diversity, abundance of submerged aquatic vegetation (SAV), and polychlorinated biphenyl (PCB) levels in white perch. The project identified thresholds for development (such as the percentage of impervious surface and distance from the water) beyond which specific estuarine indicators begin to show signs of degradation. For example, marsh bird diversity drops in a threshold-like manner when more than 14 percent of the land is developed in the area within 500 meters of a wetland boundary (Brooks et al. 2006).

The Atlantic Slope Consortium's indicators could prove instrumental for understanding the hypothetical recovery trajectory the Bay will follow. Ecological indicators such as the water clarity threshold for SAV survival, for example, provide diagnostic tools for setting a management target for water clarity — one that can be linked directly to sediment and nutrient input from development on land.

eries should to be monitored closely during the experiment. Monitoring should include a combination of routine fixed station samples, continuous observations from stationary platforms, and spatial mapping of surface characteristics. Formal protocols for analysis of monitoring data need to be established and coordinated with diagnostic modeling studies.

Recognizing Early Signs of Response

As the Chesapeake begins to respond to nutrient reductions, it will be critical for managers to recognize the early ecological signals, to make course corrections if necessary, or to push harder toward thresholds for recovery. Developing and operationalizing an early warning system for incipient thresholds that managers can use would be an important next step — one contingent upon interpretation of information inherent in long-term data sets. Although there is little experience in identifying behavior of estuarine ecosystems that foreshadows the approach of thresholds, theoretical considerations (e.g., Brock and Carpenter 2006) suggest that increases in variance of spatially explicit ecological variables tend to precede shifts in ecosystem structure and dynamics.

To become operational, the early warning system needs to incorporate two key elements. (1) Real-time data streams must include easily interpretable indicators of incipient thresholds. (2) Such indicators must be detected by an automated analysis of data streams. High-quality continuous monitoring data are available in real time through web-based interfaces, such as the Maryland Department of Natural Resources “Eyes on the Bay” and “Chesapeake Bay Observing Systems.” But rigorous retrospective analysis of existing data will be a key step in this process. This analysis should capture diverse responses to changes in nutrient loading conditions from data that reflect a wide range of sampling scales, in terms of both temporal and spatial resolutions and extent. Data need to show clear examples of the Bay system crossing thresholds and moving between ecological regimes in the past. Ultimately, diagnostic and predictive numerical simulation models need to be developed to capture observed nonlinear trends.

RECOMMENDATIONS FOR RESEARCH AND MANAGEMENT

1. Improve understanding of past threshold events in the Chesapeake Bay through rigorous analysis of historical data sets. These analyses should help identify the key variables that define thresholds and alternative regimes. Such an effort should:
 - Include data sets that cover a range of time scales — from sediment cores and tree rings to current routine monitoring data of water quality and living resources abundance.
 - Identify and analyze time periods in these data surrounding threshold events using a variety of statistical approaches, such as the analysis of variance-covariance or cluster analysis.
 - Include the analysis of climate data in conjunction with ecological data to consider the role that climate variability and climate change play in driving measured data trends.
2. Revisit current modeling approaches to evaluate whether they are capable of capturing nonlinear dynamics and state changes that follow the crossing of a threshold. Develop modeling approaches that might help better predict threshold responses to decreased nutrient loading and that could be used to help design adaptive management experiments.
3. Conduct adaptive management experiments with careful attention to key factors controlling threshold responses, including water depth, water clarity, salinity, food web interactions, and climate.
 - Target experiments to shallow, low salinity regions of the Bay that are likely to respond more quickly to reduction in nutrient loads. Specifically, these regions might include areas with existing or planned future monitoring with some of the following characteristics: marshes/wetlands, historical/current SAV or oyster beds, water quality already showing signs of improvement, and located some distance from adjacent developing land.
 - Pair experimental approaches, such as the manipulation of freshwater flow, with efforts to restore habitats (marsh/wetland construction, SAV, filter feeders) and reduce nutrients over small spatial scales in an attempt to induce “self-catalyzing” threshold responses.
 - Incorporate into the experimental design explicit predictions for the Bay’s response to climate warming (including changes in freshwater delivery, sediment, and nutrients, salinity, and temperature) in adaptive management experiments.
4. Work to manage expectations of the public with regard to the range of anticipated ecosystem responses to restoration efforts. Improve dialogue between scientists and managers by developing

teaching tools that make the concept of thresholds and nonlinear responses accessible to a broad audience.

5. Work with federal and state agencies to initiate new Requests for Proposals (or add to existing ones) that would provide funding for specific goals:
 - Compile and analyze historical data sets that quantify changes in Bay environmental quality and living resources, anthropogenic influences (e.g., point and diffuse source inputs, fishery harvest, sediment dredging), and climatic conditions.
 - Test existing models for their capacity to capture threshold responses and devise, where needed, model structures that effectively simulate these nonlinear dynamics.
 - Conduct, monitor, simulate, and analyze adaptive management experiments in targeted areas.
 - Develop educational tools geared towards communicating the concept of thresholds to a broad audience.

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APPENDIX I

Summaries of Presentations by Invited Speakers

Slides of speaker presentations are available online at: www.chesapeake.org/stac/thresholds

Below are brief synopses of the invited presentations at the workshop in February 2007

1. Recovery Trajectories, Mechanisms & Examples: Relevance for Eutrophic Chesapeake Bay

W. Michael Kemp, Walter R. Boynton (University of Maryland Center for Environmental Science) and Denise Breitburg (Smithsonian Environmental Research Center)

In aquatic ecosystems like the Chesapeake Bay, when inputs or conditions change, such as a decrease in nutrient loads, threshold-type responses may occur. Examples in the Chesapeake region include the tidal fresh region of the Potomac River proper and a tributary to it (Gunston Cove), the Patuxent River meso-haline region, and the Back River oligohaline region. These examples, which are discussed in greater detail in the Case Studies section of the report, include evidence of linear responses with and without time lags, threshold responses, and hysteretic responses where recovery trajectories differ markedly from degradation pathways. Examples of ecosystem feedback mechanisms observed in the Chesapeake include: (1) a positive feedback relationship between the growth of submerged aquatic vegetation (SAV) and a decrease in total suspended solids (TSS), leading to an improvement in water clarity, followed by abrupt SAV recovery, (2) improved benthic filtration by a clam in the Potomac (*Corbicula fluminea*), followed by improved water clarity and SAV recovery, and (3) hypoxia in the Bay reinforcing eutrophic conditions (positive feedback) through enhanced nutrient recycling efficiency despite stable or decreasing nutrient loads. Complex interactions between top-down (food web-driven) and bottom-up (nutrient-driven) controls make these kinds of ecological feedbacks difficult to document and analyze.

The take-home points here are that we need to: (1) mine existing monitoring and historical data for signs of ecological thresholds and hysteresis, (2) undertake additional research that focuses specifically on quantifying nonlinear feedback mechanisms, and (3) incorporate feedback processes into management efforts in an adaptive and iterative manner.

2. Eutrophication in the Neuse-Pamlico Estuarine System: Responses to Nutrient Reduction and Large Storm Events

Hans Paerl (UNC, Chapel Hill)

The Neuse River-Pamlico Sound estuarine system in North Carolina followed particular pathways to reach the eutrophied state that characterizes it today. Its future will be affected by a number of factors, including the prediction that more intense and frequent storms will affect this region with global climate warming.

The Neuse River has a relatively long water residence time that has exacerbated an increase in nitrogen and phosphorus loading by some 30 percent over 40 years of agricultural, urban, and industrial expansion. The region has also felt the impact of several major hurricanes, including Floyd, Dennis, and Irene (1999) and Fran (1996).

Understanding the historical pathways that led to eutrophication will help inform future management strategies. The ModMon and FerryMon monitoring systems help to provide key data by sampling the system at high-frequency temporal and spatial scales. Long-term monitoring data show that phytoplankton chlorophyll levels have decreased upstream over time, but increased downstream. This suggests that the management decision to decrease loading rates for phosphorus only, without parallel decreases in nitrogen loading, led to this regional disparity in chlorophyll abundance and the associated downstream progression of eutrophication effects. To change course, a nitrogen-input threshold must be established. Chlorophyll *a* levels could serve as the measured response indicator used to evaluate whether management actions are working.

Extreme storm events, like hurricanes, can overwhelm the impact of effective nutrient management strategies. Hurricane Floyd, for example, reduced the residence time of Pamlico Sound from one year to one week. Storms can also change the abundance and community composition of phytoplankton, which can have feedback in other parts of the food web. Establishing nutrient loading thresholds during a period of potentially elevated hurricanes will pose a clear challenge.

3. Concepts of Nonlinear Feedback Systems: Case Studies and Management Implications

Lance Gunderson (Emory University)

Efforts in the Florida Everglades and Grand Canyon provide two case studies where adaptive management has been used to mitigate undesirable shifts.

To pursue effective adaptive management, we need to understand six key concepts related to nonlinear feedback systems: (1) such feedback systems are ubiquitous and can occur in terrestrial, freshwater, or marine systems; (2) variables that drive nonlinear responses occur at different spatial and temporal scales; (3) in most instances, only a “handful” of key ecological variables (3 to 6) are largely responsible for driving state changes; (4) thresholds are dynamic and difficult to predict; (5) resilience can be lost as the result of over-capitalization (increased nutrients and biomass), hyper-connectivity in space, and loss of functional diversity (trophic cascade); and (6) ecosystem structure and function are coupled to human institutions and preferences.

The relationship between the ecological system and human institutions can be characterized by the “Pathology of Command and Control.” This feedback loop links ecosystem state → ecosystem services → human preferences → action, which then in turn feeds back to affect ecosystem state. Ecological changes and accompanying management actions can be described for the Florida Everglades and Grand Canyon examples.

Adaptive management and governance provides a set of tools for accommodating uncertainty in future ecosystem responses. Social response to ecological crisis often plays a key role in initiating management actions. Since regime shifts can be either reversible or irreversible, knowing when to adapt to change or invest in a reverse transformation is key. Ecological resilience plays an important role in this consideration, as it can

provide a buffer for experimentation. For adaptive management to succeed, institutional frameworks should be learning-based and open to change.

4. Biogeochemical Feedback Mechanisms and Effects on Ecosystem Dynamics

Daniel J. Conley (Lund University, Sweden), Jacob Carstensen (National Environmental Research Institute, Roskilde, Denmark), Raquel Vaquer, Carlos M. Duarte (both from Instituto Mediterraneo de Estudios Avanzados (IMEDEA), Esporles, Spain)

Biogeochemical feedback mechanisms play an important role in threshold responses. In Europe, the THRESHOLDS of sustainability project serves as an ongoing effort to develop operational tools to identify thresholds, threshold behavior, and point-of-no-return values for coastal systems. Through this effort, scientists hope to use these tools to set policy targets in nutrient and contaminant inputs (learn more at <http://www.thresholds-eu.org/>).

It is essential to employ appropriate methods for identifying and testing the significance of thresholds in the environment and useful to know how these approaches have been applied to various case studies, including specific statistical tools and models. Case studies presented here focused on the relationship between biogeochemical cycles and hypoxia in Danish estuaries and in the Chesapeake Bay.

As these cases show, hypoxia tends to be linked to threshold behaviors because of its effect on changes in benthic communities, with the loss of deep-dwelling organisms that oxidize the sediments and cause dramatic changes in biogeochemical processes. With the sediment's oxidation capacity diminished, sediment metabolism switches to less efficient anaerobiosis, with different pathways for organic matter remineralization. Both nitrogen and phosphorus cycles are affected by hypoxia, leading to an increase in recycling of ammonium and dissolved inorganic phosphorus, which tends to promote further algal growth. Data from both Chesapeake and Danish waters support the idea that hypoxia may cause a "stuck-in-rut" effect that inhibits a return to a less eutrophic ecological state. Global climate warming will likely make matters worse. Projected temperature increases may mean lower oxygen saturation, higher rates of respiration, and a resulting increase in system heterotrophy, where rates of respiration exceed rates of primary production.

5. Trophic Dynamics, Regime Shifts, and Thresholds in Shallow Lakes

Erik Jeppesen (NERI, Denmark) et al.

Regime shifts in various lakes in Denmark and elsewhere highlight the importance of bottom-up and top-down controls and trophic dynamics as mechanisms underpinning threshold responses. In many instances, response trajectories in lakes differed depending on whether nutrient loads are increasing or decreasing. Temperate lakes also tend to respond differently from subtropical lakes and brackish tend to respond differently from freshwater lakes.

As nutrient gradients (phosphorus in this case) increase, the trophic organization in the middle of the food web changes — especially among zooplankton and fish. The relative importance of zooplankton-feeding fish (planktivores) increases while that of fish-eating-fish (piscivores) decreases. In eutrophic lakes phytoplankton production dominates, while benthic photosynthesis tends to be more important in oligotrophic

lakes. Experimentally increasing the abundance of submerged aquatic macrophytes in lake systems can sometimes reverse this change in food web dynamics. In shallow freshwater lakes, macrophytes remove nutrients for growth and provide refuges for zooplankton (Cladocerans) which control phytoplankton and water clarity. In shallow brackish lakes, macrophytes also assimilate nutrients, enhance denitrification, and stabilize sediment — all of which helps to favor a clear water, oligotrophic state. However, in brackish and saline systems, copepods, which are less efficient in regulating phytoplankton, dominate the zooplankton.

Warm lakes tend to have many fish and few zooplankton, while colder lakes have fewer fish, but many zooplankton. Food web dynamics differ accordingly — in subtropical lakes, fish feed directly on periphyton. Salinity makes a difference too. Copepods tend to be more abundant at higher salinities. Low salinity tends to correlate with lower fish density and lower chlorophyll.

Chemical and biological resistance might cause time delays in the response of water bodies to decreased nutrient loading. Lakes take an average of 10 to 15 years to respond to changes in nutrient loading. The delay is caused by both biogeochemical factors and lag times in concomitant changes in the organization of the food web (especially birds and fish). In many cases, the delay is also caused by a combination of relatively long residence time for water volumes and by large pools of phosphorus accumulated in lake sediments.

Experiments with biomanipulation (adding/removing fish and plants from the system) have been conducted in multiple European lakes. While such efforts can have an impact, they do not prove a substitute for a decrease in nutrient loading. Treatments have to be repeated in order to have a sustained effect and, therefore, may be more useful as a management tool to maintain a state against natural odds, rather than as a restoration tool.

Reducing nutrient loading is the lynchpin to regime shifts. Take-home messages for Chesapeake Bay are: (1) reduce nutrient loading as much as possible; (2) demonstrate to the public that this works by putting the most concentrated effort toward the upper arms (shallow, freshwater) where the response is likely to be the most dramatic; (3) conduct comparative studies within and between bays and within and between years to help make decisions about where to allocate greatest effort and to set target loadings; and (4) undertake more large-scale experiments (using both exclosures and enclosures).

6. Eutrophication in a Multi-stressor World: Interactions with Climate Change, Alien Species, and River Damming

Jim Cloern (USGS)

Dramatic changes have occurred in San Francisco Bay over the past two decades. These demonstrate that the connection between changes in phytoplankton biomass and nutrient loading can be shaped by factors such as food resources, transport processes, and change in biological community structure.

Like Chesapeake Bay, San Francisco Bay has experienced human-driven nutrient loading, with increasing levels of nitrogen and phosphorus over recent decades. Although similar in scale to Chesapeake Bay, it differs in its ratio of watershed to estuary area, residence time, tidal currents, turbidity, and macrophyte abundance. Additionally, the north and south basins of San Francisco Bay differ greatly from each other — the north bay is river-driven and has low salinity, while the south bay is a marine lagoon.

In the north bay, the invasive clam *Corbula amurensis*, which first appeared in 1987, dramatically altered spring bloom dynamics and organization of the food web. Primary production decreased and populations of the zooplankton *Eurytemora* and mysid shrimp declined as a result. Numbers of juvenile striped bass have also fallen since 1987. The south bay did not experience the same changes as the result of the *Corbula* invasion, continuing to experience spring blooms with a regular pattern, although with varying intensity and duration. In 1999, the spring bloom pattern in the south bay changed, with a secondary bloom appearing that surpassed the spring bloom in magnitude.

Several hypotheses may explain the appearance of a secondary bloom at a time when nutrient loading has been declining as the result of management interventions. These involve turbidity, contaminants, physical transport, and changes in food web structure as possible culprits. Ultimately, both transport processes and trophic dynamics may be interacting in a complex way. A primary hypothesis: Upwelling intensity in the coastal Pacific Ocean has increased in recent years due to climatically driven factors, causing high phytoplankton biomass in the Pacific Ocean. When the wind relaxes or reverses, offshore biomass may be transported into San Francisco Bay. Meanwhile, the abundance of *Corbula* clams has been decreasing since the late 1990s likely due to increased predation by fish, thus diminishing their impact in limiting phytoplankton abundance. This combination of both climatically-driven and food web-driven factors can explain the change in bloom dynamics, underscoring the importance of using a multi-faceted approach when considering the interaction between phytoplankton abundance and nutrient loading.

APPENDIX II



Thresholds in Recovery of Eutrophic Coastal Ecosystems
February 14-15, 2007
Belmont Conference Center, Elkridge, MD
www.belmontconferencecenter.com



Day 1: February 14, 2007

Carriage House

TIME	ACTIVITY	PRESIDING
9:30 am	Registration and Continental Breakfast (Provided)	
10:00 am	Introduction to Workshop	Walt Boynton
10:30 am	Presentation: <i>Recovery trajectories, mechanisms, & examples: Relevance for a eutrophic Chesapeake Bay</i>	Mike Kemp UMCES, Horn Pt
11:20 am	Presentation: <i>Eutrophication in the Neuse-Pamlico estuarine system: Responses to nutrient reduction & large storm events</i>	Hans Paerl UNC, Chapel Hill
12: 10 pm	Goals and Structure of Workshop	Mike Kemp
12:30 pm	Lunch (Provided)	
1:30 pm	Break-out Discussions Group 1 – Carriage House, Conference Room Group 2 – Carriage House, Lunch Room Group 3 – Manor House, Conference Room	
3:00 pm	Coffee break (Refreshments provided at Carriage House)	
3:30 pm	Break-out Discussions	
4:30 pm	Plenary Discussion	Denise Breitburg
5:30 pm	Adjourn (Down Time)	
6:30 pm	Dinner (Provided in Carriage House, Cash Bar available)	
7:30 pm	Presentation: <i>Concepts of nonlinear feedback systems in Ecology: Case studies and management implications</i>	Lance Gunderson Emory U., Atlanta
8:15 pm	Adjourn for Social Hour at Manor House Lounge (Cash Bar available)	

Day 2: February 15, 2007
Carriage House

TIME	ACTIVITY	PRESIDING
7:00 am	Continental Breakfast (provided)	
8:00 am	Plenary Discussion: Review and Recap	Michael Kemp
8:30 am	Presentation: <i>Biogeochemical feedback mechanisms and effects on ecosystem dynamics</i>	Daniel Conley Univ. of Lund, SE
9:20 am	Presentation: <i>Regime shift in freshwater and brackish lakes: A critical view</i>	Erik Jeppesen NERI, Denmark
10:10 am	Coffee Break	
10:30 am	Presentation: <i>Eutrophication in a multi-stressor world: interactions with climate change, alien species, & river damming</i>	Jim Cloern USGS, Menlo Park
11:20 am	Plenary Discussion	Denise Breitburg
12:00 pm	Lunch (Provided)	
1:00 pm	Break-out Discussions	
2:30 pm	Coffee Break (Refreshments Provided at Carriage House)	
2:50 pm	Break-out Discussions	
3:00 pm	Plenary Discussions	Walt Boynton
4:00 pm	Workshop Adjourns	Michael Kemp
4:15 pm	“Synthesis Committee:” Debriefing & Planning Manor House Ballroom (Refreshments Provided)	Michael Kemp
5:30 pm	Depart	

APPENDIX III

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