

Predictability, Scale, and Biodiversity in Coastal and Estuarine Ecosystems: Implications for Management

This paper looks at coastal and estuarine ecosystems in terms of their unique biodiversity characteristics and the implications of these characteristics for management. With the exception of coral and other reef communities, coastal and estuarine systems are generally low in species diversity. But estuaries are typically dominated by strong aperiodic physical forces (e.g. salinity changes due to freshwater inflows, storm events) and under these conditions structure is more difficult to build and maintain. Estuaries are also characterized by a high degree of organism mobility. These characteristics point to a high degree of ecosystem resilience. The general hypothesis is that the biodiversity achievable in a system is a function of the predictability and scales of its physical environment. This hypothesis is consistent with the limited data on diversity in estuaries and other systems, and can be further tested in the future via comparative analysis. These ideas are elaborated and extrapolated to the task of managing complex and coupled ecological economic systems. Biological or species diversity is put in a systems context as a scale-dependent measure of an important system characteristic. In estuaries it is the diversity of ecological processes, and in particular certain keystone processes, that are more critical and that should be the focus of management efforts. Effective management is seen as the process of escaping from social traps that occur when local, individual incentives diverge from global, long-term goals.

COASTAL AND ESTUARINE ECOSYSTEMS

Coastal and estuarine ecosystems are the vast biomes that join continental lands and oceanic islands with their surrounding seas. Most of the world population resides in the coastal zone and the density of coastal economic development is increasing. Therefore, these ecosystems are particularly important for integrating sound ecological management with sustainable economics (1).

Estuarine ecosystems are coastal indentations with "restricted connection to the ocean and remain open at least intermittently" (2). Salinities are usually intermediate between those of fresh and seawater, but in regions where evaporation is high or rainfall low, estuarine salinities may be equal to or higher than those of the ocean. Most present day estuaries were formed during the last 15 000 years of the current interglacial period, and are thus geologically ephemeral features of the landscape.

Although estuaries vary in depth from one to several hundred meters, shallowness clearly distinguishes them from the open ocean. Depending on the mode of origin and the nature of surrounding land masses, estuaries may assume a variety of sizes and forms. Coastal plain estuaries were formed with the drowning of coastal rivers with rising sea level, while others (e.g. fjords) were formed in glacial channels with terminal sills associated with moraine deposits. Others fill the chasm left from tectonic activities or formed as part of river deltas. Estuaries also include the large

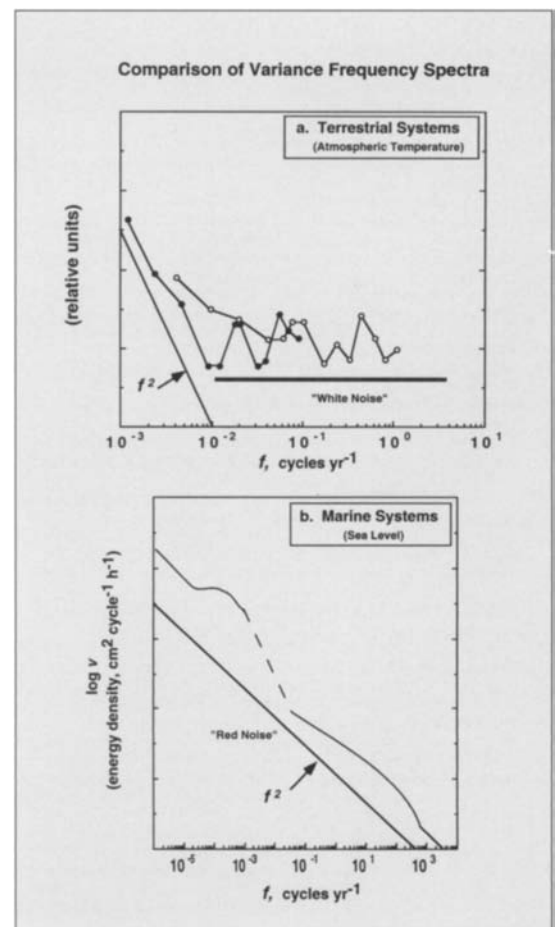
system of shallow coastal lagoons formed from oceanic sedimentological processes behind barrier islands, peninsulas, and spits.

One of the larger and more productive estuaries in the world is the Chesapeake Bay. Because many characteristics of the bay and its watershed have been well documented, it represents a good case study for further elaboration of some key concepts in estuarine science and management, and in particular, elaboration of issues of predictability, scale, and diversity.

Special Physical Characteristics of Coastal and Estuarine Systems

Perhaps the most distinctive feature that contrasts estuaries from other biomes is the nature and variability of the physical forces which influence these ecosystems. Within small geographic regions, many estuaries experience widely varying conditions of temperature, salinity, concentrations of a wide variety of chemicals, and plant and animal densities, much of which is mediated by water movement over relatively short time scales.

Figure 1. Comparison of variance frequency spectra for a) marine systems; and b) terrestrial systems. Source: (3).





Floods and storm events transport large amounts of water, sediments, and nutrients into estuaries in an unpredictable pattern. Photo: M. J. Reber.

For example, in the Chesapeake Bay, temperatures range from near 30° C in surface waters in late summer to zero by late winter. Ice cover is extensive in severe winters, but of only local importance in normal winters. Salinity also varies widely, from near zero in the upper reaches of tributaries to 30 ppt near the capes. Superimposed on these general gradients of temperature and salinity, significant, unpredictable, interannual variability also occurs related to normal climatic shifts from wet to dry periods. As a result, the spatial extent of various estuarine habitats undergoes periods of significant expansion and contraction.

Shifts from wet to dry periods also strongly influence the rate at which essential nutrients (such as nitrogen, phosphorus, and silica) enter the system from the surrounding watersheds. Since these elements are essential for plant growth, their availability determines, at least in part, the amount of organic matter available to support food webs. Recent measurements indicate that nutrient loading rates and algal production rates vary among years by at least a factor of two in the Chesapeake Bay.

In addition, the amount of freshwater entering the system is the primary factor determining the degree to which estuaries are vertically stratified, with lighter, fresher water near the surface and saltier, denser water near the bottom. One aspect of the biological significance of stratification lies in the fact that the degree of stratification determines the ease with which essential gases such as oxygen can reach deep waters and support the respiratory needs of benthic communities. In turn, the degree of stratification also regulates the ease with which nutrients released from benthic communities reach euphotic surface waters and are again available to support plant growth.

Finally, catastrophic events, such as hurricanes and severe tropical storms, cause yet another, largely unpredictable scale of variability. These storms can discharge huge amounts of

freshwater, nutrients and sediments into estuaries through a variety of mechanisms, and subject most organisms to some degree of stress. However, the "memory" of most estuaries with respect to these events seems to be relatively short (< 5 years) at least for lower levels of the food web. At higher trophic levels the long term impacts are not clear.

Although fluctuations in some physical features (like temperature) are damped in marine systems compared to terrestrial environments, the shallowness of estuaries makes them more susceptible to larger amplitude variations. In both marine and estuarine environments, spectral distributions for variations in many physical forces exhibit patterns which are inversely related to the square of the frequency (Fig. 1a). This so-called "red noise" distribution, which is associated with interactions between events at low and high frequencies, characterizes terrestrial processes at scales longer than 50 years (3). For higher frequency events, which occur within the life time of many organisms in terrestrial environments, variations in physical forces tend to be distributed independently of the frequency of occurrence, producing a pattern of "white noise" (Fig. 1b). One ecological consequence is that organisms in marine environments (as opposed to estuarine) are better able to adapt their behaviors and physiologies to the more predictable physical variations in the marine habitat.

Ecological Diversity of Estuaries

The relatively large and unpredictable variations in salinity and water movement characterizing most estuaries tend to limit the number of animal and plant species capable of adapting to these rigorous conditions (2, 4). As an ecotone between fresh and marine environments, estuaries contain a mixture of freshwater and oceanic species, but both planktonic and benthic communities

contain substantially fewer species than do similar communities in oligotrophic lakes and in the ocean. The number of benthic faunal species in the deep sea may be comparable to that of tropical forest biomes (5), while estuarine benthos are commonly dominated by a few species, with limited taxonomic diversity in any given bottom area (2).

The relatively low taxonomic diversity of estuarine communities arises because of physiological difficulties in dealing with high-amplitude unpredictable stresses (4) and because of the high organism mobility afforded by physical processes and properties of water. Osmotic stress is a primary physiological limitation for many organisms. In an estuary organisms must adapt to continually changing salinity. Other factors such as oxygen deficiency can contribute to environmental difficulties. Estuaries do provide a means for rapid dispersion and easy mobility for resident organisms due to the buoyancy of water and the rapid hydrodynamic transport associated with tides, winds, and pressure gradients. Many coastal marine organisms have high fecundity and depend on water transport for larval dispersal, so that isolated populations are rare. Many fish and swimming invertebrates migrate long distances (10^2 – 10^3 km) during portions of their life-cycles. Consequently, functional replacements for a given estuarine species are virtually always available (6) so that the selective advantages of specialization are minimal. There are relatively few endemic species in estuaries; most originate from freshwater or oceanic environments, and many marine organisms require estuarine environments for a portion of their life-cycle.

For example, during each year many adult striped bass (*Morone saxatilis*) spend a portion of the summer in coastal waters, the winter in deep waters of the coastal bays, and the spring in the tidal-freshwater portions of tributary rivers. Small-scale vertical movements also occur during summer in response to prey distributions, water temperatures, and oxygen conditions.

Other organisms, especially those without the mobility of fish and larger crustaceans, have developed physiological mechanisms to deal, often for extended periods of time, with adverse environmental conditions. The American Oyster (*Crassostrea virginica*) has often been cited as a premier example of an estuarine organism. The oyster can grow well across an extreme salinity range, feeds successfully on a broad range of algal species and detritus, stops feeding during cold periods of the year when food supplies are limited, and can survive extended periods of hypoxia or anoxia by closing tightly and switching its metabolism to a form of anaerobic respiration. On the scale of the whole estuary, reproduction is favored in some years in one location and in other locations at other times. Pelagic larval stages insure wide dispersal and colonization of available habitats and replenishment of areas that have become depopulated.

Finally, estuaries are truly open systems and this has implications for maintenance of species assemblages as well. Both the ocean and landward end of these systems are open to active and passive migrations of both indigenous and exotic species. For example, estuaries are characterized by having both anadromous (ocean dwelling but spawning in estuaries) and catadromous (freshwater dwelling but spawning in seawater) species. In addition, exotic species find their way into these systems attached to commercial ships or recreational boats. The constant exchange of fresh and saltwaters insures a constant seeding of planktonic organisms as well. Thus, despite the rigorous environment typical of estuaries and intense fishing pressure and degraded habitats in some instances, local extinctions are relatively rare and generally of short duration. Normal migrations, passive entry via river and tidal water flows, and accidental introductions insure a continual supply of normal and new species.

In addition to the physical stresses, another factor which may limit the number of species in estuarine environments is the virtual absence of the physical structures and associated habitats created by organisms, e.g. plant canopies, which typify terrestrial

environments. In very shallow coastal environments, generally less than 10 m, however, rooted vascular plants (seagrasses) and attached algae, e.g. kelp, often do create complex physical structures which lead to multiple physical niches and relatively high taxonomic diversity. Similarly, reefs formed by colonial animals (oysters, mussels), in estuaries can produce complex physical structures containing relatively more species. In very stable tropical marine environments, coral reefs develop unparalleled taxonomic diversity. Coral reefs cannot survive in highly variable environments, and such high-diversity systems do not occur in estuaries.

In general, the relationship in any ecosystem between taxonomic diversity (number and distribution of species) and functional diversity (variety of ecological processes) is unclear. The basic ecological processes involved in biogeochemical cycles and trophic interactions are the same in estuarine ecosystems as in any other biome. In estuaries, however, a given species is relatively less specialized for performing a single or a limited repertoire of ecological function(s). For example, the cosmopolitan estuarine clam, *Macoma balthica*, acts as a suspension-feeder, filtering food from the overlying water in environments with low rates of organic deposition to sediments, but acts as a deposit-feeder, scavenging food from the sediments, in organic-rich environments (7). Indeed, most estuarine animals appear to be opportunistic feeders, altering their diets to focus on foods which are relatively abundant (2). Similarly, most estuarine bacteria have alternative metabolic pathways for obtaining energy (8), and the same algal species can be found dominating benthic diatom, phytoplankton or epiphytic communities under different estuarine conditions (2). One measure of the functional diversity of estuarine ecosystems is the variety of different responses displayed by organisms to the range of physical environmental changes that occur (6). Thus, the relatively large scales of physical, and attendant biological, variability in estuaries might suggest that despite low taxonomic diversity estuarine ecosystems have high functional diversity (9).

Estuarine Productivity

Estuaries and coastal marine ecosystems are cited among the most productive biomes of the world (10). One reason for the high primary productivity of estuaries is the high nutrient loading rates, characteristic of these systems, compared to agricultural systems and other biomes (11). Rates of carbon fixation in estuaries rival those reported for the most productive terrestrial environments and substantially exceed those for oceans and many lakes (Fig. 2a). While benthic algae and seagrass can contribute substantially to estuarine production in shallow and clear coastal environments, phytoplanktonic algae tend to be the dominant autotrophic group. In addition to the relatively high rates of nutrient inputs to estuaries, their shallow depth and proximity of sediments to the euphotic zone promote efficient nutrient recycling. Physical circulation, characterized by landward flow of more saline waters and particle trapping, with density-driven stratification, leads to efficient nutrient retention (13).

Secondary production of estuaries is also large compared to other biomes of the world (13). Biomass production of certain benthic suspension-feeding bivalves in estuarine ecosystems exceeds the highest protein yield of pond-cultured herbivorous fish and rivals the areal production of highly subsidized cattle farms (14). These remarkable production rates for estuarine animal tissue result, again, from the natural energy subsidy associated with hydrodynamic transport of food and wastes to and from benthic animals. Thus, food-chains associated with benthic communities in shallow estuaries are likely to be more efficient in producing animal tissue. The omnivorous diets of many estuarine animals, and particularly their ability to grow on combinations of living plant material and detrital (dead plant and animal) foods, also results in relatively high trophic efficiencies

in organic-rich estuaries (13). Indeed, compared to freshwater ecosystems, the relative yield of fish per unit primary production is considerably greater in coastal marine ecosystems (Fig. 2b). This appears to be associated primarily with the mechanical boost associated with physical transport in estuaries (15). There is, therefore, considerable potential for production of human foods in coastal ecosystems (16), but the same physical processes and their associated variabilities which provide estuaries with natural work subsidies leading to high trophic efficiencies, also impair the ability of humans to cultivate the coastal seas.

In summary, we find that estuaries and other shallow coastal ecosystems represent unique biomes in which variabilities in certain physical properties, e.g. salinity, and processes, e.g. water movement, are relatively large and unpredictable. As a consequence of natural environmental stresses and the mobility afforded by buoyancy and hydrodynamic transport, taxonomic diversity in estuaries tends to be low with few endemic species. Estuarine functional diversity, however, appears to be relatively high compared to that in other biomes, especially in benthic dominated subsystems. Rates of primary production of estuarine ecosystems are among the highest in the biosphere, and trophic transfer of this production to growth of animal populations is relatively

efficient. These high conversion efficiencies of sunlight to plant tissue to animal biomass in estuaries are attributable largely to the mechanical subsidy of hydrodynamic processes.

Resilience and Keystone Processes in Estuarine Ecosystems

It has been suggested that many ecosystems exhibit resilient responses to external and internal perturbations by developing mechanisms which allow them to "absorb, buffer, or generate change" (1). In this context, ecosystems contain key organisms and processes which play crucial roles to insure long-term resilience by modifying the impact on ecosystem structure resulting from environmental changes. One mechanism for conferring ecosystem resilience is to establish alternating replacement structures that are switched periodically but which avoid accumulations of excessive structure. Examples of such keystone species or processes have been cited for a variety of terrestrial ecosystems. For instance, periodic outbreaks of the spruce budworm serve to release accumulated ecological structure for temperate coniferous forests (17). Few, if any examples of these kinds of key organisms have been identified for estuarine ecosystems. The term "keystone" organisms has also been used to describe organisms that play pivotal roles in the trophic structure of an ecosystem (18). In this case, predation by keystone organisms effectively preserves community structure by relieving competitive pressure between organisms at lower trophic levels or serving to keep lower-level predation levels in check (19). This latter kind of keystone organism or process has been identified for shallow benthic ecosystems in coastal marine environments (20), but they are poorly documented for estuarine plankton systems.

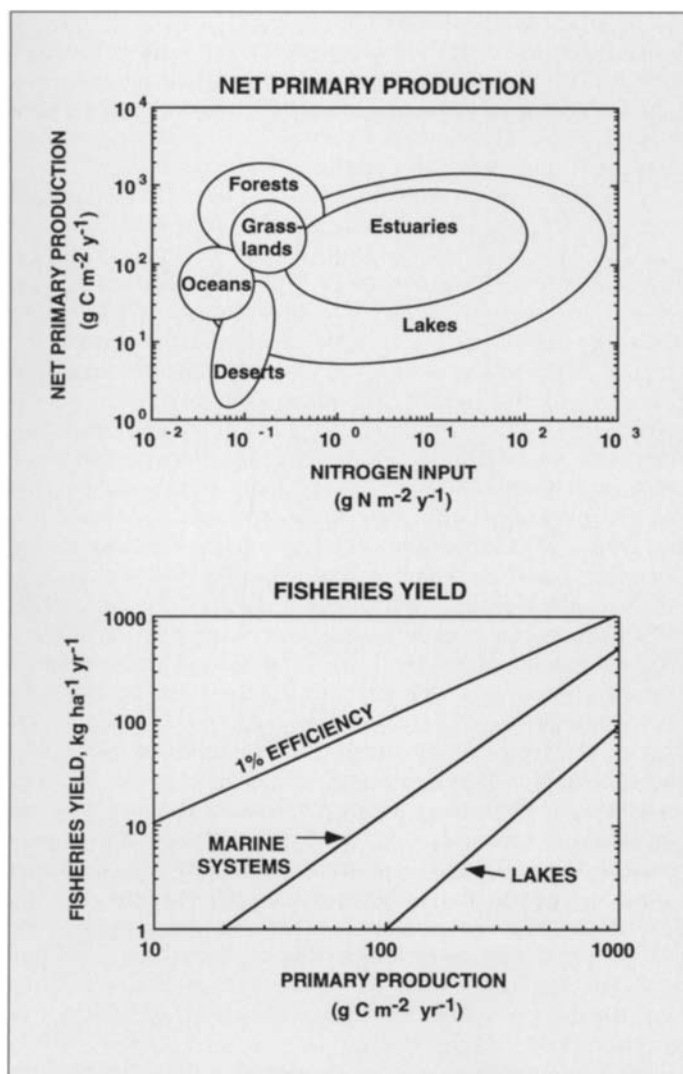
In spite of the sparseness of keystone organisms in estuaries, there is strong evidence that these ecosystems are relatively resilient to perturbations, at least for time scales less than 10^3 years. Estuarine ecosystem processes have been shown to return to pre-disturbance levels within months after perturbations from major meteorological events, e.g. hurricanes, floods, droughts, and winter freezes. For example, the Chesapeake Bay experienced a 200-year event in June of 1972 when a tropical storm created an unprecedented flood in the lower watershed. Sediment loading to the Bay during the 4–5 days of the storm were equivalent to inputs from the previous decade. Sufficient freshwater was delivered to remove virtually all seawater from the estuary for several days. Despite this dramatic change in environmental conditions, plankton community production and abundance returned to prestorm levels within 2–3 months. Although there were massive mortalities of benthic faunal populations, they recovered within a year (21). Similarly, there were no apparent effects on the annual fisheries yields comparing 1972 with previous and subsequent years. Numerous other examples are well documented illustrating estuarine ecosystem resilience to major disturbances; e.g. Hurricane Hugo in North Inlet, South Carolina. A few coastal ecosystems such as coral reefs are much less resilient to environmental changes (22), but organisms in these systems are not adapted to the same kind of high-frequency/high-amplitude variations in physical and chemical environmental conditions as are those in estuaries.

It appears that this well-buffered disturbance-response displayed by various estuarine ecosystems rests on three primary factors:

- i) the relatively small standing ecological structure;
- ii) the high degree of organism mobility;
- iii) the prevalence of generalist species.

Unlike forests, estuaries and other aquatic ecosystems contain relatively low levels of standing biomass. Hence, the time required to regenerate any losses in ecological structure is relatively short for estuarine systems. The combination of strong hydrodynamic transport and active motility insure that seed organisms are readily available to replace those lost with perturbations from both the land and marine ends of estuarine systems. Furthermore, the high degree of functional generalism among estuarine

Figure 2. Synthesis diagrams of a) nitrogen inputs vs. productivity for various ecosystem types; and b) primary production vs. fisheries yield for marine and freshwater systems. Source: (15).



organisms increases the probability that any ecological processes lost with species declines from external perturbations can be replaced by other organisms. In many estuarine ecosystems, the rapid plankton turnover resulting from hydrodynamic transport tends to keep any species from dominating the broad ecological niches of estuaries. This tends to facilitate species coexistence and stabilize community structure against internal disruptions such as overgrazing (23).

Conventional ecological views of keystone organisms may not be sufficiently inclusive for estuarine systems. There are, nevertheless, a number of key organisms and processes which play fundamental roles in the functioning of estuarine ecosystems. Although the loss of these critical ecological attributes may not jeopardize the resilience of an estuarine ecosystem, it may significantly change its ecological structure. Many of these critical processes are most evident in the benthic subsystems of estuaries. An example of such a process is nitrification-denitrification which is crucial in nature and is generally not fully recognized until after its loss has occurred.

A complex but essential component of nitrogen cycling in estuaries is the coupled process of nitrification-denitrification. In this process the reduced nitrogen salt, ammonium, which is released in microbial decomposition and animal excretion, is converted to gaseous forms—predominantly di-nitrogen gas (N_2), which comprises almost 80% of the earth's atmosphere. Whereas the reduced salts of nitrogen such as ammonium are essential for plant growth, the gaseous forms of nitrogen are virtually unavailable for use by estuarine plants. Under normal conditions the rate of nitrification-denitrification is directly proportional to the rate of nitrogen loading to the estuary (24) so that this coupled process buffers the ecosystem, maintaining an intermediate level of internal nitrogen. In all biomes of the world, including estuaries, nitrifier bacteria are highly specialized organisms with strict nutrient requirements, especially for oxygen and ammonium, necessary for growth. Thus, nitrifiers are an exception to the rule of few specialist organisms occurring in estuarine ecosystems. Because ammonium concentrations are highest in sediment porewaters, the highest rates of nitrification tend to be concentrated in surface sediments in the narrow zone into which oxygen penetrates. In contrast, denitrifier bacteria are generalists capable of numerous alternative metabolic processes for growth. To metabolize via denitrification pathways, however, they require an abundance of the nitrogen salt produced by nitrifiers (nitrate) as well as total absence of oxygen. Therefore, denitrification will not occur without nitrification and the critical coupling of nitrification and denitrification occurs only at the interface between anaerobic and aerobic environments (25).

In certain estuaries, such as those with deep channels, a high ratio of river flow to tidal flow, and/or limited turbulent mixing, and excessive inputs of nitrogen from the watershed can lead to depletion of oxygen from bottom waters. This results from nitrogen-stimulated growth of planktonic algae and decomposition of algal matter near the benthic surface at rates which consume oxygen faster than reoxygenation from the air-water interface. The anoxic conditions which ensue result in massive mortality of bottom-dwelling animals and elimination of any aerobic bacterial processes, e.g. nitrification, which might otherwise occur at the sediment surface. Hence, whereas under normal conditions a significant portion, approximately 50%, of the nitrogen entering the estuary is removed via nitrification-denitrification, under these eutrophic conditions of excessive nitrogen loading and anoxia, this nitrogen removal process is inhibited (26). However, within months after oxygen is restored to the Bay bottom, rates of nitrification-denitrification return nearly to the levels occurring prior to the anoxic disturbance. This is, therefore, another example of a key estuarine process that is susceptible to change and which controls the nature of the ecosystem, but which is quickly restored once the perturbation is removed.

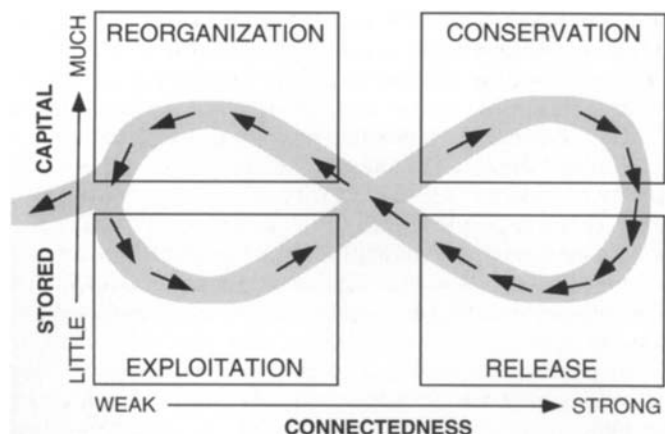
TOWARD A GENERAL THEORY OF PREDICTABILITY, SCALE, AND BIODIVERSITY

Given the foregoing discussions and insights about biodiversity in estuaries, we have formulated an embryonic hypothesis about the relationship of biodiversity to the scale and predictability of the environment. This hypothesis may be useful in sorting out the value of biodiversity, both to the ecosystems themselves and to human consumers of ecosystem services, and to devising better policies and management systems (27, 28).

In the discussion that follows, we employ the 4-box model of Holling (29, 30). Holling proposes four basic functions common to all complex systems and a spiraling evolutionary path through them (Fig. 3). The functions (boxes) are: i) *Exploitation* (r-strategists, pioneers, opportunists, entrepreneurs, etc.); ii) *Conservation* (K-strategists, climax, consolidation, rigid bureaucracies, etc.); iii) *Release* (fire, storms, pests, political radicals, etc.); and iv) *Reorganization* (accessible nutrients, abundant natural resources, etc.). Within this model, systems evolve from the rapid colonization and exploitation phase, during which they capture easily accessible resources, to the conservation stage of building and storing increasingly complex structures. Examples of the *exploitation phase* are early successional ecosystems colonizing disturbed sites or pioneer societies colonizing new territories. Examples of the *conservation phase* are climax ecosystems or mature, large bureaucracies. The *release* or *creative destruction phase* represents the breakdown and release of these mature structures via aperiodic events like fire, storms, pests, or political upheavals. The released structure is then available for *reorganization* and uptake in the exploitation phase. The amount of ongoing release or creative destruction that takes place in the system is critical to its behavior. The *conservation phase* can often build elaborate and tightly bound structures by severely limiting creative destruction—the former Soviet Union is a good example—but these structures become brittle and susceptible to massive and widespread destruction. If some moderate level of release is allowed to occur on a more routine basis, the destruction is on a smaller scale and leads to a more resilient system. Creative destruction, in terms of shocks or surprises, seems to be crucial for system resilience and integrity. Similarly, it has been argued that episodic events, such as the Chernobyl accident, the Rhine chemical spill, the death of seals in the North Sea, are shocks to the social-cultural value system and may stimulate change towards more resilient ecological economic systems (31).

Fire climax systems such as the pine forests of Yellowstone

Figure 3. The Holling 4-box model. Source: (29, 30).



Extensive shoreline development in Annapolis, Maryland, USA.
Photo: M.J. Reber.



National Park are a good example of the range of possibilities for creative destruction. In its unmanaged state, Yellowstone burned over extensive areas relatively often, but because of the high frequency the amount of fuel was insufficient to allow highly destructive fires. The more frequent, small to moderate size fires would release nutrients stored in the litter and support a spurt of new growth without destroying all the old growth. On the other hand, if fires are suppressed and controlled, fuel builds up to high levels and when the fire does come it wipes out the entire forest.

Estuaries, in this context, are awash in creative destruction due to the strong physical forces of tides and currents that dominate this unpredictable environment. They are constantly reset to the exploitation phase and rarely build up enough structure to make it to the conservation phase. They are resilient, low taxonomic diversity systems. Only systems with relatively predictable environments can build and maintain a diverse set of specialist species. Tropical rainforests and coral reefs are the extreme case of both environmental predictability and biodiversity. In this view a stable environment allows biodiversity to develop, rather than the reverse argument, that high biodiversity leads to a more stable ecosystem response. But the process is seen as a feedback loop. Ecosystems in unpredictable environments at one scale can build structures at a larger scale to smooth out and stabilize that unpredictability. For example, forests build structure to smooth out lower scale unpredictability. But this process can be tampered with, e.g. the Yellowstone forest fire management policy, by artificially reducing the amount of release or creative destruction, and the system can become brittle.

In estuaries the unpredictability is at several scales, including the large scales, and the organisms usually cannot build large biostructures and therefore the system remains at a relatively low diversity. An exception which proves the rule is the case of artificial structures like bridge pilings, on which diverse biological communities do grow because of the smoothing effect of the artificial structure. To a lesser extent, seagrasses and oyster reefs are also exceptions that prove the rule. To the extent that organisms can establish and maintain fixed structure in the face of the large and unpredictable physical forces in estuaries, they can

begin to counter the unpredictability and support specialization and diversity. But even oyster reefs and seagrass beds are fairly low diversity systems that occur only in special conditions within the estuaries. Oyster reefs rely on the large and unpredictable changes in salinity in estuaries to keep them free of disease organisms and intense predation. Seagrass beds are very sensitive to nutrient enrichment and turbidity.

Estuaries do have high functional diversity, however, and high resilience. Figure 4 summarizes our view of estuaries and their relationship with their physical environment. The top half of the diagram shows the effects of the high variance, low predictability physical forces driving estuarine ecosystem dynamics with high efficiency secondary production and high fisheries yields. The bottom half of the diagram shows the effects of the physical forces and linkages with ecosystem dynamics on ecosystem structure, with low taxonomic diversity, moderate biomass, and high functional diversity. Large and unpredictable physical forces cause structural losses and keep high taxonomic diversity from developing, but also enhance productivity.

From this analysis of estuaries we have developed an hypothesis about the general relationship of resource predictability to scale and biodiversity. The biodiversity (or taxonomic diversity) in a system is a function of the predictability of the resource environment on the time and space scales at and above the scale of the system of interest. Smaller scale unpredictability can be filtered out by the structure of the system. All else being equal, the higher the predictability of the environmental resources and forcings, the higher the biodiversity that can potentially develop in an attempt to maximize the efficiency of use of these resources. The absolute amount of biodiversity is limited by the absolute size of the resources and forcings. The system can also be tampered with by artificially restricting the relationship between structure and predictability as in the Yellowstone and the former Soviet Union. These attempts lead to brittle systems that ultimately collapse, however.

We think that the above hypothesis is testable using comparative analysis of various systems' resource predictability, diversity, and structural dynamics over several scales. It is applicable to both

economic and ecological systems and may help us to better understand the role of diversity in systems performance and value—a key issue in modern conservation policy.

MANAGING COASTAL AND ESTUARINE ECOSYSTEMS

Estuaries in general have rather low biodiversity, but are nonetheless very productive and resilient ecosystems. Because of the dominance of large, unpredictable physical forces in estuaries, and the lack of a stable base on which to build biological structure to smooth out this unpredictability, these systems are dominated by a relatively few generalist species. The economic value of estuaries focuses on these few species. For example, in the Chesapeake the American oyster, striped bass, American shad, and blue crab have been economically important species for both commercial and recreational fisheries (32–34).

Estuaries are generally open-access resources, and this fact, combined with the relatively high unpredictability of physical forces and living resource stocks, and the rapidly growing coastal population, has led to overexploitation and eventual decline of critical organisms and processes, as discussed above. How do we manage these ecosystems in light of their special ecological characteristics? Assigning private property rights has met with only very limited success in these systems because of the difficulty of preventing the use of resources by other than their owners. Leased oyster beds have been fairly successful in some locations, e.g. in Louisiana, because it is possible with relatively small enforcement costs to exclude non-owners from harvesting the oysters from these beds. But, in general, because of the unpredictability and mobility of estuarine resources, it is very difficult to assign and enforce property rights, and it is difficult to assess when the resilience of the system has been stretched to the breaking point.

A fundamental reason for the mismanagement of these systems is the inherent mismatch between the characteristics of the ecological system on the one hand and of the human institutions

developed to manage it on the other. Our management institutions have largely been based on systems of private property rights adapted from terrestrial systems and agriculture, and assume a relatively high degree of predictability. But, as we have noted, these rights are difficult to define and enforce in estuaries and unpredictability is the norm. One critical feature is the incentive structures that these institutions produce. Society's response has been to develop systems of direct regulation of the potentially damaging activities like fishing. But the incentive structures these regulatory systems produce often lead to behavior that is directly counter to the long-term health of the whole system, and often even to the stated goals of the institution itself. How does this happen and how can we fix it?

SOCIAL TRAPS

This process of short-run and local incentives moving out of sync with long-term and global goals has been well studied in the last decade under several rubrics (35, 36), but one particularly effective representation is John Platt's notion of "social traps" (37–41). In all such cases the individual decision-maker may be said to be 'trapped' by the local conditions into making what turns out to be a bad decision viewed from a longer or wider perspective. People go through life making decisions about which path to take based largely on road signs, i.e. the short-run, local reinforcements that we perceive most directly. These short-run reinforcements can include monetary incentives, social acceptance or admonishment, and physical pleasure or pain. In general, this strategy of following the road signs is quite effective, unless the road signs are inaccurate or misleading. In these cases we can be trapped into following a path that is ultimately detrimental because of our reliance on the road signs. For example, overfishing is a social trap because by following the short-run economic road signs, fishermen are led to exploit the resource to the point of collapse.

The elimination of social traps requires intervention; the modification of the reinforcement system. Indeed, it can be argued that the proper role of a democratic government is to eliminate social traps, no more and no less, while maintaining as much individual freedom as possible. Cross and Guyer list four broad methods by which traps can be avoided or escaped from. These are education about the long-term, distributed impacts; insurance; superordinate authority, i.e. legal systems, government, religion; and converting the trap to a trade-off, i.e. correcting the road signs.

Education can be used to warn people of long-term impacts that cannot be seen from the road. Examples are the warning labels now required on cigarette packages and the warnings of environmentalists about future hazardous waste problems. People can ignore warnings, however, particularly if the path seems otherwise enticing. For example, warning labels on cigarette packages have had little effect on the number of smokers.

The main problem with education as a general method of avoiding and escaping from traps is that it requires a significant time commitment on the part of individuals to learn the details of each situation. Our current society is so large and complex that we cannot expect even professionals, much less the general public, to know the details of all the extant traps. In addition, for education to be effective in avoiding traps involving many individuals, all the participants must be educated, and this is usually not possible.

Governments can, of course, forbid or regulate certain actions that have been deemed socially inappropriate. The problem with this direct, *command-and-control* approach is that it must be rigidly monitored and enforced, and the strong short-term incentive for individuals to try to ignore or avoid the regulations remains. A police force and legal system are very expensive to maintain, and increasing their chances of catching violators increases their costs exponentially, both the costs of maintaining a larger, better-

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The Institute was established in 1991 as one of the research institutes of the *Royal Swedish Academy of Sciences*, to promote interdisciplinary research between ecologists and economists. The objective of the Institute is to improve our understanding of the links between economic and ecological systems, in order to ameliorate the management of these interconnected systems. The Institute brings together leading scholars from economics, ecology and related disciplines in a number of research programs. The first four programs relate to the *Ecology and Economics of Biodiversity Loss*, *Complex Ecological Economic Systems Modelling*, *Property Rights and the Performance of Natural Systems* and *The Baltic Drainage Basin*. The Institute also organizes training workshops and international research seminars on environment and development, and international training programs. Professor Karl-Göran Mäler is Director of the Institute. For further information please contact Ms Christina Leijonhufvud, *The Beijer International Institute of Ecological Economics*, Royal Swedish Academy of Sciences, Box 50005, S-104 05 Stockholm, Sweden.

equipped force and the cost of the loss of individual privacy and freedom.

Religion and social customs can be seen as much less expensive ways to avoid certain social traps. If a moral code of action and belief in an ultimate payment for transgressions can be deeply instilled in a person, the probability of that person's falling into the "sins" (traps) covered by the code will be greatly reduced, and with very little enforcement cost. On the other hand, the problems with religion and social customs as means to avoid social traps are that the moral code must be relatively static to allow beliefs learned early in life to remain in force later, and it requires a relatively homogeneous community of like-minded individuals to be truly effective. This system works well in culturally homogeneous societies that are changing very slowly. In modern, heterogeneous, rapidly changing societies, religion and social customs cannot handle all the newly evolving situations, nor the conflict between radically different cultures and belief systems.

Many trap theorists believe that the most effective method for avoiding and escaping from social traps is to turn the trap into a trade-off. This method does not run counter to our normal tendency to follow the road signs; it merely corrects the signs' inaccuracies by adding compensatory positive or negative reinforcements. A simple example illustrates how effective this method can be. Playing slot machines is a social trap because the long-term costs and benefits are inconsistent with the short-term costs and benefits. People play the machines because they expect a large short-term jackpot while the machines are in fact programmed to pay off, say, USD 0.80 on the dollar in the long term. People may win hundreds of dollars playing the slots in the short run, but if they play long enough they will certainly lose USD 0.20 for every dollar played. To change this trap to a trade-off, one could simply reprogram the machines so that every time a dollar was put in USD 0.80 would come out. This way the short-term reinforcements, USD 0.80 on the dollar, are made consistent with the long-term reinforcements (USD 0.80 on the dollar), and only the dedicated aficionados of spinning wheels with fruit painted on them would continue to play.

Modifying Incentives for Improved Management

In the context of social traps, the most effective way to make global and long-term goals consistent with local, private, short-term goals is to somehow modify the local, private, short-term incentives (37-41). These incentives are any combination of the reinforcements that are important at the local level, including economic, social, and cultural incentives (42). We must design the social and economic instruments and institutions to bridge the gulf between the present and future, between the private and social, between the local and global, between the ecological and economic parts of the system.

One policy that has often been recommended, and which is consistent with this idea of modifying local incentives, is the "polluter pays principle." This principle would require the payment of pollution taxes (43) to account for the damages to ecological systems by private polluters or resource users. One factor limiting the adoption of this approach has been the high degree of uncertainty and unpredictability associated with ecological damages. How big should the tax be? If it is too low the polluters are not paying

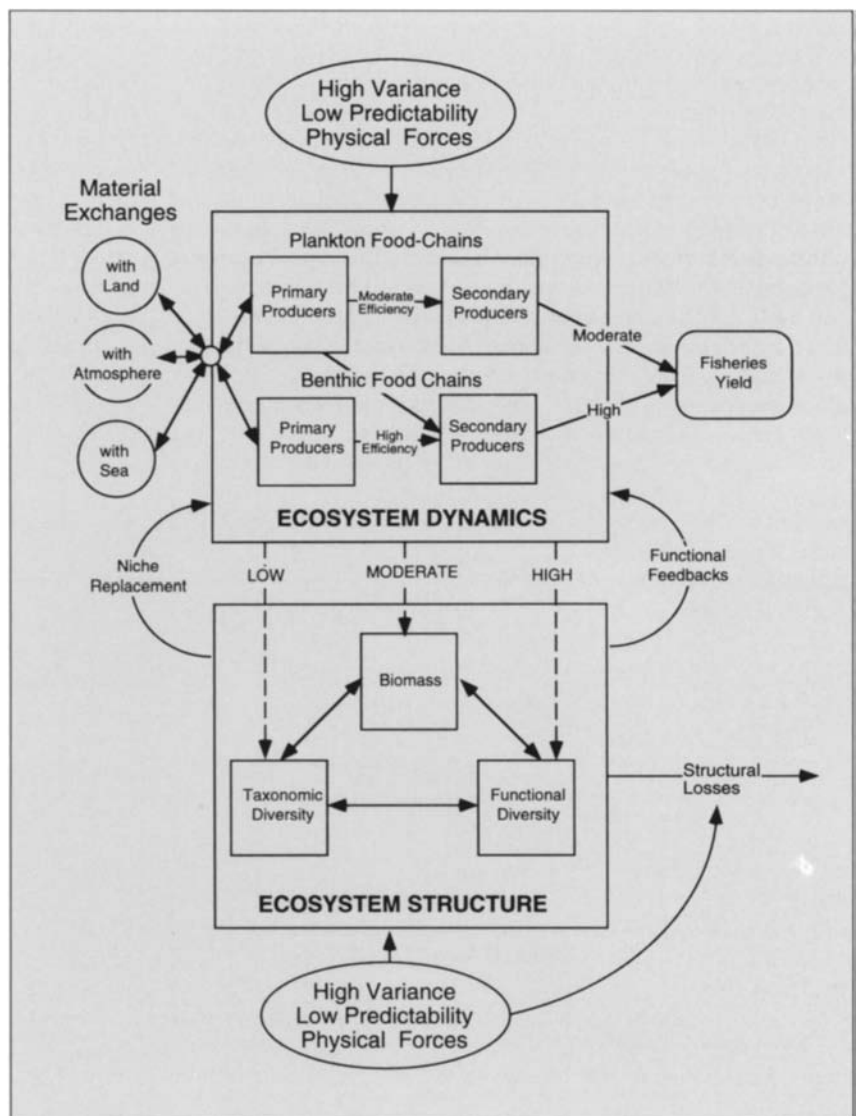


Figure 4. Conceptual diagram of the relationships between physical forcings and ecosystem structure and dynamics in estuaries.

the full cost to society and will continue to overpollute. If it is too high the polluters will be subsidizing society and the cost of their products will be too high.

One way to handle this uncertainty about the true damages is the idea of a flexible environmental assurance bonding system (44, 45). This variation of the deposit-refund system is designed to incorporate environmental criteria and uncertainty into the market, and to induce positive environmental technological innovation. It works in this way: in addition to charging for known environmental damages, an assurance bond equal to the current best estimate of the largest potential future environmental damages, would be levied and kept in an interest-bearing escrow account for a predetermined length of time. In keeping with the precautionary principle, this system requires the commitment of resources now to offset the potentially catastrophic future effects of current activity. Portions of the bond, plus interest, would be returned if and only if the agent could demonstrate that the suspected worst case damages had not occurred or would be less than originally assessed. If damages did occur, a portion of the bond would be used to rehabilitate or repair the environment, and possibly to compensate injured parties. By requiring the users of environmental resources to post a bond adequate to cover uncertain future environmental damages, with the possibility for refunds, the burden of proof and the cost of the uncertainty is shifted from the public to the resource user. At the same time, agents are not

charged in any final way for uncertain future damages and can recover portions of their bond in proportion to how much better their performance actually was compared with the worst case.

Deposit-refund systems, in general, are not a new concept. They have been effectively applied to consumer policy, conservation policy, and other efficiency objectives. Deposit-refund systems can be market generated or government initiated and are often performance based. For example, deposit-refund systems are currently effectively used to encourage the proper management of beverage containers and used lubricating oils (46).

Strong economic incentives are provided by the bond to reduce pollution, to research the true costs of environmentally damaging activities, and to develop new innovative, cost-effective pollution control technologies. The bonding system is an extension of the "polluter pays principle" to "the polluter pays for uncertainty as

well" or the "precautionary polluter pays principle" (4P) (43). It would allow a much more proactive, rather than reactive, approach to environmental problems because the bond is paid up front, before the damage is done. It would tend to foster prevention rather than cleanup by unleashing the creative resources of agents on finding more environmentally benign technologies since these technologies would also be economically attractive. Competition in the marketplace would lead to environmental improvement rather than degradation. The bonding system would deal more appropriately with scientific uncertainty and the inherent unpredictability of ecosystems.

The 4P approach has several potential applications. Any situation with large, true uncertainty is a likely candidate, and these situations abound in the modern world, especially in ecosystem management and especially in managing coastal and estuarine ecosystems.

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