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The Importance of the Natural Sciences to Conservation

(An American Society of Naturalists Symposium Paper)*

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ABSTRACT: The last century has seen enormous environmental degradation: many populations are in drastic decline, and their ecosystems have been vastly altered. There is an urgent need to understand the causes of the decline, how the species interact with other components of the environment, and how ecosystem integrity is determined. A brief review of marine systems emphasizes the importance of natural sciences to understanding the systems and finding solutions. These environmental crises coincide with the virtual banishment of natural sciences in academe, which eliminate the opportunity for both young scientists and the general public to learn the fundamentals that help us predict population levels and the responses by complex systems to environmental variation. Science and management demands that complex systems be simplified, but the art of appropriate simplification depends on a basic understanding of the important natural history. It seems unlikely that meaningful conservation and restoration can be accomplished unless we recover the tradition of supporting research in and the teaching of natural history. We must reinstate natural science courses in all our academic institutions to insure that students experience nature first-hand and are instructed in the fundamentals of the natural sciences.

Keywords: conservation, ecosystem, education, fisheries, natural history, recoverability, restoration, stability, taxonomy.

On-line enhancements: color versions of photographs.

Our biosphere faces an increasing rate of biological extinctions and ecosystem alterations resulting from human impacts. In many cases, species become extinct even before they are described. The past few decades have seen growing concern in the scientific community, with the concurrent development of specializations in theory, molecular biology, and restoration ecology. Almost a decade ago, Graeme Caughley (1994) observed that conservation biology had split into two lines of research. He identified the first as a paradigm focusing on the generic effects of small populations declining or becoming isolated. Caughley observed that powerful molecular and theoretical tools with easily defined questions and objectives have recently dominated the field, have received almost all the financial support, and have resulted in many publications and careers vested in this line of research. The groups working on molecular biology and theoretical ecology have been highly successful within their own circles and have branched into many specialties. These specialists have produced many breakthroughs important to those respective fields. However, Caughley also observed that this reductionist approach has contributed rather little toward actual solutions for the increasingly severe global realities of declining populations, extinctions, or habitat loss.

The second line of research discussed by Caughley addresses the difficult problem of why populations are in decline in the first place. It is here where real solutions must be found, and this progress must rely on a profound understanding of taxonomy, natural history, and complex ecosystem dynamics. While extremely important, this line of thinking and research has fallen from favor in academe.

Conservation and Restoration

Populations decline for a variety of reasons, and we have a rich history of debating the ecological processes that determine the distribution and abundance of individuals within a population. The debate includes disputes about the relative roles of density-independent and -dependent factors, the importance of inter- and intraspecific competition, predation, parasites, and mutualistic relationships. Ecosystem re-

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search has produced another rich history focusing on fluxes and large-scale generalized dynamics. There is a decoupling between the two lines of classical ecology (population and ecosystem approaches), and this disconnect has retarded progress. Depressingly, it seems that much of this debate also has been divorced from the applied literature, and academics have fiddled while the natural world they argue about has burned.

We need to stand back and to consider some of the important questions and processes urgently in need of study. The following list is a small sample of some of the basic issues that need far better understanding. The reader is encouraged to contemplate whether such understanding can be achieved without careful research in natural history.

Cumulative Effects: How Much Is Too Much? What Defines Limits and Thresholds?

What describes species vulnerability? Are some species redundant and expendable? Can cumulative impacts of human perturbations be predicted?

Ecosystem or Habitat Stability and Recoverability

How do we define and measure stress in multispecies systems? How do we define habitat or ecosystem stress? How do we define system collapse? Why do systems collapse? What are the thresholds? What are the processes that maintain stability? What are the processes that define recoverability? What are the processes that define strong and weak interactions?

Trend Analysis

How do we differentiate human-induced trends from natural ones? What determines whether trends are general or peculiar to particular systems? What spatial and temporal scales are appropriate for such trend analysis? How can society acquire trend data from already perturbed systems?

Restoration Ecology

How do we define the desired state? What are realistic goals? How are they determined? How should we manipulate succession processes that are little understood? What are the most efficient means of restoration? How do we value species in mitigation considering mixtures of endemic and invasive species?

These and many similar issues and questions must be understood if we hope to recover our natural heritage. No monitoring or restoration ecology programs can succeed if they are not based on appropriate questions. Such questions must be defined and prioritized, and this absolutely depends on excellent natural history, systematics with voucher collections, and careful field research.

Selected Marine Ecosystems at Risk

Marine biota are remarkably diverse. Of >50 phyla on the earth, only one (the Onychophora) is strictly terrestrial; all the rest have marine representatives. Interestingly, all of these phyla had differentiated by the dawn of the Cambrian, almost 600 million years ago, and all evolved in the sea. Since that time, the sea has been frozen, has experienced extensive anaerobic conditions, has been blasted by meteorites, and has undergone extensive sealevel variations. The sea has been fragmented and coalesced, resulting in a plethora of habitats. The present diverse biota reflect the combination of historical events coupled with physical, chemical, and biological dynamics. Far less is known about marine species than about terrestrial. Not even the actual species diversity in the ocean is known; only tiny fractions of the species have been described (National Research Council 1995). One of the rare recent efforts to sample all of the mollusk species at a tropical site found 2,738 species of marine mollusks in a limited area near New Caledonia (Bouchet et al. 2002).

In contrast to terrestrial systems, many marine species are in decline because of directed killing: the goals of many fishery management plans are to reduce populations well below the criteria for World Conservation Union listing. Though an obvious and immediate first step is to stop killing so many animals, the solutions to most of the questions listed above are not obvious and are based on understanding the ecosystems of multiple species. Managing people in a way that protects ecosystems has proven extremely difficult, largely because we know so little about how marine ecosystems function.

Bottom habitats in the ocean include a gradient of substrata—from cliffs, cobbles, and boulders to soft sediments ranging from gravels to fine muds. The substrata define the general benthic habitats. Most of these habitats are characterized by biological construction in which the organisms provide structures that are critical to many other parts of the ecosystem. Examples include reefs of mussels, oysters, sponges, and corals with roles that include filtering the seawater and affecting its flow while creating a biological structure that furnishes critical habitats and predator protection to new recruits. The architectural complexity supports a diverse association of feedback loops that define the biological complexity of seafloor processes. These important ecological roles are as yet poorly understood.

I briefly consider selected marine systems at risk and suggest the types of information needed to solve ecological problems. Different habitats have different problems—bioturbation in some, ecosystem functioning in others, and cascading effects of selected removals in others. The following summaries of benthic marine ecosystems are presented with the objective of demonstrating how much they differ and how hard it is to generalize between these systems. The next section will review common processes that need much better understanding.

Estuaries and Coastal Wetlands

Estuaries and coastal wetlands are critical transition zones linking the land and sea (see review by Levin et al. 2001). Important nutrient cycling and fluxes, primary and secondary productivity, nursery areas, and critical habitats of many birds and mammals are examples of essential services provided by these once ubiquitous habitats. Most of these functions are mediated via sediment-associated biota, including macrophytes (mangroves, salt marsh plants, and sea grass beds, as well as macro algae), heterotrophic bacteria and fungi, and many invertebrate taxa. Vascular plants regulate many aspects of the nutrient, particle, and organism dynamics both below- and aboveground and provide critical habitats for many species of animals. Retention of deposited materials is enhanced by the stabilization provided by these plants as they constitute structurally complex habitats offering refugia and other nursery services for larvae and juveniles of many species.

The invertebrates have countless roles, including shredding and recycling organic debris, both marine and terrestrial; they resuspend organic material and transport it across the water-sediment interface. For example, some 90% of particulate organic matter entering the coastal zone is transferred to the sediments by flocculation, adsorption, and physical deposition that occurs where fresh and salt water meet (see Levin et al. 2001). Bioturbation oxygenates the sediment and moves material into and out of the seabed. Importantly, a wide variety of animals move in and out of this habitat for many reasons, including completion of life cycles, feeding, using larval nurseries, and migration. The bioturbation itself is an important structuring mechanism providing mounds and depressions, both of which are critical habitats to hundreds of small invertebrate species.

An appalling litany of anthropogenic impacts have virtually eliminated this essential estuarine habitat in many areas. These impacts and their consequences include eutrophication, nonnutrient pollutants, overfishing, invasions of exotic species, and most importantly, the loss of essential habitat and the loss or destruction of almost all of the watershed. Poor management of watersheds, including poor grazing practices that destroy natural riparian habitats, results in floods and the burial of natural habitats under silt and enriched sediment. Often these impacts combine with nutrient loading, which causes large coastal areas to become anoxic. An extreme example is the massive (to 15,000 km^2) dead zone in the Gulf of Mexico (Turner and Rabalais 1994). Urbanization of watersheds interrupts the flow of both essential fresh water and nutrients. Nutrient loading and eutrophication cause prolonged ecological degradation as algae take over bottom habitats and the water column and alter entire ecosystems (Levin et al. 2001). Restoration depends on sensitivity to facilitative and inhibitory succession, processes that cannot be understood without detailed life histories.

Estuarine systems are among the most invaded ecosystems in the world (e.g., San Francisco Bay has >210 exotic species, many of which are now dominant). Grosholz (2002) reviewed the ecological consequences of invasions, which include habitat loss and alteration, altered water flow and food webs, the creation of novel and unnatural habitats subsequently colonized by other exotic species, abnormally effective filtration of the water column, hybridization with native species, highly destructive predation, and pathogenic disease. The natural processes that bestow resistance to invasion are complex and virtually unknown. For example, in many cases the exotic species exist as very rare members of the fauna for decades and are suddenly ecologically released, and we have no understanding of such processes. Indeed, without excellent taxonomy and voucher specimens, we would not know to ask such important questions.

Rocky Intertidal Systems

Because it has been subject to extensive small-scale experimentation, local processes in rocky intertidal systems are among the best-understood marine communities in the world. Here, I compare representative communities from the U.S. Pacific coast to emphasize ecological differences. These communities are characterized by patch dynamics based on frequent disturbance, effective dispersal, and both inhibitory and facultative succession. Strong and weak interactions are well studied at small scales (Paine 2002). However, there is a dearth of understanding of when and why these mechanisms work in some areas but not in others. Conspicuously lacking in most systems is an appreciation of the large-scale processes that define the more fundamental and generic questions. Generalizations based on very small-scale research often are not accurate on a large scale. Furthermore, discerning the differences between direct human impacts and natural changes or changes related to regional or global change will prove very difficult. For example, in central California, Barry et al. (1995) capitalized on an opportunity to resample a much earlier study based on permanent quadrates and excellent taxonomy. They found that warm-water species increased and cold-water species disappeared from the quadrates; they associated these changes with ocean warming.

The rocky intertidal habitats in southern California differ from those in the northeast Pacific since they are characterized by extensive patches of algal turf mixed with classical mussel associations in which the predator *Pisaster* once appeared important. But more important than *Pisaster* were lobsters foraging over the turf, removing mussels (Robles 1987), and helping prevent the turf from being overgrown by the once ubiquitous mussel *Mytilus californianus*. In many cases, there seem to be two community types in southern California: an algal turf community and relatively bare rock with chitins and limpets and patches of barnacles, mussels, and fucoids. The algal turf is maintained by a few species of articulated coralline algae that trap sand, resist sand burial, and offer a substratum for almost 100 species of small fleshy algae (Stewart 1982). The chitins and limpets prevent expansion of the algal turf by maintaining relatively clean rock surfaces that tend not to accumulate sand. Food and bait collection and human trampling have substantially depleted the mussels and rockweeds (Murray et al. 1999, 2001; Smith 2003). Presently, *M. californianus* is very rare and *Pisaster* is almost never seen (Engle and Davis 2000). In addition, the abundant black abalone (*Haliotis cracherodii*; fig. 1) is practically absent from southern California, as are some dozens of species of formerly abundant nudibranchs, none of which can be found without very extensive searches. Similar trends have been observed elsewhere (e.g., Keough and Quinn 1998).

Kelp Systems

The productivity of kelp ecosystems rivals that of the most productive land systems. These systems characterize temperate coastal habitats, and they are remarkably resilient to natural disturbances. They are highly diverse systems organized around large brown algae, where the complex biological structure supports a high diversity of species and interactions; they support fisheries of a variety of invertebrate and finfish, and the kelps themselves are harvested.

Kelp communities consist of several distinct canopy types and are patchy in many dimensions. There are many herbivores, but the most important are sea urchins capable of overgrazing nearly all fleshy algae in most kelp systems. Factors affecting the abundance of sea urchins and the kelps themselves are important to the integrity of kelp ecosystems. In almost all kelp systems, overfishing the predators results in sea urchin barrens varying in size and covering anywhere from hectares to >1,000 km of coastline. In southern California, sea urchin predators that were functionally removed included first sea otters and then very large lobsters (fig. 2) and sheepshead, a fish in which the large males have been heavily exploited. Unfortunately, the animal populations in the kelp forests are destabilized by fishing to such an extent that they retain only ghosts of their former diversity (Dayton et al. 1998; Tegner and Dayton 2000).

Figure 1: Black abalones on Santa Rosa Island, California, before succumbing to a disease. Early divers reported pavements of abalones and said they could capture 1–2 tons per dive. Abalones at such densities profoundly alter space allocation; they possibly prevented the formation of sea urchin barrens. Credit: Gary Davis, U.S. National Park Service.

The paradigm of fishing's impact on coastal habitats cascading down to much simplified sea urchin–dominated barren grounds has proven to be very general (Sala et al. 1998; Steneck 1998), but the actual mechanisms vary across systems. No kelp system is pristine, and humans have vastly reduced expectations of how the systems should exist. Hence we can conclude that there often are enormous system responses to human impacts, but without integrated retrospective and community understanding, we have little chance to understand and to correct the changes. In southern California, once abundant large fish such as the black sea bass (fig. 3) are now extremely rare. Black sea bass were bottom feeders that may have consumed young lobsters and fish such as sheepshead, two of the species that are important predators of urchins. It is impossible to understand ecosystem functions from archival photographs. Large northwest Atlantic fish such as halibut, wolfish, and cod are key predators of sea urchins, and these predators also have been largely removed from the system; as a result, sea urchin populations exploded (Witman and Sebens 1992; Steneck 1998). More recently, directed exploitation and disease have led to a collapse of the urchin populations, leaving a once healthy and productive ecosystem characterized by waves of exotic species (Harris and Tyrell 2001).

Restoration and subsequent management should be based on understanding the sources of propagules of the

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2*B*

Figure 2: The large lobsters (*A*) were extremely important predators, capable of eating all the other shellfish, including sea urchins. While a fishery continues in California, the very large lobsters with their ecological roles are missing. In addition, it is obvious that the catch in the first part of the century (*B*) was much larger than it is now. These lobsters also had important ecological roles, now much diminished. Credit: (*A*) Jim Steward ("Children's Pool, 1948"; photo, Lamar Boven) and (*B*) San Diego Historical Society, Photograph Collection ("Coronado Lobster Dump, may actually be Rosarito Beach in Baja, California, a few kilometers south of San Diego, ca. 1915").

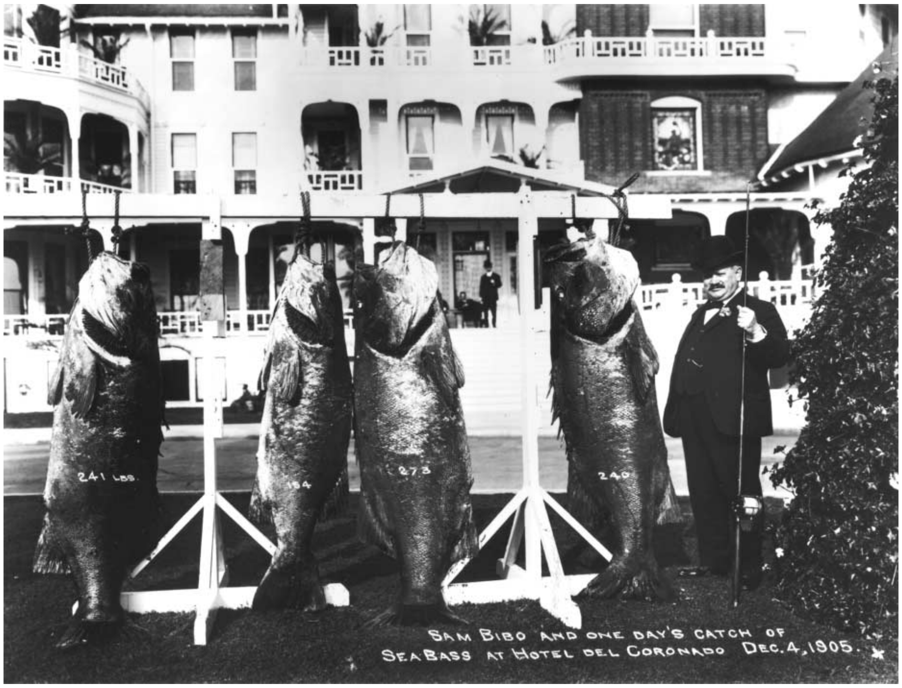


Figure 3: Popular literature at the turn of the century reported that large numbers of sea bass were routinely captured in the southern California kelp forests. There is no way of guessing the ecological roles that they maintained in the kelp systems, but it is likely that they consumed small lobsters and sheepshead. Their removal may have resulted in interesting cascading effects. Credit: San Diego Historical Society, Photograph Collection ("Sam Bilbo and One Day's Catch of Sea Bass at Hotel del Coronado, December 4, 1905").

target species, and understanding propagule sources requires understanding the strong interactions (Sala and Graham 2002) and a definition of the target species in urgent need of management. There is an urgent need to understand better the Allee effect (the need for concentrations of reproduction aggregations), in which sources of propagules and the population thresholds in their respective spawning aggregations are defined. It is important to distinguish between larval nurseries and sinks and the relative abundance of each. A clear understanding of successional processes is also important.

Encrusting Associations on Subtidal Rocky Habitats

Hard-bottom habitats below the photic zone tend to be dominated by sponges, corals, bryozoans, and compound ascidia. The architectural complexity provided by these colonies of organisms attracts other species, provides them refuge from predators, and generally plays an important role in maintaining the biodiversity and biocomplexity of seafloor habitats. In the more stable habitats, these species are usually clones and long-lived individuals, and the associations are stable over decades and perhaps centuries. The populations are marked by very low dispersal, often with larvae that crawl only centimeters. These relatively stable associations are characterized by extreme resistance to competition, invasion, or predation (reviewed in Dayton 1994). These encrusting communities differ from other marine habitats in many ways. For example, while there is not much free space, poor competitors for primary space depend on other tactics, such as long-term survival during periods of overgrowth, asexual division, clever larval settlement, growth adaptations including vinelike growth, or simply reduced attachments with siphons or tentacles above the overgrowth.

While encrusting species tend to be protected by chemical defenses, they have a wide array of predators. Some predators, such as sea stars, sea urchins, fishes, and some snails, are generalists; most, especially nudibranchs and lamellarians, are specialists. In general, however, predators do not have limiting effects on their prey populations. Indeed, they rarely kill entire clones. While they are robust to natural disturbances from predation, competition, and biofouling, the fact that the species in this system tend to have extremely limited larval dispersal means recolonization and recovery following a disturbance can be very slow. The recovery dynamics depend on the size of the disturbance relative to the dispersal patterns (Lissner et al.

1991). The communities recover from small disturbances via lateral growth and short-dispersing larvae in such a way that recovery is from the margins of the disturbance. Alternatively, those communities subjected to large disturbances, such as widespread damage from fishing gear, may need centuries to recover, if they ever do.

Encrusting communities often appear to have several examples of alternative stable states that are self-perpetuating in the face of normal disturbances (Sebens 1986). The mechanisms include powerful, often chemical, defenses against predation and biofouling, asexual reproduction or nondispersing larvae, and the ability to protect juveniles from predation. Overfishing along the coastal zone greatly reduces the top predators and releases their prey from predation, especially crustaceans and echinoderms (Witman and Sebens 1992). This in turn has changed much of the community structure. Aronson (1991) argues that this overfishing has virtually eliminated many evolutionarily "new" predators and caused a "rebirth" of the Mesozoic communities dominated by echinoderms. The natural processes involved in such large-scale system responses are not known.

The deepwater edges of continental shelves may once have been dominated by massive bioherms of deepwater corals, including over 670 species of deepwater corals that may tower >40 m above the sea floor (Cairns 1999). These intricate reefs furnish critical habitat to hundreds of species of other animals (Rogers 1999). Obviously, these systems are highly vulnerable to trawling (Fossa et al. 2002) and are now relatively rare. The vast expanse of the deep ocean floor's soft sediment is interrupted in places by highly structured seamounts. The fauna of these seamounts often differ greatly from that found on soft sediments because the presence of hard substrata projected above the sea floor and of the intensified currents around these projections supports very long-lived suspension-feeding corals. These corals offer structure to very diverse communities of associated species (fig. 4). A brief survey of Tasmanian seamounts, for instance, found hundreds of species, about 30% new to science, and some 30%–60% endemic to the seamount (Koslow et al. 2001).

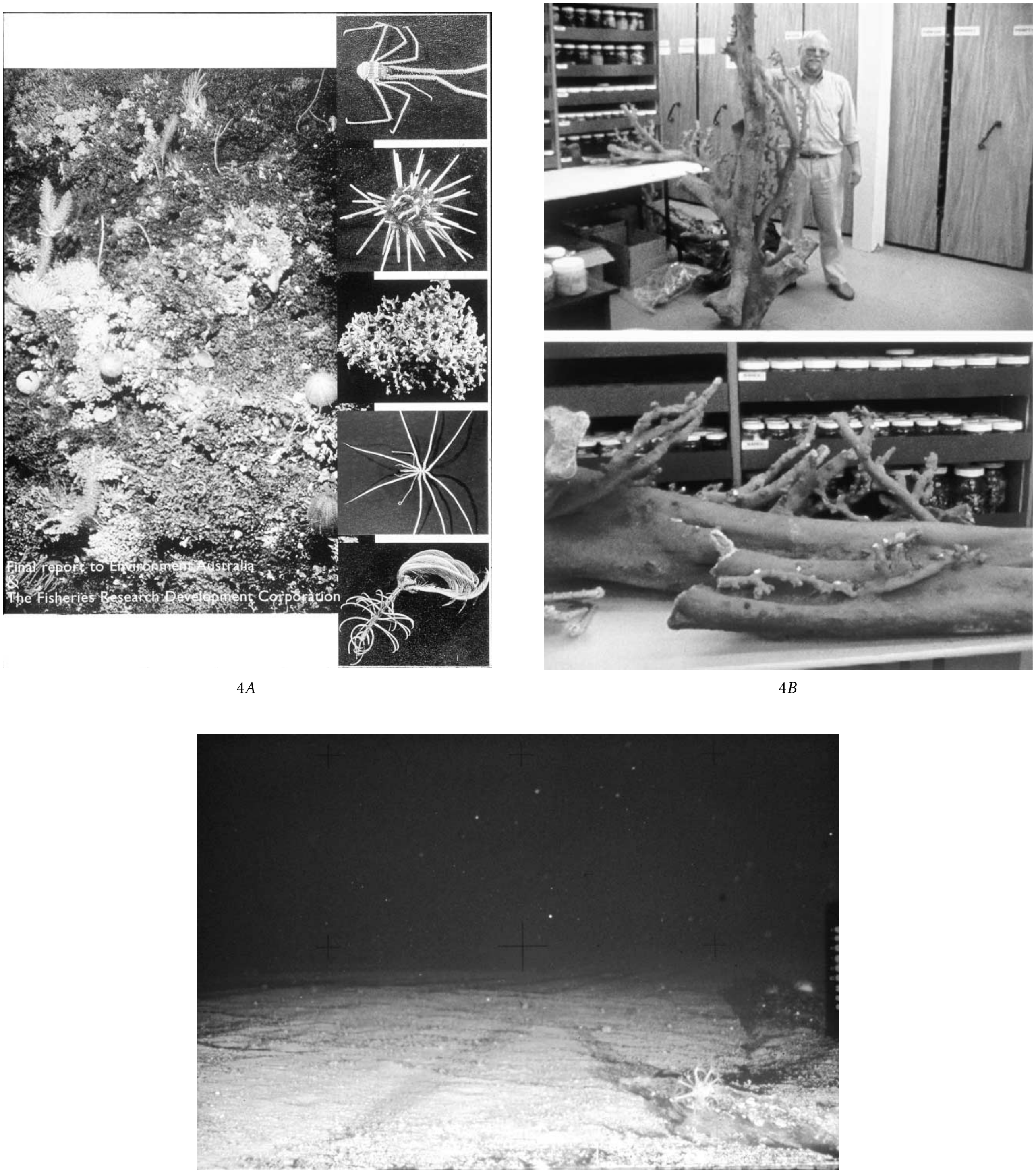
Soft-Bottom Ecosystems

About 70% of the earth's seafloor is composed of soft sediment. In coastal and continental shelf environments, habitats can be highly heterogeneous owing to both broad-scale factors (e.g., hydrodynamic and nutrient regimes) and smaller-scale physical and biological features. Although soft-sediment habitats do not always appear as highly structured as some terrestrial or marine reef habitats, they are characterized by extremely high species diversity. In fact, the organisms that live in sediments often create much of the structure in soft-sediment habitats, ranging from the microscale changes around individual animal burrows to the formation of extensive biogenic reefs (Thrush and Dayton 2002).

Apart from their extremely high species diversity, soft-sediment marine organisms have crucial functional roles in many biogeochemical processes that sustain the biosphere. Within the sediments, microbial communities drive nutrient recycling, while the movement, burrowing, and feeding of organisms such as worms, crabs, shrimps, and sea cucumbers markedly increase the surface area of sediment exposed to the water column, thus recycling nutrients back into the water column where they can again fuel primary production. Organic debris produced on the continental shelf finds its way to the shelf edge, where it accumulates in canyons that act as sinks to the deep ocean. There, it supports extremely high densities of small crustaceans that in turn serve as prey for both juvenile and mature fish (Vetter and Dayton 1998).

There has long been concern about the environmental effects of fishing, but the vast scope of ecological destruction is only recently becoming apparent on soft-bottom habitats. The removal of small-scale heterogeneity associated with the homogenization of habitats is an important cause of the loss of biodiversity. Once the functionally important components of an ecosystem are missing, the anthropogenic disturbances are less obvious, and it is extremely difficult to identify and to understand ecological thresholds that are violated beyond the point of recovery. Ecological systems can shift into alternative states through the loss of ecosystem functions, and we need to be able to identify and to assess the consequences of these shifts in terms of loss of diversity and ecological services. Spatial mosaics that result from local biological disturbance events, as well as the organisms that create them, can be obliterated by intense broader-scale disturbances. Restoration of the system depends on a model of what is to be restored; it depends on an understanding of a great deal of structure in time and space, of biological thresholds for all of the species that create and maintain the structure, including the large bony fish and rays that disturb it.

The present debate over fisheries management and marine conservation highlights both the challenges and opportunities to test our current understanding of how broad-scale habitat disturbance to seafloor communities influences benthic ecosystems. There is strong evidence of effects on seafloor communities that have important ramifications for ecosystem function and resilience. Given the magnitude of disturbance by trawling and dredging and the extension of fishing effort into deeper, more sensitive benthic communities, this type of human disturbance is one of the most significant threats to biodiversity and the provision of ecosystem services (Thrush and Dayton 2002).



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4*C*

Figure 4: *A*, Tasmanian seamount below the depth of the orange roughy trawlers had hundreds of species associated with the fragile deep-sea corals. *B*, A deepwater soft coral brought up in an orange roughy trawl off New Zealand. *C*, A Tasmanian seamount exposed to orange roughy trawling. Credit: (*A*) Tony Koslow, Commonwealth Scientific and Industrial Research Organization ("Final Report to Environment Australia and the Fisheries Research Development Corporation, J. Anthony Koslow and Karen Gowlett-Holmes, March 9, 1999), (*B*) Les Watling, ("Paragorgia sp. from the deep water off the coast of New Zealand in the collection of NIWA, Wellington. Photographed March 9, 1999"), and (*C*) Tony Koslow, Commonwealth Scientific and Industrial Research Organization Marine Research.

Importance of Natural History in Understanding and Restoring Marine Systems

Ecological systems are extraordinarily complex and confusing. Yet they must be studied with the classical scientific techniques of simplification, analysis, and synthesis: testing theory remains the cornerstone of science. The process of simplifying the complex natural world is difficult and invariably relies on a keen sense of natural history. A commonly seen trap is that hypotheses are based on inappropriate simplifications and assumptions contradict natural history. The trap is that the bad assumptions can be mensurate and precise, esthetically pleasing, and appear heuristically useful, but the tests might be irrelevant or make the right predictions for the wrong reasons (see Dayton 1973; Dayton and Sala 2001).

Clearly, our goal in ecological science is to make interesting accurate generalizations about nature on the basis of relevant and parsimonious parameters. The relevant parameters are meant in an exclusive sense, and a central challenge in ecology is to weed out the marginally relevant parameters because all of nature is trivially related. But our generalizations should be based on those few parameters that account for most of the uncertainty or the ecological structure under study. Creative ecology is based on a deep sensitivity to natural patterns and processes. Naturalists have the ability to synthesize perceptions of nature into hypotheses about the processes that cause the patterns and then use the powerful scientific procedures for testing hypotheses.

In the same sense, the environment must be managed in ways that are responsive to the population thresholds and vulnerable aspects of the natural systems so poorly understood. Perhaps the only way this type of management can be accomplished is with acute sensitivity to the natural history of the particular system. And arguably the most important message from this essay is that current ecological model systems do not generalize very well. Because the life-history patterns are so different, different ecological systems, especially marine ones, may be based on fundamentally different ground rules, and these rules are not easily extrapolated between systems. Management must be generated from the important natural history that is often idiosyncratic to the system at hand. Understanding complex systems must be based on how populations behave under different environmental situations, on how their life histories both restrict and provide different demographic options that can respond to different environmental stresses. This type of natural history can help us predict population and system responses to environmental variation in complex systems. Excellent natural history is necessary to help us focus and prioritize questions for study and identify areas to monitor. In summary, science and management demand that complex systems be simplified, but the art of appropriate simplification depends on a basic understanding of the important natural history: there are no shortcuts.

Examples of Critical Life-History Stages

Conservation and restoration decisions rest on understanding the processes that result in population declines, ecosystem stability, and the successional processes necessary for recovery. There are important practical as well as theoretical reasons to define and to understand extinction thresholds in populations and ecosystems. These thresholds often relate to critical stages in the life histories of the populations as well as to the roles that the populations have with regard to the resilience of the ecosystems to natural and anthropogenic stress.

Recruitment dynamics represent an important focus for marine systems. Ecologists have attempted to identify sources, sinks, and essential habitats as important factors for recruitment processes. But how does one operationally define sources and sinks or rank habitat qualities? How can habitats be placed along a source-sink gradient? Critical periods and thresholds or bottlenecks can vary in time and space: how do we rank and study them with regard to declining populations and fragile ecosystems? In most marine systems, the following life-history components are important and have distinct thresholds. These represent important but by no means general examples of critical processes that contribute to correct generalizations.

Fertilization

Many marine organisms broadcast their gametes directly into the sea, where dilution implies that individuals must release sperm and eggs within a meter or so of each other (Tegner et al. 1996). Fertilization of relatively sedentary species such as abalone, scallops, sea urchins, and bivalves often depends on the existence of dense patches of both males and females or on mass spawning tactics. Many species of fish also aggregate to spawn. In many cases, the feature that attracts spawning aggregations seems to be a biologically produced physical structure. For example, Koenig et al. (1996) report that Florida groupers traveled >100 miles to gather around deepwater *Oculina* coral reefs to spawn. The same affinity for biological structures is likely to be true of other species associated with deepwater coral reefs. Unfortunately, many of these reefs have been virtually obliterated near the Aleutian Islands, Nova Scotia, Scotland, Norway, and especially the Southern Ocean seamounts. The number of gametes released often follows power function relationships between individual size and fecundity. Thus, instead of targeting large individuals, we should protect them. Simple natural history demands protection of both large individuals and spawning aggregations.

Larval Growth and Survival

Critical periods in the planktonic life of many fish larvae have been known for almost 100 yr. Critical periods include their first feeding, the successful dispersal to appropriate habitats, and successful settlement and metamorphosis (Hjort 1914). The first feeding periods are defined by the abilities of the larvae to handle prey as well as the sufficient density of appropriate prey. Invertebrates have much more complicated life-history patterns and much more complicated dispersal tactics, with postfertilization and dispersal processes varying from seconds for brooding species to many months for species with feeding larvae.

Dispersal

Most but not all propagules depend on oceanographic transport. The larvae of most species with planktonic dispersal drift for periods from 3 to 60 d. Because of complicated coastal oceanography, the variance within this period of time for a given species often encompasses spatially and temporally complex physical transport systems. This is especially true in the very near shore areas such as those within/between bays or kelp forests or unstable gyres where "relaxation" modes are important and the oceanography is further complicated by topography. The difference between 3 and 7 d can be the difference between flushing and retention, and the differences above 10 d can result in transport to very different oceanographic regimes and localities. The variability in these factors complicates the definition of sources and sinks for species such as lobsters, crabs, and some echinoderms with very long larval periods.

Dispersal processes are highly variable both from the evolutionary adaptations and the physical transport systems. Marine ecologists often focus on dispersal biology, but many systems such as the clonal encrusting systems have virtually no dispersal as most species reproduce by budding or crawl-away larvae. In the same sense, many other soft-bottom groups, including peracarid crustaceans and capitellid polychaetes, are brooders and disperse as adults; often their transport mechanisms include the bottom flocculent layer or being picked up and carried by breaking internal waves.

Settlement, Growth, and Survivorship

Successful settlement is another critical period (Tegner and Dayton 1977). Food availability and temperature strongly influence the length of time spent in the water column; the larva may continue to drift, exposing itself to increased risk of predation before it settles. The period at which a larva becomes capable of settlement is known as the competent phase. The models of Jackson and Strathmann (1981) imply that critical parameters are mortality rates, the length of the precompetent period, and the ratio of competent/precompetent time. The availability of appropriate settlement habitats or nurseries can be an important bottleneck. Once larvae arrive in the right habitat, many require inducements to settle and to metamorphose. It is interesting to note that the species with the longest precompetent periods also have very specific recruitment habitats that help avoid predation, disturbance, and stress (Dayton et al. 1995). These factors are poorly understood but extremely important and probably account for the common observation of episodic settlement; their understanding can only come from natural history–based research.

Juveniles and adults often have different habitats. For example, nurseries of many Pacific rockfish are in kelp forests, and many other species rely on sea grass beds, mangroves, corals, various associations of encrusting species, or depressions in soft-bottom habitats. In many cases, the adults live in very different habitats, and the passage to other habitats may be tenuous and risky. Without understanding this natural history, artificial settlement habitats such as artificial reefs may simply be killing zones if the appropriate adult habitats are not available and accessible.

Discussion

While society is concerned about the rapidly declining quality of the biosphere, most anthropogenic stresses are protected through rabid political resistance to conservation in favor of short-term economic gain. Representative natural areas are almost impossible to find, and few endangered species show signs of recovering, even with millions of conservation dollars spent on their behalf. A sad commentary is that our ability to respond and to defend natural systems has been eroded within academe by scientific elitism against natural history and systematics. Biology undergraduates increasingly have little opportunity to learn classic zoology or botany, invertebrate zoology, mammalogy, herpetology, ornithology, ichthyology, and so forth. Many first-year graduate students do not know the major phyla or the life history—and sometimes even the anatomy or developmental biology—of their own study organisms. Unfortunately, the study of minor phyla is a thing of the past. Without this grounding, it is no wonder that the respect for natural history has been lost despite the fact that this grounding seems vital. In almost all cases, we lack appropriate natural history to evaluate relationships and population thresholds, and we have lost virtually all instruction in taxonomy; it is a poignant paradox to lose biodiversity while simultaneously losing the scientific knowledge base of what it is (Zanetell and Rassam 2003). The academic foundation necessary to solve these problems is often missing. Those attempting to study these problems must start from scratch to describe what they are seeing.

The past 2–3 decades of biological research has seen the virtual elimination of the understanding of declining populations in Caughley's dichotomy; we have lost an enormous amount of evolutionary and cultural wisdom, and by destroying the natural sciences in academe, we may have foreclosed our future options to try to evaluate declining populations and ecosystem collapse. Most of the constructive efforts along the lines of Caughley's second paradigm seem to be done by applied workers, who often labor anonymously and without mentoring students in their sciences. What is the future with regard to understanding the questions posed at the beginning? Can we measure environmental stresses? How do we mitigate the impacts? What are the most important gaps in our knowledge? What are the ecosystem consequences of the loss of biodiversity? Loreau et al. (2001) argue that advances in functional understanding based on small-scale work are difficult to scale up to regional levels or to generalize across ecosystems. It is clear from this review that there is an urgent need to classify the community roles of many species and that much better syntheses of natural history across many scales will be necessary to understand the consequences of the loss of biodiversity.

As in the terrestrial realm, the last century has produced a large marine literature. But the value of much of this literature for application to conservation is truncated by the limited appreciation of the important scales in time and space. While the focus on small scales is understandable for many practical reasons, arguably the most important lesson of the past several decades is the importance to local communities of oceanographic processes operating on much larger scales in time and space. With the exception of the very large-scale California Cooperative Oceanic Fisheries Investigations program that has compiled complete oceanographic surveys for >50 yr, there are no time series observations that allow a holistic definition of what is natural for the ocean ecosystem. Within habitats, descriptive understanding is woefully inadequate even to pose and to prioritize critical questions.

A consistent thread in every case is that any understanding must be based on sophisticated knowledge of ecological processes, such as facultative and inhibitive succession, and that these studies will be stillborn without taxonomy, natural history, or realistic life-history biology. Conservation must be based on excellent taxonomic foundations (Vecchione and Collette 1996). Many of the most important contributions from the past relate to the virtuoso systematic contributions of the early workers. Consider the importance of plant taxonomy going back at least to Theophrastos (reviewed by Egerton 2002), and remember that most human cultures evolved intimate and knowledgeable relationships with nature (Johannes 1998). The importance of taxonomy has been emphasized by the National Academy of Sciences (1995) and seems self-apparent, yet influential authors publishing in *Science* and *Nature* advocate disposing of this very essence of the understanding of nature in favor of web-based illusions that species can be treated as bar codes (see review and critiques by Knapp et al. 2002).

Unfortunately, very few students are being trained in taxonomy, and our ability to identify any of the species in extremely important habitats, such as the continental shelf ecosystems, which include perhaps hundreds of thousands of species, will be lost with the retirements of the aging experts. This loss means that we will not perceive any but the most massive changes. Without systematics, we are not likely to identify, much less to study, those species that have weak interactions; thus, we are not able to debate questions of species redundancy or food web stability. Without collections and voucher specimens, we will not be able to interpret the work of the old literature. Not only do we need better natural history to understand these trends, but also such research depends on retrospective analyses utterly dependent on well-curated biological collections (Levitan 1992; Shaffer et al. 1998). Yet institutions everywhere react to declining budgets by eliminating the collections and the necessary curators: it is ironic that the same administrators who decry the loss of the library at Alexandria can move quickly to sacrifice their collections, the natural equivalent of that famous library.

The goal of this essay is to recover the biological natural science courses in all our academic institutions and to insure that students experience nature firsthand and be instructed in the fundamentals of the natural sciences. Unfortunately, this training has not been available for so long that students have not been trained so that teachers are now unavailable. A solution to this vicious cycle is to offer the classes, to hire the best applicants available, and to insure that they actually teach the material well even as they learn on the job. A parallel exists with many indigenous cultures that have lost an entire generation of people no longer conversant in their languages or cultures; now their grandparents are training the young people. In this sense, dedicated professors can still find academic grandparents who can help them learn the natural sciences. But like the native languages and cultures, we must move quickly if we are to save this critical component of our scientific culture.

Children grow into tomorrow only as they live and learn today. Yet so complete has been the elimination of natural history from academe that there are virtually no teachers being trained to inspire and to mentor children from kindergarten through college. This might be the most insidious result of the loss of respect for "old-fashioned" natural history: very few students are offered the opportunity of observing nature and accumulating the background natural history essential to the ecological understanding necessary to ask relevant questions. Political support for conservation depends on public passion, which must be based on their real understanding of what they wish to protect. The value system within academe must change so that the public also understands natural history. This understanding can only come via our academic system. We cannot protect or restore what we do not know.

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