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Managing for ocean biodiversity to sustain marine ecosystem services

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Managing a complex ecosystem to balance delivery of all of its services is at the heart of ecosystem-based management. But how can this balance be accomplished amidst the conflicting demands of stakeholders, managers, and policy makers? In marine ecosystems, several common ecological mechanisms link biodiversity to ecosystem functioning and to a complex of essential services. As a result, the effects of preserving diversity can be broadly beneficial to a wide spectrum of important ecosystem processes and services, including fisheries, water quality, recreation, and shoreline protection. A management system that conserves diversity will help to accrue more "ecoservice capital" for human use and maintain a hedge against unanticipated ecosystem changes from natural or anthropogenic causes. Although maintenance of biodiversity cannot be the only goal for ecosystem-based management, it could provide a common currency for evaluating the impacts of different human activities on ecosystem functioning and can act as a critical indicator of ecosystem status.

Compelling evidence is accumulating from terrestrial, freshwater, and marine systems to suggest that sustainable ecosystem services depend upon a diverse biota (Daily *et al.* 1997; Loreau *et al.* 2001; Tilman *et al.* 2001; Wall *et al.* 2004; MA 2005; Sala and Knowlton 2006; Worm *et al.* 2006; Butler *et al.* 2007; Hector and Bagchi 2007). In principle, such knowledge should be useful in guiding a national ocean policy that maintains the services provided by oceans into the future. But does knowing the link between diversity and services usefully

inform policy? We argue that management to sustain biodiversity could provide a critical foundation for a practical, ecosystem-based management (EBM) approach to the oceans.

Globally, 60% of ecosystem services are degraded (MA 2005). These ecosystems provide food, shelter, recycling, and other support mechanisms that human communities require, but fundamental services are declining as ecosystems are unraveled by human impacts (Palmer *et al.* 2004). Marine ecosystems (Figure 1) provide a constellation of services: they produce food, receive and assimilate wastes, protect shorelines from storms, regulate the climate and atmosphere, generate tourism income, and provide recreational opportunities (Covich *et al.* 2004; MA 2005). The extraordinary diversity of the world's oceans – across the different levels of ecosystems, habitats, species, functional roles, and genetic diversity (Carpenter *et al.* 2006; Sala and Knowlton 2006) – and the interconnections of marine, coastal, freshwater, and terrestrial ecosystems make managing ocean ecosystems crucial for long-term prosperity. Although degradation of ecosystems might be reversed through appropriate policies (MA 2005), there are substantial information gaps in our understanding of ecosystem processes (Carpenter *et al.* 2006), which impede practical ideas about implementing policy.

EBM involves incorporating knowledge of ecosystem processes into management, but defining EBM and specifying how it can be implemented has been difficult, particularly for marine ecosystems (Arkema *et al.* 2006). Grumbine (1994) surveyed 33 definitions of EBM, and Arkema *et al.* (2006) detailed 17. However, even with this large number of definitions, fewer than 10% of plans created by resource managers addressed priority EBM criteria, such as sustainability (Arkema *et al.* 2006; Figure

In a nutshell:

- Natural biodiversity broadly promotes the provision of marine ecosystem functions, including those critical to human survival and well-being
- Conserving natural biodiversity increases the likelihood that marine ecosystems can continue to provide such services and serves as a hedge against environmental change, increasing the chance that ecosystems can adapt and recover following disturbance
- Conserving biodiversity should become a common aim of ecosystem-based management for all agencies involved in regulating the marine environment
- Management for biodiversity may have to rely, in part, on management of surrogates, such as habitat types, population size, and related biodiversity characteristics

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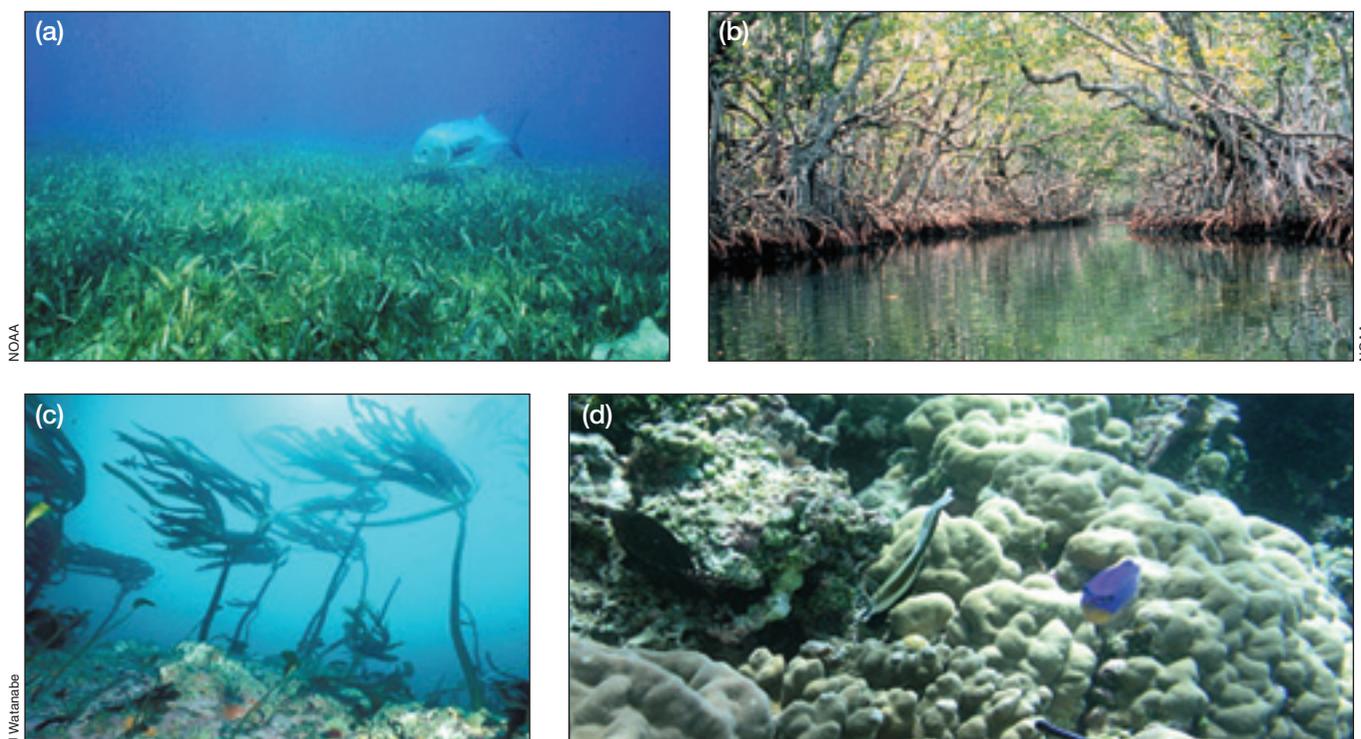
Figure 1. *(a) The high diversity of marine habitats provides a wealth of important marine ecosystem services. The species in these grass beds in Florida serve to consolidate sediment, protect shallow shores, and provide nursery and forage grounds for fish. (b) Mangrove forests protect coastlines from wave and tsunami damage, provide wood, shelter juvenile fish, recycle terrestrial runoff, and produce almost as much food per acre as a commercial shrimp farm. These complex services are provided by thousands of plant, animal, and microbial species. (c) Kelp forests and (d) coral reefs are some of the most productive ecosystems on Earth. Recreational, commercial, and subsistence fishing, as well as shore protection and tourism revenue, are derived from these ecosystems.*

2b). Despite increasing agreement on the principles and criteria of EBM among academics, managers do not include these in current plans (Arkema *et al.* 2006). Calls for EBM usually include the need to create a balance between services and to incorporate input from all stakeholders, managers, and policy makers (Arkema *et al.* 2006). However, this complex balancing act requires a high level of coordination, a great deal of cooperation, and the ability of managers to enforce trade-offs among different services. How can such positive interactions best be achieved? We posit that a common focus on management to conserve natural biodiversity could provide a foundation for such interactions and a practical basis for beginning EBM.

■ Showing that diversity matters

Biological diversity includes diversity at genetic, species, and ecosystem levels (Norse and McManus 1980). Sala and Knowlton (2006) succinctly defined marine biodiversity as "the variety of life in the sea, encompassing variation at levels of complexity from within species to across ecosystems". Experiments on, and observations of, species diversity in sessile invertebrates and seaweeds (Stachowicz *et al.* 2002; Allison 2004), grazing crustaceans (Duffy *et al.* 2003), and predators (Byrnes *et al.* 2006), as well as genetic diversity in seagrasses (Hughes

and Stachowicz 2004; Reusch *et al.* 2005), salmon populations (Hilborn *et al.* 2003), and oceanic cyanobacteria (Coleman *et al.* 2006), suggest that more diverse assemblages provide either higher productivity, greater resilience, or both. Analyses over larger temporal and spatial scales suggest similar linkages (Sala and Knowlton 2006; Worm *et al.* 2006). In addition, some of the key elements of ecosystem resilience, such as recovery, resistance, and reversibility, are bolstered by natural levels of biodiversity (Coleman *et al.* 2006; Palumbi *et al.* 2008).

These and other studies provide evidence for a generally positive relationship between biodiversity and ecosystem processes and services (Figure 2). A spectrum of mechanisms might generate this positive diversity effect, including complementary resource use, positive interactions among species, and increased likelihood of having key species present when species diversity is high. Ecological research suggests that these mechanisms are commonly in operation in the sea. For example, *complementarity*, in which species have slightly different roles in their environment, is probably widespread, because of the high frequency of niche partitioning among marine species (Kohn 1959). *Facilitation*, which occurs when one species improves environmental conditions for others, is well documented in such marine ecosystems as salt marshes, coral reefs, and kelp forests (Knowlton 1999; Bruno *et al.* 2003). By contrast, in some cases, a single species may play a central (sometimes

called keystone or foundational) role in an ecosystem. For well-known keystone species like sea otters, managing for their abundance is an obvious plan. However, other species play hidden but important roles, with impacts that may vary over time and space. High diversity assemblages have a higher chance of including such species than low diversity assemblages, which also helps to generate a diversity effect (Sala and Knowlton 2006). Structure-forming species, such as corals, oysters, kelps, sea- and marsh grasses, and mangroves, may be especially important, because their physical form provides numerous microhabitats and niches.

Even when high diversity results in species with similar ecological roles, the apparent biological *redundancy* can provide protection against changes in ecosystem function, because such species are usually not ecologically identical and are not redundant in the typical sense of the word (Levin 1999). Species richness (the number of species) provides a reservoir of biological options that help to ensure that an ecosystem can respond to some level of perturbation without catastrophic failure. This "insurance effect" of species richness is easily observed in ecosystems that are highly disturbed by human intervention (Nystrom and Folke 2001; Tilman *et al.* 2006), and probably plays a critical role in sustaining functions in these ecosystems. This can occur when similar species respond differently to environmental variation (Yachi and Loreau 1999), or when a substantial reduction in population size of one species is buffered by the presence of backups (eg through "guilds" or groups of species that perform similar functions within the ecosystem; Naeem and Li 1997). In addition, ecosystem stability may increase with diversity due to a *portfolio effect*, in which variations are dampened due to statistical averaging (Tilman *et al.* 2006). We infer that redundancy is common in the sea because many marine species have generalized diets, creating overlapping food web links that may generate a biodiversity insurance effect. Although species cannot be both perfectly complementary and perfectly compensatory, the complex mix of similarities and differences among species often results in a reduction in the fluctuations of ecosystem properties for systems that retain a larger number of slightly different functional elements (Tilman *et al.* 2006).

Invasive species add complexity to these issues. Although they nominally add to biodiversity by increasing the number of species present, their addition can often have a destabilizing effect on natural community abundance patterns and ecosystem services, especially if they become dominant. In such cases, they are better seen as a disturbance to the community, and we do not
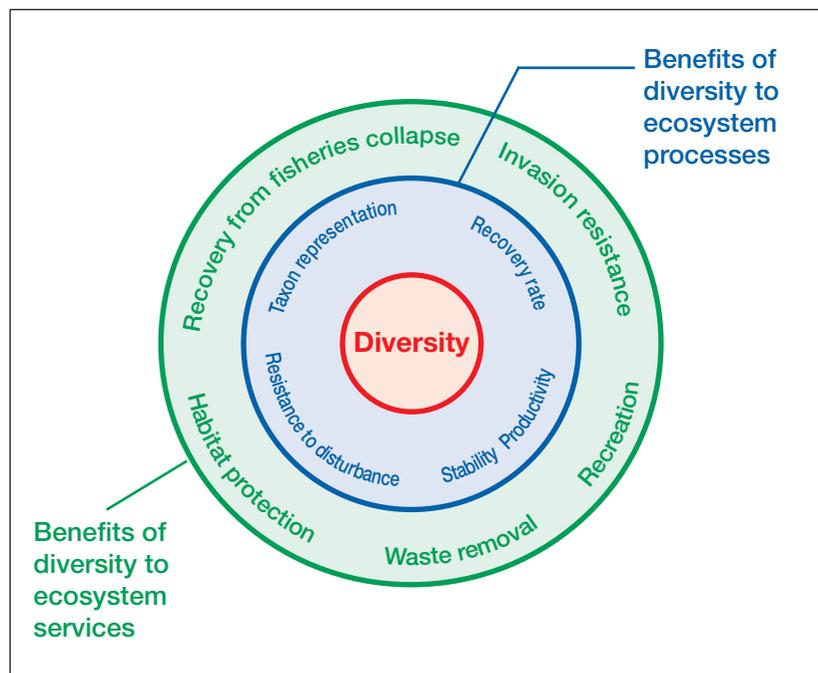
Figure 2. *A schematic view of the benefits of biodiversity. Diversity (red ring) enhances a variety of ecological processes (blue ring). These enhanced processes accelerate benefits that ecosystems provide in terms of recovery, resistance, protection, recycling, recreation, etc (green ring). Results are summarized from Loreau* et al. *(2001); Stachowicz* et al. *(2002); Duffy* et al. *(2003); Hilborn* et al. *(2003); Allison (2004); Hughes and Stachowicz (2004); Wall* et al. *(2004); Reusch* et al. *(2005); Byrnes* et al. *(2006); and Worm* et al. *(2006).*

include them in our consideration of the role of natural levels of biodiversity in ecosystem function.

■ Complex services provided by diverse communities

Even a simple-sounding ecosystem service may depend on complex ecological processes that, in turn, depend on high biological diversity. For example, waste detoxification depends on the breakdown of many pollutants by microbes. The broad range of metabolic processes needed for this action demands a diverse microbial community (Nystrom and Folke 2001).

Most other ecosystem services, including fisheries that target dozens of species simultaneously, also depend on complex ecological linkages. Diversity among and within species can stabilize the delivery of these complex services (Hilborn *et al.* 2003; Hughes and Stachowicz 2004; Reusch *et al.* 2005; Palumbi *et al.* 2008). For example, Worm *et al.* (2006) showed that marine ecosystems with high diversity had slower fisheries collapse rates and higher rates of fisheries recovery than marine ecosystems with lower diversity.

The link between diversity and services is not limited to the sea. Hector and Bagchi (2007) found that different ecological processes in grassland ecosystems rely on different species. Thus, the list of species considered important to ecosystem function grows with the number of ecosystem functions included in the analysis. Soil biological commu-

nities also contribute strongly to services such as water quality, food, erosion control, and pollutant degradation (Kibblewhite *et al*. 2008), suggesting that the link between ecosystem services and biodiversity crosses ecosystem boundaries. Clearly, however, agricultural and aquacultural systems represent situations in which artificial monocultures provide particular services, such as food. Here, the value of one particular service is enhanced at the expense of others. Such trade-offs may be a common feature of detailed management plans in any large ecosystem, but should be considered part of a larger ecological mosaic in which other services are supported by natural biodiversity.

■ Existing mandates for maintenance of marine biological diversity

Some authorization to protect marine biodiversity exists for many US federal and state agencies, although the term "biodiversity" may not be specifically mentioned. Relevant US federal laws include the National Environmental Policy Act, Clean Water Act, Magnuson-Stevens Fishery Conservation and Management Act (MSA), Endangered Species Act (ESA), Marine Mammal Protection Act, and National Marine Sanctuaries Act. However, no single administrative and legislative framework exists for integrated ocean management in the US, despite urgent calls for such a structure (Pew Oceans Commission 2003; USCOP 2004).

Progress toward EBM in fisheries (Pikitch *et al*. 2004) culminated in the US Administration's commitment to EBM in the US Ocean Action Plan (2004). The central issue is no longer *whether* to apply an ecosystem approach to management, but rather *how* to apply it. Current agency efforts are dominated by consideration of harvestable resources, and these are only a fraction of the important ecosystem services at stake. An approach emphasizing the role of biodiversity and multiple services (Figure 2) would be much more comprehensive.

■ Using diversity to manage multiple, conflicting services

Here, we propose a fundamental shift in orientation, one that would move us away from management of one service at a time and allow us to focus instead on the conservation of multiple services through protection of natural biodiversity. Biodiversity would become the central element tying management of different sectors together, constraining some sectors for the benefit of others, but ultimately producing a net benefit for all sectors. We argue that consistent management across agencies to sustain natural biodiversity – via conservation of species richness, genetic diversity, species composition, and habitat diversity – will help to maintain ecosystem integrity and stability. Our approach establishes the maintenance of natural biodiversity (sustaining all of an ecosystem's biological parts at functioning levels) as a common core principle, guiding decision mak-

ing in agencies at local, state, and federal levels.

The suite of services provided by marine ecosystems can create management conflict and overuse of the environment through cumulative impacts, if different managers are required to optimize for different services. For example, if improving waste management demands changes that decrease fisheries yield, then separate management for these services may generate regulatory conflict and the inability of either management body to reach its goals (Figure 3). Thus, a management focus on one service at a time may compromise the multifunctionality of the ecosystem. So, how can managers balance conflicting needs for a given ecosystem, to produce many complex, linked services?

We suggest an approach based first on the link between diversity and ecosystem function and, second, on experimental studies showing that increased biodiversity can simultaneously increase and stabilize multiple measures of ecosystem functioning (Hooper and Vitousek 1998; Duffy *et al*. 2003; Worm *et al*. 2006). In this approach, different agencies, regardless of their primary focus (eg fisheries, water quality, coastal zone management), would also be required to manage for sustained biodiversity, because sustained biodiversity would increase the likelihood that multiple, important ecosystem services would be sustained as well (Figure 3). Such clear mandates will probably need to come in the form of amendments to existing laws or new laws, or could be incorporated into comprehensive ocean area-based management. Although politically difficult, development of such mandates would generate broadly parallel management goals in different agencies, creating much-needed coordination, as agencies would be managing for similar outcomes.

Coupled with a clear specification of other management objectives and establishment of strategies for evaluation of trade-offs and conflicts among different ocean-use sectors, maintenance of biological diversity can serve as a focal point for the specification of management options and constraints on human impacts. Maintenance of biodiversity cannot be the only approach to managing ecosystem services, because inflexible enforcement might limit many ongoing uses of ecosystems. Instead, it can serve as a way to evaluate the ecosystem impacts of management decisions, using a common currency that can be applied across agencies. It can also be used as a "tie-breaker" for different management options that might both fulfill agency mandates, but have very different impacts on biodiversity. By evaluating the impact of different human activities on ecosystem functioning, a focus on biodiversity can serve as a critical indicator of ecosystem status. Implementation would require a governance structure that coordinates among sectoral managers.

We do not argue for maintenance of all natural biodiversity, everywhere, all the time. But we do suggest that the following requirements make good policy and market sense: (1) each agency or management entity understands its role in the conservation of biodiversity, including impacts and benefits derived; (2) each agency focuses at

least part of its energies and resources on the conservation of biodiversity; and (3) a coordinated management structure focused on integrated assessments of the environment and human impacts, and on trade-offs between various ocean-use sectors, is created.

We envision that the overall objective for EBM will involve maintaining or optimizing the provision of ecosystem goods and services, subject to a set of constraints that maintain biological diversity. Protecting biological diversity will provide long-term, direct benefits to several ocean-use sectors. Some sectors (eg mineral extraction, transportation) may benefit little from this approach; for these sectors, preservation of biological diversity may serve primarily as a constraint on activities. Yet, even here, a focus on biodiversity could still provide an important framework for evaluating trade-offs among ocean-use sectors. Adopting maintenance of biodiversity as a core element of EBM provides a basis for evaluating cumulative impacts, which can lead to decision tools to guide management of diverse sectors. Our goal would be to define strategies for utilization that minimize impacts on biodiversity, while permitting continuation of ecosystem use and a broad mix of goods and services.
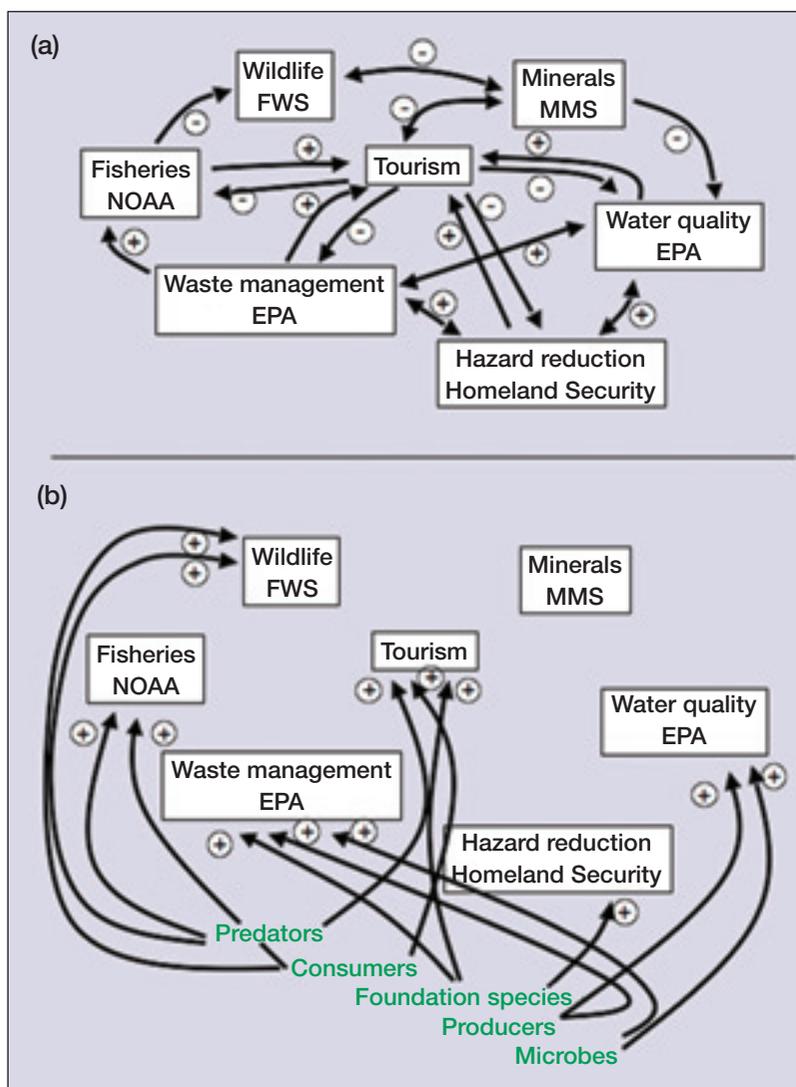
Although our proposal would need to be implemented on a region-by-region basis, it could form the core of a well-defined national strategy focused on biodiversity rather than only on individual ecosystem services. Clearly, the simple idea of focusing on conservation of biodiversity cannot solve every problem. But it could force explicit recognition of the importance of trade-offs among sectors and provide a way of addressing them, as opposed to the current practice of neglecting to document such effects.

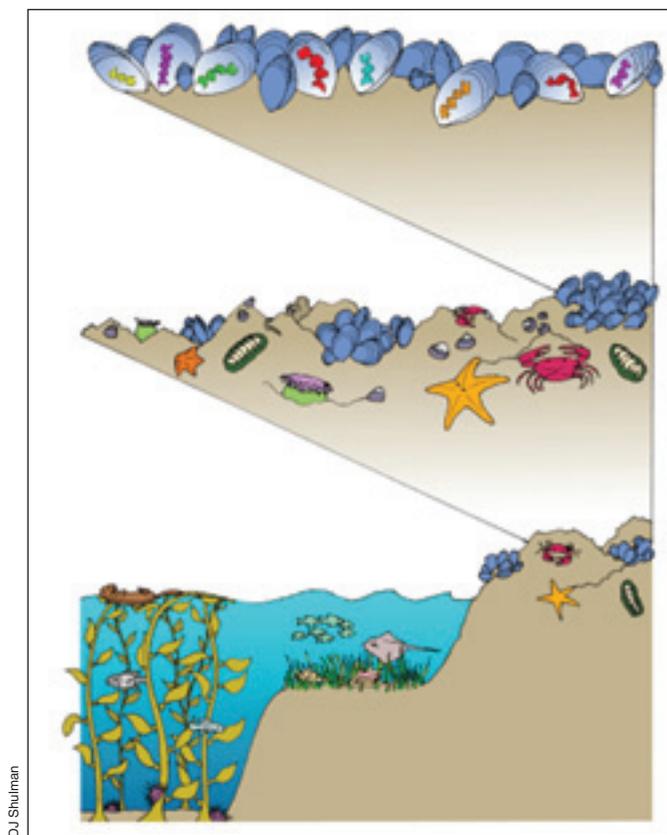■ **How to measure diversity so that we can conserve it**

Using biodiversity as a national master variable to enable EBM will require that it be measured in consistent ways and over the multiple regional, temporal, depth, and geographic scales relevant to management. Such measurement systems are currently lacking (Rosenberg and McLeod 2005). However, web-based tools for biodiversity assessment are now under development and show promise for global information transfer and quality control (Guralnick *et al.* 2007), as do broadly based marine biodiversity research efforts, such as the international Census of Marine Life and regional Marine Life Observatories. There is also considerable

Figure 3. (a) Complex positive and negative correlations among marine ecosystem services create an intricate web of relationships that will be difficult for managers to simultaneously optimize. Environmental changes that affect any one service (eg water quality) will probably impact others as well, making ecosystem-wide decisions difficult to achieve. (b) Likely relationships between each ecosystem service and the biodiversity of marine habitats. Positive effects of diversity on services may make it easier to enhance or maintain multiple services at the same time, providing a basis for a coordinated regulatory framework. NOAA = National Oceanic and Atmospheric Administration; EPA = Environmental Protection Agency; FWS = US Fish and Wildlife Service; MMS = Minerals Management Service.

potential for mining additional information from existing datasets. Nevertheless, even for taxa that are well studied, the choice of appropriate metrics has not been completely resolved. For example, the use of species richness as a measure of species diversity fits naturally into existing legal mandates (eg ESA, MSA), but does not address concerns related to loss of ecological function as population levels decline or loss of adaptability as genetic diversity declines.

We suggest that measuring biodiversity in ways that will be useful in a management context probably requires a

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Figure 4. Measurement of biodiversity must occur at several levels. The lower level includes different habitat types within a region – in this case, the rocky intertidal zone, seagrass beds, and kelp forests along the California coast. The middle level focuses on species diversity, here illustrated as the set of macroinvertebrates of the rocky intertidal zone. The upper level represents the diversity within each species, here cartooned by different DNA types within intertidal mussels.

three-tiered approach (Figure 4). First, fundamental measures of biodiversity could be accomplished at the seascape level by mapping distinct biological habitats within regions. Second, monitoring within habitat types for key species would provide assays of species-level diversity. Third, diversity within species, including genetic variability and physiological or life history diversity, adds the last layer (Beck 2003; Guinotte *et al*. 2006; Pittman *et al*. 2007). As Sala and Knowlton (2006) point out, "an effort to map marine ecosystems and ecoregions – similar to those conducted for terrestrial ecosystems – will be essential, because conserving habitats to preserve species might be an immediate and practical management strategy, regardless of the number of species present". One of the outstanding challenges is to relate the nature and magnitude of services to the extent of habitats and communities, the biodiversity that they contain, and the types and levels of disturbance they can endure, because there will always be a need to use the marine environment. The goals of conserving biodiversity – thereby conserving ecosystem function – and of sustaining human use and benefits require an understanding of the interplay between these factors.

In measuring diversity within habitats, we will need

assessment and ongoing monitoring to verify species' occurrence and abundance. Defining habitats within regions and enumerating the species that depend upon them are fundamental requirements. Practical considerations will probably force the adoption of a subset of surrogate taxa, preferably ones that are critical to ecosystem services, as the targets for assessment. These surrogates must include taxa that provide a variety of services, such as habitat-forming species (eg corals, sponges, oysters, seagrasses, kelps), pollutant-recycling species (eg marsh grasses, macroalgae), fisheries species, and microbes, and not just fished species or large fish and invertebrates. Other diversity indicators for the pelagic and deep-sea realms might focus on planktonic prokaryotes and micro-eukaryotes, thermal vent communities, deep-sea coral and sponge assemblages, seamount communities, mixed-species fisheries, and sediment microbial communities. Species across the size and phylogenetic spectrum should be included, with the most appropriate candidates being those with the greatest amount of biological knowledge and taxonomic certainty. Based on such evaluation, a set of species should be selected for monitoring (Vecchione *et al*. 2000). Over time, maps of habitat types and temporal changes in abundance could be combined to paint a dynamic picture of species occurrences over the seascape.

Managing for biodiversity will require the incorporation of new technologies, in addition to established techniques. In particular, biodiversity assessments will necessitate employment of more taxonomists and parataxonomists, as well as the use of information-based tools designed for quicker assessments (Pittman *et al*. 2007). Certain species (especially microbes) may best be enumerated with DNA arrays or other automated techniques (DeSantis *et al* 2007). Whatever automation can be applied to these surveys will free resources for measurement of species that cannot be assessed in these ways. Similarly, sophisticated tags for fish and invertebrates can record a variety of environmental and physiological parameters (eg temperature, depth, hormone levels) that may reveal environmental associations that would otherwise be hidden from view (Weng *et al*. 2005).

Long-term study sites will be critical to effective management in the coming decades, as increasing anthropogenic stressors and climate change affect ocean and coastal ecosystems. A wide range of marine protected areas will be invaluable experimental and control sites for such investigations. To conduct the requisite studies, the scientific community will have to develop new tools for the remote and continuous measurement of microbial diversity, oceanic and coastal zooplankton and phytoplankton, and mega- and meiofauna in the benthos and the ocean. Such tools will probably include genomics; more robust marine biosensors; automated aerial, surface, and underwater drones equipped with sonar or acoustic monitoring; cameras for detection of ocean fauna; other biological monitors and samplers; and new mathematical models to chart energy flow within food webs. Such a combination of efforts amounts to creation of marine life

observatories that will complement ocean-observing systems focused on physical measurements of the sea.

While new approaches must be developed to acquire consistent measures of biodiversity across all marine habitats, the efforts we outline here have their basis in the current wealth of taxonomic and ecological knowledge. For our approach to become practical, existing data for well-known ecosystems will need to be summarized in a comparative framework. In addition, new data on poorly known ecosystems, especially their taxa, habitats, and levels of natural diversity, need to be collected. The end result would be a system in which information on trends in the biodiversity of marine habitats is accessible to managers and decision makers. Political will is needed to mandate management for conservation of biodiversity and to allocate reasonable resources to support the requisite scientific (eg habitat mapping, taxonomy) and management work.

Case studies that test our concept of managing for biodiversity to sustain ecosystem services are generally lacking, though some ongoing activities appear to offer opportunities for such evaluation. One might be the snapper–grouper fishery in the US South Atlantic Bight. This complex fishery, which includes 73 of the 98 fish species managed by the South Atlantic Fishery Management Council (SAFMC), is administered using a multi-species Fishery Management Plan (see www.safmc.net/ for information and documents). At least in part because many of the species in the snapper–grouper complex are highly dependent on specific habitats, the SAFMC has developed a Habitat Plan as a precursor to a broader Fishery Ecosystem Plan. Although the SAFMC is currently constrained to accommodate only a single ecosystem service (fishing), if the Council included management efforts dealing with biodiversity of the habitats important for the snapper–grouper complex, we believe this would have positive effects on numerous other ecosystem services.

■ Future directions and conclusions

Broadly speaking, new data suggest that biodiversity helps to increase, maintain, and promote marine ecosystem function (Sala and Knowlton 2006; Worm *et al.* 2006; Hector and Bragchi 2007). The ecological mechanisms of diversity effects, such as complementarity and redundancy, may be widespread in the oceans, making this a general rule. The ecosystem services demanded by humans are complex, and are probably best supported by diverse biological communities (MA 2005). In addition, conservation of biodiversity for its own sake remains a valid and valuable goal for our society; we should do all we can to maintain the rich and fascinating life of this planet (McCauley 2006). Thus, conservation and management of biodiversity include both philosophical and practical concerns. The current rate of decline of ocean ecosystems makes them urgent.

Because sustained diversity is likely to bolster most services, a system managed in a coordinated fashion for

diversity will accrue more "ecoservice capital" for human use than do current practices. In almost all investment or allocation schemes, having more capital makes investment choices and conflicts easier to resolve. If we use conservation of biodiversity as a primary aim of EBM, we will automatically also conserve many of the myriad interconnections among species and their environment. These interactions represent a major target of EBM, because they result in essential ecosystem services.

This proposal represents a core idea, but there are many aspects that need to be resolved in any specific application. Acceptable trade-offs between maintaining diversity and modifying it through ecosystem use need to be defined, and are likely to be system specific. There may be cases where direct management of all core ecosystem services simultaneously results in better function than an indirect approach emphasizing biodiversity. In many cases, our simple biodiversity approach might be a starting point of EBM, with more focus on coordinated management of different ecosystem services later. By maintaining biodiversity as a national core variable through conservation of key species, overall species richness, functional diversity, habitat diversity, and variation in genetic diversity within species, we will generate a cost-effective way to coordinate diverse agency goals, manage trade-offs in service provision, and ensure maximum ecosystem function and resilience.

■ Acknowledgements

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