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Essential ecological insights for marine ecosystem-based management and marine spatial planning

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ABSTRACT

The abrupt decline in the sea's capacity to provide crucial ecosystem services requires a new ecosystem-based approach for maintaining and recovering biodiversity and integrity. Ecosystems are places, so marine spatial planners and managers must understand the heterogeneity of biological communities and their key components (especially apex predators and structure-forming species), and of key processes (e.g., population connectivity, interaction webs, biogeochemistry) that maintain them, as well as heterogeneity of human uses. Maintaining resistance and resilience to stressors is crucial. Because marine populations and ecosystems exhibit complex system behaviors, managers cannot safely assume they will recover when stressors are reduced, so prevention is a far more robust management strategy than seeking a cure for degraded systems.

1. Introduction

Three recent assessments report that goods and services provided by marine ecosystems are seriously compromised [1–3]. These assessments call for a dramatic shift in marine science toward solution-driven research, and, in ocean policy, from management of individual sectoral activities toward ecosystem-based management [4,5]. Ecosystem-based management is "an integrated approach to management that considers the entire ecosystem, including humans" [6]. Ecosystems at sea, in the water column and on the seafloor, occur at various scales and are bounded primarily by physical and biological features. Although there are ecosystem approaches to managing particular resources that are not necessarily place-based (e.g., Pikitch et al. [7]) ecosystems are places, and ecosystem-based management is therefore inherently place-based [6]. Moreover, social, cultural, economic, and political attributes overlay these biophysically defined places. Thus, approaches that integrate natural and social scientific perspectives on defining and managing places at sea are necessary to implement ecosystem-based management.

The escalating crisis in marine ecosystems—from biodiversity losses and transformed food webs to marine pollution and warming waters—is in large part a failure of governance [4]. All the recent assessments have called upon policymakers and managers to transition from managing sectoral activities toward ecosystem-based management, but implementation is constrained by the lack of a clear way forward. Current governance of marine systems is by sector, leading to fragmentation and spatial/temporal mismatches in governance [4]. We argue that place-based management and marine spatial planning (MSP) can provide a far more promising approach to implementing ecosystem-based management. Rather than individual sectoral agencies managing their activities everywhere, responsible sectoral authorities could work together to manage all the human activities in a place. These places could align with ecosystem boundaries, socio-economical boundaries, and/or jurisdictional boundaries. Management always occurs in a delimited space, with many processes that transcend boundaries [8]. Refining and integrating our concept of place in the sea is critical to implementing ecosystem-based management.

An important first step in defining place is to map biophysical conditions and human uses in the oceans. The objective in mapping biophysical conditions is to identify distinctive assemblages or communities of marine organisms, such as kelp forests, coral reefs, or shellfish beds. Simultaneously, researchers should map human uses of the area and political and legal arrangements that relate to these places. Socio-economic overlays would identify the spatial distribution of recreational boating, scuba diving, fishing, aquaculture, oil and gas development, shipping, and so forth (see also St. Martin and Hall-Arber, in this issue). Jurisdictional overlays would delineate areas covered by existing management arrangements, such as the regional fishery management councils, or areas closed to fishing by state or

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federal regulation, marine sanctuaries, and military zones. Taken together, these biophysical, socioeconomic, and jurisdictional overlays can produce meaningful mosaics of places suitable for the practice of place-based management of marine ecosystems.

The biophysical component of marine ecosystems provides the basic template on which all human activities occur and that various forms of governance regulate. Approaches to MSP and ocean zoning outlined elsewhere in this volume require consideration of some basic ecological concepts so that human activities can be conducted in ways that maintain ecosystem functioning, provide sustainable ecosystem services on which people depend, and maintain resilient ecosystems that can respond to environmental change. We outline some of those key concepts below.

2. Heterogeneity of marine areas

Borders matter, and their placement can bring endless benefit or pain, depending on the thought invested in their placement. The borders of Iraq with its neighbors reflect decisions made by the League of Nations after the British and French defeated the Ottoman Empire in World War I, rather than the distributions of deserts, floodplains, mountains, and oil—or those of Sunni Arabs, Shi'a Arabs, and Kurds. An unmistakable lesson of the current US effort in Iraq is that lines on maps that do not reflect real-world patterns and processes are destined to fail. The same is equally true in the sea. And because we cannot afford to lose valuable marine resources, planning based on faulty premises is a risky management strategy.

Anybody who flies over the land sees a complex mosaic of landforms, weather phenomena, ecosystems, and human uses. But to a casual observer from a ship or airliner, the wavy ocean surface often seems homogeneous from horizon to horizon. That is misleading because the sea conceals its spatially heterogeneous patterns of topography, water stratification and movement, living things, and human interests and impacts. A thoughtful observer will also realize that the sea is heterogeneous in time, with some important things happening on time scales of hours, days, or months, and others happening over years, decades, or centuries. The complexity of natural processes in the sea and resulting mosaic patterns in space and time mean that any "one-size-fits-all" management regime that treats the sea as uniform or divides it in ways that does not reflect its real heterogeneity is likely to fail. Successful marine management, therefore, requires managers who understand and work with the sea's heterogeneity in space and time [9].

Virtually all jurisdictions, e.g., as demarcated by national, state, and county borders, were created long before scientists had much understanding of the boundaries of marine populations and ecosystems. As a result, legal boundaries in the sea do not reflect natural processes or the shared socio-economic interests of humans. When most of our knowledge came from plumbing ocean depths with weighted hemp lines, management had only a limited empirical or conceptual basis and so was, in a way, doomed to be ineffective. But a growing suite of new research tools—scuba, submersibles and remotely operated vehicles, multi-beam sonar, ocean sensors on Earth-orbiting satellites, vessel monitoring systems, electronic satellite tags, and fixed ocean monitoring stations—have revealed oceans to be a complex spatial mosaic, a dynamic patchwork of physical features, distributions of marine organisms, and human uses. Now we have much more information as the basis for spatial management than those who drew the initial biophysically and socio-economically artificial lines we see on maps.

Ecosystems occur on all spatial scales from the whole Earth to particular habitats, and the differences among these scales are fundamental to any effective management. On the largest spatial scale, scientists know that each of the oceans basins is ecologically distinctive. The Pacific is strewn with far more chains and clusters of islands and seamounts than the other oceans, which affects migratory corridors and distributions of species, as well as the history of human colonization of the Pacific. The Southern Ocean is the only ocean not defined by landmasses, but by an ocean boundary, being surrounded entirely by the Antarctic Circumpolar Current. Upwelling, a crucial factor in productivity and marine food webs, is more frequent on the east sides of oceans. Tropical and temperate waters on west sides of the Atlantic and, Pacific oceans go farther toward the poles than on the east sides, that affects population sizes and ranges of species. There are important latitudinal effects on human dimensions of marine ecosystems on an ocean basin scale as well. Most marine scientists work in temperate latitudes, so we tend to know more about their marine ecosystems than those in warmer or colder waters. That is crucial because people tend to pay the most attention to what we know best, not necessarily what needs the most attention.

Heterogeneity among ecosystems at smaller scales also affects on marine management. The inshore waters and offshore banks from Labrador, Canada, to New England, USA, were bountiful fishing grounds until fisheries overexploited cod by treating them as one large population and failing to appreciate the complex patterns of subpopulations distribution, migration and larval dynamics. Now many of the apparently discrete subpopulations appear to be severely depleted or extinct [10], and cod, overall, have not recovered even after fishing for them has largely stopped. The failure of fishery managers to recognize that there were many interacting subpopulations of cod, not just one homogeneous cod "stock" helped to ruin one of the premier fisheries of the world and damaged the human communities that depended upon these resources.

Similarly, seamounts are undersea mountains, mostly extinct volcanoes, which modify ocean currents and provide hard substrates that are shallower than the surrounding muddy abyssal plains. Because their geology and oceanography is so different than their surroundings, these island-like marine ecosystems attract pelagic animals (such as tunas and albatrosses) above them and many kinds of animals (corals, sponges, and associated fishes) onto their crests and slopes that are quite different than those of the abyssal plains.

At the finer spatial scale, ecologists know that habitats having greater spatial complexity or three-dimensionality often have a higher diversity of species, because they create more physical opportunities for species to feed, hide from predators, and reproduce. It is not entirely surprising, therefore, that coral reefs, which comprise less than 1% of the ocean area of the world, are home to 25% of the world's fish species [11].

Indeed, perhaps the most important insight that marine ecologists can share with managers is that some places have much greater importance than others for particular species, ecosystems or processes, and hence for humans. In other words, "real estate values" in the sea vary enormously, just as they do on land. Knowing which places are the most important to conserve is central to the art of marine spatial management. For example, some groupers and snappers in tropical shallow coral reefs, and orange roughy in deep-sea banks, ridges and seamounts, aggregate to spawn in specific, predictable places [12]. Knowing this, fisheries have targeted these spawning aggregations. It would be difficult for managers to have designed a more effective strategy for wiping out a species. An alternative strategy would be to protect these places for their extraordinary value, a management approach used in Belize and some other countries.

Size matters. In an unpredictable world, conserving enough well-chosen places, comprising enough cumulative area, so that populations in these places will be self-sustaining, is an essential objective. Because heterogeneity occurs on different spatial scales, it is useful for managers to have ways to envision it from the largest scales (ocean basins and realms), through provinces and ecoregions [13], to specific habitats. Using a nested hierarchy of spatial patterns and conducting gap analyses will allow governance and management to set priorities that reflect oceanographic, ecological, and human use patterns as well as the processes that underlie them, a quantum improvement over sectoral approaches.

A large number of scientific studies have now demonstrated that in places where we do not kill fishes, there are more of them. Especially when we know that there is heterogeneity, but do not know everything, the best planning and management decisions err on the side of protecting places that support sustainable populations and communities we value. Ensuring that some places where marine wildlife aggregate, and are most vulnerable, become zones where people are not allowed to kill them, and others become zones where mortality of fishes is kept within prudent limits, is probably the most fail-safe tool in a marine spatial planner's toolbox. But it is not enough to maintain isolated bits of functioning ecosystems. Rather, we must maintain the connections that bind living things together, both their physical connectivity and their interaction webs.

3. Population connectivity

Charismatic megafauna, such as tunas, jacks, leatherback turtles, albatrosses, and common dolphins, range over wide areas, exploiting predictable or temporary patches of food animals. But the distribution of most marine species is driven by currents. Unlike terrestrial animals that walk or fly from one habitat to another, these animals disperse in the larval stage with the assistance of currents. Populations of both groups of animals, therefore, occur in patches because of the underlying heterogeneity of the environment and the different mechanisms populations have for moving among suitable habitats, which ecologists call connectivity [14]. For this reason, marine populations are often held together by immigration and emigration among habitat patches.

Recruitment is the biological process through which animals are added to a population. And variability in recruitment drives population fluctuations in many marine organisms, including valuable fishes, so understanding the linkages in space and time between recruitment and environmental variation is critical to effective management. Fishing and other human activities happen at particular places and times, so understanding how fishing relates to the population dynamics of target and non-target species in a dynamic, patchy ecosystem is critical to good conservation decision-making. Scientists consider many marine populations with dispersive stages to function as "metapopulations" with interconnected subpopulations that exchange individuals [15]. Moreover, many marine species are also likely characterized by what ecologists call "source–sink population dynamics" [15–17]. In such metapopulations, some organisms occupy "sink" habitats that are colonized by larvae produced elsewhere. In contrast, a critical part of the metapopulation occurs in "source" habitats, where the output of individuals from the spawning stock is sufficient to maintain populations in both source and sink habitats [18]. Ultimately, good source habitats are defined both by their potential to produce ample larvae and the potential for those larvae to be transported to good developmental habitats nearby [19]. As in investing in real estate, it is about location, location, and location. Marine spatial planners seeking to protect critical, productive habitats for marine animals need to understand how particular places support populations of interest. If we know where the best habitats are, indeed where source habitats are, they should be protected. If we protect sinks and redirect fishing effort to source habitats, the whole fishery can decline [16]. Absent this information, a precautionary management strategy is to protect a diversity of representative habitats as discussed above.

Of course, not all connectivity results from the dispersal of planktonic larvae. Some marine animals are sufficiently large (or fast) to migrate (with or without the assistance of ocean currents) over vast distances, making dramatic seasonal migrations for feeding and breeding. Satellite and GPS tags attached to individual organisms and oceanographic sensors built into the tags can provide valuable information as to the distribution and movements of key marine species relative to habitat features. For smaller animals, scientists have attached acoustic tags that can be interrogated by acoustic arrays on the seafloor to determine animal movements. Soon it will be possible to develop models that allow researchers to forecast the distribution and movements of animals relative to remotely sensed oceanographic measurements.

Obviously, understanding migratory routes of large marine animals clarifies where they intersect with human activities. These migratory corridors could be protected as they have been for terrestrial wildlife. Scientists are also identifying hotspots occupied by animals for feeding or breeding where human activities can have disproportionate effects. Including marine reserves in comprehensive marine spatial plans can protect vulnerable animals from damaging human activities, such as fisheries. The reserves might be fixed in the location of particular habitat (e.g., coral reef), or they might be dynamic reserves that respond to dynamic ocean features (like eddies or fronts) or to seasonal migrations of protected species [20]. Once again, marine spatial planners can use such information to minimize the effects of human activities with these highly vulnerable organisms.

4. Interaction webs

Food webs are the road maps of species interactions and so display another sort of ecological connection in marine systems [21]. A very simplified version of a food web is the widely known food chain where smaller organisms are consumed by larger ones. Primary producers such as phytoplankters and seaweeds are eaten by herbivores and herbivores are eaten by carnivores. In practice, however, things are a bit more complicated, one reason being that species feeding at more than one trophic level (omnivores) are not easily categorized and many marine organisms feed at different trophic levels at different life stages. A larval fish may begin feeding on microscopic algae, later feed upon zooplankton and larval fishes (even those of species that are predators upon it later in life), and finally switch to eating other fishes.

Descriptive food webs display the complexity of natural systems, but they treat all linkages as equivalent. Other food webs weight linkages by the amount of material or energy they transfer. "Interaction webs" emphasize those linkages with high interaction strength. The notion of "interaction strength" measures how changes in the abundance of one species affects other species in the web whether directly (via predation) or indirectly (via competition or other effects). An interaction is considered "strong" when a change in the abundance of one species has a relatively large effect on the mortality, growth, or recruitment of other species in the web. Strong interactions may arise due to behavioral rather than trophic interactions. Tunas drive food fishes to the surface, benefiting foraging seabirds (in marked contrast with a trophic scheme, in which they are competitors). *Trapezia* crabs defend *Pocillopora* corals from predation by crown-of-thorns starfishes. From a trophic perspective, the crabs are parasites of the corals, but they provide protective benefits when the predatory starfish are around [22]. Focusing on trophic linkages alone can provide us incorrect insights in these cases. Scientists draw interaction webs to distill an assemblage of organisms down to its most important ecological features and to identify possible indirect effects that develop as a consequence of interaction web manipulations, such as the removal of apex predators in fisheries [23]. Planners and managers who wish to avoid surprises need to be aware that unanticipated results occur commonly when interaction webs are overlooked or are manipulated by managers.

Although we do not have a field guide to strong interactors in marine food webs, strong interactors repeatedly occupy two major roles, top predators and structure-forming species. Removing top predators including marine mammals, sharks, and other large fishes can have effects that cascade down the food web [24–26]. These cascades can link factors not linked in the minds of most managers. For example, an increase in abundance of killer whales in the North Pacific could drive declines in threatened kelp rockfishes—when *Orca* increase, they reduce the abundance of sea otters, releasing herbivorous sea urchins from predation. Abundant urchins can then overgraze giant kelp, reducing habitat for juvenile rockfish. In a recent example, Myers et al. linked the decline of sharks in the Northwest Atlantic to the collapse of the bay scallop fishery in North Carolina estuaries [26]. The nearly 90% declines in a guild of predatory sharks are correlated with an increase in cownose rays and other elasmobranches that eat shellfish. This example brilliantly shows how a stovepipe sectoral approach (in which coast-wide shark fishing and local estuarine scallop fishing have nothing to do with one another) is inherently inappropriate.

Jackson et al. show that effects of fishing and other human activities (including nutrient pollution) alter marine ecosystems in unexpected ways, largely due to impacts on strong interactors [27]. Species that build habitat for other species including reef-building corals, giant kelp, oyster reefs, seagrasses, and mangroves play a critical role. If these species are lost or decline, all the species that feed in or hide in these habitats are compromised. No coral reefs, no coral reef fish! Given that coral reefs contain extremely high species diversity (they are the marine equivalent of tropical rainforest), loss or damage to coral habitat leads to loss of many other species and the ecosystem services they provide.

Marine spatial planners need to be aware that some species are more important than others in maintaining the function and resilience of marine ecosystems. Planning should protect a variety of key habitats, especially those produced by structure-forming organisms, and maintain adequate populations of apex predators.

5. Biogeochemistry

In the sea, and entering the sea from the land (via rivers and the air), are many chemical substances of fundamental importance to biological processes. Marine organisms take up, transform or store these chemicals in ways that affect human interests. Scientists call this "ocean metabolism" biogeochemistry. Many human activities alter biogeochemical processes that affect the distribution of these substances.

Carbon is a major element in all living things, and the amount of dissolved inorganic carbon in oceans is 50 times the amount of carbon in the atmosphere [28]. Carbon dioxide makes the sea more acidic and is the most important greenhouse gas contributing to global warming. Marine phytoplankton remove billions of tons of carbon dioxide from the atmosphere by incorporating it into their cells. This carbon flows to zooplankton and other organisms that eat phytoplankton, then to fishes that eat zooplankton, etc. Of course, not all the carbon in the sea is in fishes; much of it sinks to the seafloor as dead organisms and fecal pellets, where it forms an immense carbon storehouse. Anything humans do that changes the rate of this carbon "rain" to the seafloor, or the rate at which seafloor carbon is oxidized to carbon dioxide, affects ocean acidity and global warming, two major threats to marine ecosystems.

Nitrogen is far less abundant in living organisms than carbon, but, as a major component of proteins and nucleic acids (such as DNA), is no less essential. Indeed, the concentration of chemically fixed nitrogen (in forms such as ammonium and nitrates) limits productivity in many marine ecosystems. Until the 20th Century, atmospheric nitrogen entered ecosystem metabolism mainly through nitrogen fixation by bluegreen bacteria in the sea and plants (such as legumes) on land. Since then, human activities have approximately doubled the amount of fixed nitrogen compounds entering the biosphere [29], and a large fraction winds up in the oceans. That is a problem because these nitrogen compounds stimulate blooms of phytoplankton, which may die in such large numbers that the bacteria decomposing them deplete all the oxygen in the water column, resulting in "dead zones". For several decades now, a dead zone devoid of fishes, crabs, and shrimp has formed seaward of the mouth of the Mississippi River in the Gulf of Mexico off Louisiana, USA, thanks to nitrogen washed off the land or discharged into streams throughout the Mississippi River watershed, from golf courses in Montana and sewage treatment plants in Illinois to hog farms in Tennessee. Even tiny amounts of nitrogen increase phytoplankton populations, reducing water clarity, which matters for tourists and divers no less than to marine animals that search visually for food.

These are only two of many examples of chemicals whose distributions profoundly affect human interests. Managing human activities that affect their movements and transformations is a key consideration in marine ecosystem-based management. This includes polluting activities, but also activities such as fisheries. The combination of increased nitrogen inputs, diseases, and overfishing of the oysters that filtered phytoplankton from Chesapeake Bay, USA, for example, has dramatically reduced water clarity, which has thereby reduced the area of the Bay in which eelgrass and other submerged plants can grow. These plants once provided nursery habitat for young blue crabs and fishes that are now far less abundant. Avoiding alteration of biogeochemical cycles is therefore one of the most important objectives in marine spatial management.

6. Marine ecosystems are complex systems

People (e.g., taxpayers and officials who represent them) pay for marine spatial planners who understand enough about marine ecosystems to maintain or recover what people value. That requires both understanding of the components of marine ecosystems and their interactions; that is, how these complex systems function.

Simple systems are easy to understand: the more you push them, the more they respond. Their response to external influence (forcing) is linear, which makes their behavior easy to predict, which, in turn, facilitates decision-making. But while it may be "a gift to be simple," simple systems are not common gifts. Most things behave simply and predictably only under certain limited conditions. Outside those limits, systems become complex and harder to control. Overall, therefore, their behavior is complex. Moreover, if you add the behavior of one complex thing (system)—say a species—with another—another species—and another—the weather—things start getting very complex very quickly. Marine ecosystems have many more interacting components than this, including the complex socio-political system underlying management, so robust strategies for dealing with complexity that we do not fully understand are especially important for marine spatial planners.

The behavior of a complex system cannot necessarily be predicted from understanding the behaviors of the individual parts because these parts interact. This is central to the widespread observation that sophisticated and expensive fishery population models have not necessarily led to successful fishery management. We might understand the behavior of each population in isolation, but populations behave differently in the context of their ecosystems. Both fish population sizes and ecosystem contexts change over time due to changes in fisheries, pollution, habitat damage, invasive species, and climate change. No matter how much is known about what a population of small fish does in the presence of large fish species, the system behaves differently when those large predators are removed by overfishing or when you have multiple predators, including marine mammals and seabirds, consuming the same small fish.

Complex systems exhibit a kind of stability, in that they generally resist change when they are being forced until the forcing exceeds some threshold (now popularly known as a "tipping point") and the system reorganizes. This is true of both individual populations that have complex behavior, and of whole ecosystems. Species and ecosystem reorganizations can be sudden, leading to a new stable state. The field of fisheries biology critically depends on the assumption that these thresholds do not exist, such that reducing mortality from fishing can always allow an exploited population to recover. In some species that clearly is true. For example, New England, USA, sea scallop populations recovered rapidly within years after areas where they had been over-fished were closed. But Atlantic cod in the same ecosystems have not recovered. There are several plausible theories why this might be so, but all of them involve some threshold that has been exceeded. The message for marine spatial managers is clear. It is not always safe to assume that slight adjustments in human behaviors can recover species populations. And the same is true of ecosystems. The key, then, is to maintain them within limits where they are resistant to change or are resilient, able to return to their former (desirable) state even after they experience a perturbation that puts them (temporarily) in a different state. It is difficult to imagine a better goal for managers than maintaining resilience.

As with species, ecosystems can reorganize quickly to a new state. Coral reefs prevailed in many shallow coastal areas of the Tropical West Atlantic for millennia until very recently. In these ecosystems, herbivores, such as parrotfishes and *Diadema* sea urchins, previously removed algae from patches of reef rock, creating spaces that corals could colonize. In the last three decades, as fishing and disease caused drastic reduction of herbivore populations, coral reefs throughout much of the Tropical West Atlantic, including the Caribbean Sea, have undergone a profound phase shift from domination by stony corals to domination by fleshy algae. Scientists interpret this as a system reorganization to a new state that resists change [27]. It seems unlikely that managers could reverse this change by reintroducing corals to sites that have lost them. Allowing herbivore populations to recover seems a more promising approach.

Similarly, as mentioned earlier, oysters were once phenomenally abundant in Chesapeake Bay, USA, so abundant that they kept phytoplankton abundance low, allowing enough light to penetrate to the Bay floor that benthic eelgrasses grew in many areas, and, consequently, the water was clear and oxygen-rich. The near-disappearance of oysters due to over-fishing, nutrient pollution, and disease precipitated an ecosystem phase change that now resists reversal. Unless oysters can resume their crucial role as filters—which requires much, much higher populations of oysters than the Bay now supports, a recovery that low oxygen concentrations now inhibits—managers are unlikely to see a Chesapeake Bay ecosystem like the one that prevailed before the oysters disappeared [30].

It is not easy to manage in an information-poor environment, and it would be understandable if a marine spatial manager were to think, "It's hopeless! Marine ecosystems are too complex to understand and manage!" In one sense that might be true. Marine ecology cannot yet make highly accurate predictions about all components of marine ecosystems in response to all kinds of forcing. However, there are some principles that seem robust. That is, they are true in many ecosystems under many circumstances. And if one starts by managing according to the principles outlined above, our capacity to maintain or recover what people value will only grow as scientists learn more and provide managers with better guidance.

7. How key ecological concepts relate to ecosystem-based management

Until quite recently, management in marine ecosystems has focused largely on issues such as how many cod can be caught without depleting their populations or what is the minimum gillnet or trawl mesh size that can be used in a particular fishery. These questions often have no geographic constraints or no spatial structure within the broad area where they are applied. In each place there are many managers, each focusing on only a subset of all the marine issues that affect that place, each one largely ignoring what the others do. As Crowder et al. note, this is a recipe for conflict [4]. An exception in some countries has been leasing for oil and gas operations, which usually has much more specific geographic boundaries, although, as with other sectors, biodiversity is seldom a primary consideration in oil leasing decisions. But the increasingly widespread call for change—to a management system that is ecosystem-based and therefore shifts the focus to having a single authority for managing the suite different activities in each place—is a momentous change. The authority does not need to be an individual; it can be a partnership, council or other joint decision-making process—but having one authority is critical to avoiding the pitfalls and resolving the inevitable conflicts in such a planning process.

We have already mentioned that one of the most important insights both natural and social scientists can offer is that different places have differing values in both the biophysical and human dimensions. Another is that they have differing sensitivities. Some ecosystems, or species of concern within them, are more resistant or more resilient to disturbance than others. For the small percentage of the very most sensitive ones, e.g., seabird-nesting colonies, minimizing disturbance is the best strategy; these should be "no-go" areas. In other important areas that are less sensitive, a set of "no-take" marine reserves is more appropriate. In other areas, the higher resilience of some populations allows more sustainable extractive activities to occur. So long as the productive capacity and resilience of the ecosystem is left undiminished, these areas can be managed for limited uses that do not harm ecosystem functions. Finally, areas that are least sensitive or where biodiversity protection is least important can allow a broad range of human activities. This simple four-level hierarchical system of management objectives can be the basis for classifying most or all marine areas, and thus, the basis for MSP and zoning within large marine areas.

Knowing where marine communities, human activities, and jurisdictional borders occur is a key first step in spatial planning. A strategy that many marine ecologists favor is protecting truly unique places and representative examples of all ecosystem types to a degree sufficient to maintain the biodiversity and ecosystem services people value in our changing world. Building resistance and resilience into this system is essential because even the best crystal balls are foggy. In a world that is certain to send us surprises, it is important to have as many interconnected, protected places as needed to provide a high level of assurance that we will not lose what we value. In other words, when the cost of making mistakes is very high but important information is lacking, it is essential to build redundancy into MSP to allow for inevitable mistakes and for learning. This robust strategy allows subpopulations of species that disappear from one place to be replaced by recolonization from subpopulations in other places that are part of the same larger metapopulation. Undoubtedly socio-economic considerations will modify mosaics based on purely ecological criteria, and jurisdictional issues will further modify these. But the odds of success go up dramatically when we get the ecology right from the outset and build in safety margins.

Because scientists know less than we would like, but know that some species have much greater impact in ecosystems than others, it is logical to conserve the ones we know are important. These include large predators, which can play a "keystone" role in their ecosystems, and structure-forming species, which provide habitat for many other species. In many ecosystems, other species including herbivores, e.g., the suspension-feeding oysters discussed above, play different but very important roles, and merit special fail-safe conservation mechanisms.

Knowing these principles makes it clear why bottom trawling, which once occurred very widely, is increasingly being restricted around the world. Bottom trawling is the least discriminating of all fishery methods; it often kills very large numbers of organisms that are not targeted by the fishery. It also causes unequaled habitat destruction [31,32], so this combination of collateral damage makes it is the most destructive of fishing methods. It is not difficult to imagine a time not too far in the future when marine spatial planners will restrict bottom trawling to "general use" zones where biodiversity value is low and/or resilience is high.

8. The place-based approach to managing marine ecosystems

Marine ecologists and oceanographers have been actively developing and using new tools, including geospatial analysis, remote sensing, molecular techniques, telemetry, modeling, and quantitative analysis to understand the spatial and temporal dynamics of marine ecosystems and their component organisms in relationship to environmental variation. These new tools have broadened our understanding of the linkages between marine habitat mosaics and population dynamics, and between spatial and temporal dynamics and the function of marine food webs. Formerly, management in marine systems dealt only broadly with space or places, but the detailed information now available allows spatially explicit analyses and management possibilities previously considered impossible. Spatial planning with respect to networks of marine reserves, migratory pathways of endangered marine megafauna, even zoning of large coastal regions, e.g., the Great Barrier Reef Marine Park, are now possible. The ability to produce a dynamic map of the distribution and movements of marine animals relative to fixed and dynamic oceanic features and to model their behavior is also within reach. The next step is to develop a MSP approach that can incorporate the biophysical with the socio-economic and jurisdictional layers

Marine space has typically been seen as "unpeopled", with users entering and leaving for resource extraction, recreation, or travel, but with little attachment to particular places. To 'place' people in marine environments, we need to improve our understanding of the value of specific marine resources to people, how these resources have been managed or allocated by user groups (if at all), human distribution in and dependence on particular places, the compatibility of human activities with one another, human behavior in marine space, and linkages between at sea activities and shore-side communities (see St. Martin, in this issue). Social scientists from a variety of disciplines (anthropology, geography, economics, political science) bring a diverse set of skills to understanding these issues [33]. Sustainable marine ecosystems must support both the biophysical and human dimensions of these coupled social–ecological systems [34].

As mentioned previously, the escalating crisis in marine ecosystems is in part institutional, resulting from fragmentation in governance systems together with spatial and temporal mismatches between biophysical systems and the mechanisms we have created to manage human interactions with these systems [4]. MSP has the potential to become an important means to reduce or avoid problems arising from single-species management, sectoral decision-making, and gaps between ecological and jurisdictional boundaries. Place-based approaches call for integrated management of the full suite of human activities occurring in spatially coherent areas identified on the basis of a combination of biological, physical, and socioeconomic criteria (8).

Place-based management of marine ecosystems requires a hierarchy of management practices starting at the most general level with the concept of ecosystem-based management and moving toward the development of an integrated approach that accords priority to the maintenance of healthy, biologically diverse, productive, and resilient ecosystems. This approach explicitly recognizes that people are part of marine ecosystems and any approach to managing the resultant socio-ecological systems must take into account human–environment interactions and the governance systems that guide or steer these interactions. The key to success in place-based management of marine ecosystems is to design governance systems that align the incentives of stakeholders with the objectives of management—we need governance systems that are designed to work. MSP that fully incorporates the underlying ecosystem template and explicitly integrates the socio-economic and governance overlays can form the basis for adequate protection of marine ecosystems and sound use of marine resources.

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