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Guiding ecological principles for marine spatial planning

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ABSTRACT

The declining health of marine ecosystems around the world is evidence that current piecemeal governance is inadequate to successfully support healthy coastal and ocean ecosystems and sustain human uses of the ocean. One proposed solution to this problem is ecosystem-based marine spatial planning (MSP), which is a process that informs the spatial distribution of activities in the ocean so that existing and emerging uses can be maintained, use conflicts reduced, and ecosystem health and services protected and sustained for future generations. Because a key goal of ecosystem-based MSP is to maintain the delivery of ecosystem services that humans want and need, it must be based on ecological principles that articulate the scientifically recognized attributes of healthy, functioning ecosystems. These principles should be incorporated into a decision-making framework with clearly defined targets for these ecological attributes. This paper identifies ecological principles for MSP based on a synthesis of previously suggested and/or operationalized principles, along with recommendations generated by a group of twenty ecologists and marine scientists with diverse backgrounds and perspectives on MSP. The proposed four main ecological principles to guide MSP—maintaining or restoring: native species diversity, habitat diversity and heterogeneity, key species, and connectivity—and two additional guidelines, the need to account for context and uncertainty, must be explicitly taken into account in the planning process. When applied in concert with social, economic, and governance principles, these ecological principles can inform the designation and siting of ocean uses and the management of activities in the ocean to maintain or restore healthy ecosystems, allow delivery of marine ecosystem services, and ensure sustainable economic and social benefits.

1. Introduction

The health of global marine ecosystems is in serious decline, and multiple stressors, including overfishing, pollution, invasive species, coastal development, and climate change, compromise the ability of ocean and coastal ecosystems to support and sustain the goods and services people want and need [1–4].

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Uncoordinated expansion of existing uses of the ocean and the addition of emerging uses, such as renewable energy and large-scale aquaculture, along with a rapidly growing coastal human population, are likely to further exacerbate the decline of marine ecosystem health. Maintaining the well-being of ocean ecosystems, as well as their ability to provide essential ecosystem services for human populations [5,6], will require an alternative strategy to replace the current patchwork of complex, uncoordinated, and often disjointed rules and regulations governing use of coastal and ocean waters around the world [7]. The future of the oceans depends on successful, immediate implementation of a comprehensive governance framework that moves away from a sector-by-sector management approach to one that (1) balances the increasing number, diversity, and intensity of human activities with the ocean's ability to provide ecosystem services; (2) incorporates appropriate ecological, economic, social, and cultural perspectives; and (3) supports management that is coordinated at the scale of ecosystems as well as political jurisdictions [1,7–9]. Each of these goals demands spatially explicit consideration of multiple human uses and their compatibility, conflicts, and synergies with each other and with the ecosystem [10–14].

Such comprehensive, integrated management of marine uses and activities can be achieved in part through ecosystem-based marine spatial planning (MSP). Ecosystem-based MSP is an integrated planning framework that informs the spatial distribution of activities in and on the ocean in order to support current and future uses of ocean ecosystems and maintain the delivery of valuable ecosystem services for future generations in a way that meets ecological, economic, and social objectives [15]. In addition, this integrated planning process moves away from sectoral management by assessing and managing for the cumulative effects of multiple activities within a specific area [14]. An MSP process also emphasizes the legal, social, economic, and ecological complexities of governance, including the designation of authority, stakeholder participation, financial support, analysis of current and future uses and ocean condition, enforcement, monitoring, and adaptive management (Fig. 1; [16]).

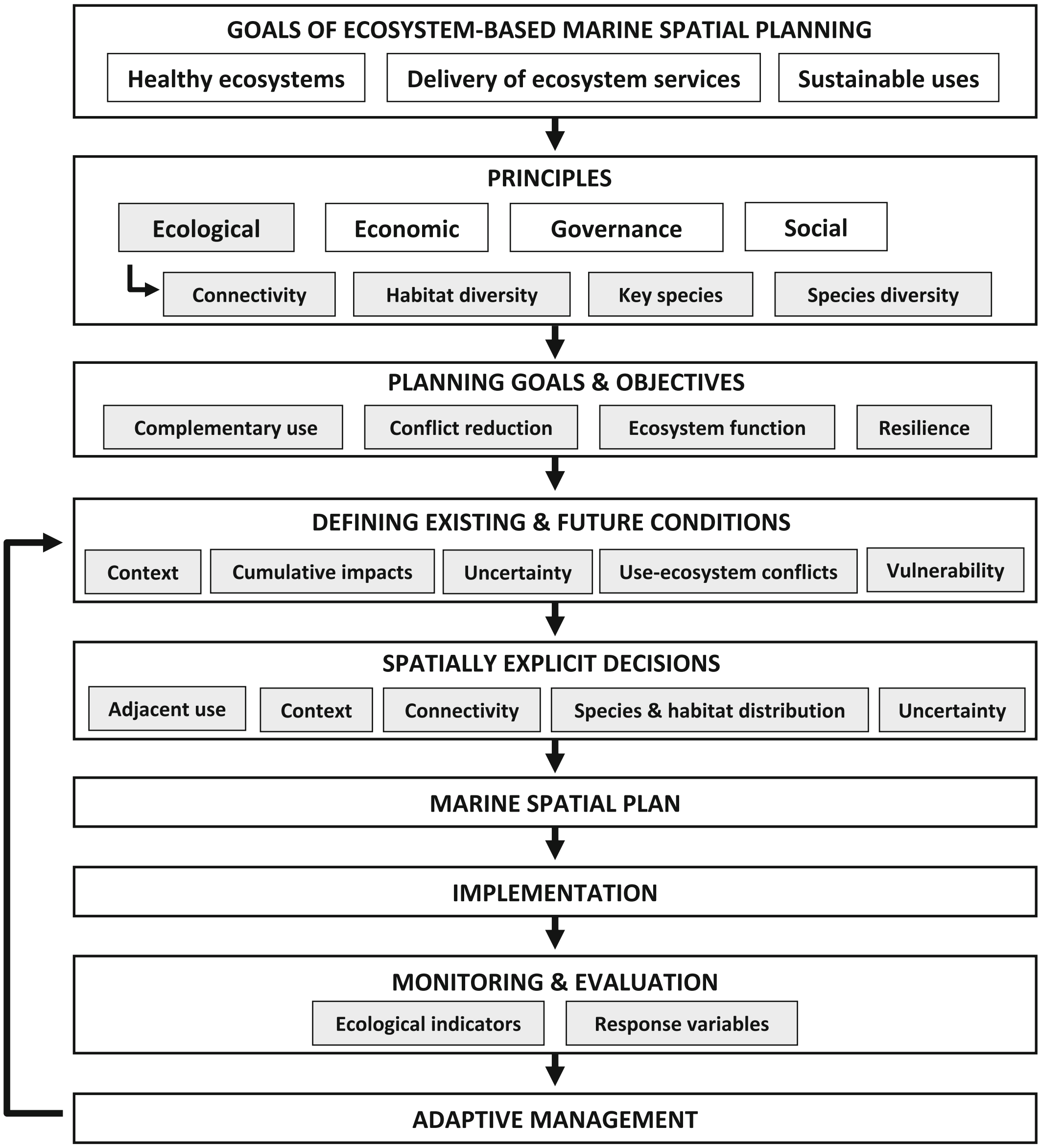

Fig. 1. Flow diagram outlining the key aspects of any marine spatial planning process with an emphasis on how ecological principles can be used throughout the planning and implementation process. Boxes that specifically pertain to components of an ecosystem-based approach are shaded in gray. This diagram would be used in conjunction with similar diagrams outlining the components of economic, governance, and social principles to develop and implement a comprehensive marine spatial plan.

Policy makers in the US have begun to consider MSP a viable strategy for managing human uses in federal waters. In June 2009, President Obama issued a memorandum calling for the development of a National Ocean Policy (NOP) that protects, maintains, and restores coastal, ocean, and Great Lakes ecosystems [17]. The President's directive established an Interagency Ocean Policy Task Force (OPTF) to develop recommendations for a national ocean policy and framework for effective coastal and marine spatial planning. In its Interim Report [17], the OPTF identified ecosystem-based management (EBM) as a key element of the NOP, with MSP as a crucial approach to implementing EBM. The Interim Framework for Effective Coastal and Marine Spatial Planning (www.whitehouse.gov/oceans) was released on December 14, 2009, and the final report will be issued following a 60-day comment period.

The Obama Administration's efforts are one part of a larger trend toward the implementation of comprehensive marine spatial planning and management in coastal and ocean ecosystems. To date, multiple countries have undertaken MSP initiatives to spatially mange current or emerging human uses, including the United Kingdom's part of the Irish Sea [18], Belgium's part of the North Sea [19], the sea areas of China [20], Canada's Eastern Scotian Shelf [21], the high seas [22], Australia's Great Barrier Reef Marine Park [23] and, within the USA, the coastal waters of Massachusetts (Draft Ocean Plan 2009, http://www.mass.gov/Eoeea/docs/czm/v1-complete.pdf), Rhode Island (http://www.crmc.ri.gov/samp_ocean.html), and North Carolina [24]. However, many of these MSP efforts have a relatively limited scope and have not yet developed a comprehensive planning process that includes all existing uses of the ocean. For example, the Massachusetts Ocean Plan has no authority over fishing or nearshore activities; in California, the Marine Life Protection Act Initiative (http://www.dfg.ca.gov/mlpa) focuses on marine protected areas and fishing. In contrast, others have explicitly addressed multiple sectors, including fishing, oil and gas development, aquaculture and shipping activities (e.g., the integrated management plan of the Norwegian part of the Barents Sea) [25]. In addition, although nearly all planning efforts have outlined one goal of MSP as protecting marine ecosystem health, in many cases, ecological goals and objectives were not fully incorporated into the planning process.

This paper focuses on articulating ecological 'principles,' or guiding concepts, that can be used to meet the goals and objectives of ecosystem-based MSP (Fig. 1). Although the importance of ecosystem health and functioning is implicit in most MSP processes (i.e. if an ecosystem is not functioning well, many services cannot be provided), it is not guaranteed to serve as a foundation of the process. In some cases, ecosystem health may not be the primary goal (e.g., siting multiple industrial uses in the Norwegian part of the Barents Sea); in others, ecosystem goals may not be well defined. In either case, social and economic goals have often been prioritized to the detriment of ecological goals and objectives.

Two notable examples of resource management processes that have incorporated ecological principles into a planning process are Australia's Great Barrier Reef Marine Park Authority (GBRMPA) [23] and Canada's Eastern Scotian Shelf Integrated Management project (ESSIM) [26]. In the mid-1990s, the GBRMPA rezoned the Great Barrier Reef Marine Park through a process that included intense involvement of users, scientists, and the public in order to increase the number and types of species and habitats that were represented in either no-take or habitat protection zones. This rezoning process increased the spatial extent of protected zones, while maintaining a large portion of the park in general-use zones to minimize negative impacts on users. The ESSIM project used a multi-stakeholder approach to assess human uses, ecosystem features, and the interactions between these components to develop planning objectives based on the ecological well-being of the region and sustainable human use [27]. The GBRMPA rezoning process and ESSIM project are examples that illustrate how specific ecological objectives can be incorporated into the planning process from the beginning to achieve the goals of ecosystem-based MSP.

This paper does not seek to resolve the debate over the relative roles of social, economic, and ecological objectives in developing MSP, but argues that ecological principles should be at the foundation of any ecosystem-based MSP process. Since ecosystem-based MSP is based on the notion that functioning ecosystems support multiple ocean uses, such planning processes should include guiding principles to ensure that those eco system functions are in fact provided. These ecological principles should be carefully considered along with social, economic, and governance principles that are being developed through parallel and complementary efforts (Fig. 1). The goal of this paper is to present core ecological principles that represent a synthesis of the best current scientific understanding of the attributes of healthy, functioning ecosystems and that can guide ecosystem-based MSP regardless of scale or context. To achieve this goal, previous delineations and applications of ecological principles used for MSP and other ecosystem-based planning frameworks were synthesized and supplemented with input from an expert workshop held in Monterey, California, in March 2009.

2. Synthesis

2.1. Previously proposed ecological principles

The biophysical characteristics of marine ecosystems and the nature of perturbations to these systems constrain the range, types, and intensities of human activities that can be conducted in a given area without impairing ecosystem function and services [10]. To fulfill the purpose of sustaining valuable ecosystem services, ecosystem-based MSP must be grounded in ecological principles that are based on the best readily available science so that activities can be reconciled with the objective of maintaining or restoring functioning, resilient ecosystems [10]. A variety of ecological attributes and principles have been used to guide the design of existing (e.g., MPAs) and emerging (e.g., MSP) area designation processes (Table 1). Although MPA designation and MSP have different goals (conservation vs. sustainable delivery of ecosystem services and human use, respectively), the goals are at least partially related and there is value in looking at both processes for ecosystem-based principles, goals, and lessons learned.

Two ecological attributes—connectivity and native species diversity—have been most commonly identified as essential for maintaining functioning marine ecosystems (Table 1). Connectivity, or the exchange of individuals among geographically separated subpopulations [28], is necessary for a wide range of ecological and evolutionary processes, including population replenishment, recovery from major disturbances, maintenance of genetic diversity, and persistence of species in the face of environmental change. Species diversity—the variety and abundance of species within an area or ecosystem—tends to be positively correlated with ecosystem health by increasing the functioning of marine ecosystems [29] and the provision of several ecosystem services [30–32].

Additional attributes identified in the literature as important to sustaining healthy marine ecosystems include habitat heterogeneity, habitat structure, and land-sea connectivity, which can be considered manifestations of diversity at the larger, landscape scale. These further recognize the fundamental importance of heterogeneity and spatial dynamics in promoting resilient and productive ecosystems (e.g., [10,33,34]). Uniqueness or rarity and vulnerable life stages or habitats were also identified to

Table 1
Previously suggested ecological attributes for existing and suggested planning processes.

Source			Ecological attributes																	
	Connectivity	Species diversity	Habitat heterogeneity	Habitat structure	Land–sea connectivity	Uniqueness/ rarity	Resilience	Vulnerable life stages	Biological productivity	Natura lness	Species interactions	Vulnerable habitats	Aggre- gations	Biogeo- chemistry	Bio- geography	Ecosystem integrity	Fitness con- sequences	Proportional importance	Extremes	Water quality
GBRMP [36]		x	x		x	x														
Roberts et al. [34]	x		x		x			x				x			x					
Derous et al. [35]						x		x		x			x				x	x		
Rogers et al. [145]		x		x	x				x											
Crowder and Norse [10]	x		x	x							x			x						
Appledoorn [136]	x			x																x
Convention on biological diversity		x				x	x	x	x	x		x								
Gaydos et al. [146]	x		x				x				x					x			x	
MLPA [147]	x	x	x	x	x	x		x	x	x	x	x			x	x				
Tissot et al. [148]	x	x					x													

acknowledge the differential susceptibility of life stages, organisms, and habitats to human uses and activities (Table 1). These attributes also play fundamental and often irreplaceable ecological roles in maintaining populations and ecosystems [34–36]. Finally, some authors highlight the fundamental importance of biogeochemistry, biogeography, and water quality in recognition of key abiotic factors that structure ocean ecosystems (Table 1). These ecosystem attributes highlight the necessary overlap between conservation and MSP goals—many species and ecosystem processes are essential for providing the services desired from the oceans. For ecosystem-based MSP to be effective, it must ensure that this suite of species is abundant and sustainable and important biotic and abiotic processes are maintained. In the MSP process, however, these ecosystem attributes will necessarily be incorporated into a larger framework that also involves maintaining existing and future uses of the ocean.

2.2. *Ecological principles for marine spatial planning*

To augment the review of proposed ecological principles for MSP (Table 1), a group of academic, government, and NGO scientists was convened for a 2-day workshop with the goal of producing a synthetic list of ecological principles for ecosystem-based MSP and operational guidelines for implementation. Based on this input and synthesis of information from the literature, four basic ecosystem principles are proposed to guide ecosystem-based MSP (Table 2)—maintain or restore (1) native species diversity, (2) habitat diversity and heterogeneity, (3) key species, and (4) connectivity. These four points are expanded below and highlight current scientific evidence that suggests maintaining or restoring these attributes is necessary for healthy marine ecosystems and the provision of services from those ecosystems. Although these principles are allied with conservation goals, they do not require conservation beyond the fundamental goal of maintaining those species and ecosystems that are necessary to support the activities that people pursue on and in the oceans. Two overarching guidelines are also outlined, the need to consider (1) context and (2) uncertainty, that should be addressed along with the four ecological principles in each planning and management area to ensure that temporal and spatial variability and non-linearities that characterize all ecosystems are adequately addressed. Although the four ecological principles and two overarching guidelines have been discussed before in different combinations and contexts, they are presented here in a unified synthesis and should (1) form the scientific foundation of any ecosystem-based MSP process; (2) inform the goals of the planning process; and (3) be incorporated into the operational decisions of MSP (Fig. 1). One potential application of these principles is presented for coastal California that, once integrated with socioeconomic and governance principles, could provide a framework for the implementation of MSP in California and other marine regions.

2.2.1. *Maintain native species diversity*

Maintaining or restoring species diversity, composition, and functional redundancy (e.g., the degree to which multiple species perform similar ecological functions) is essential for sustaining productive and resilient ecosystems [30–32]. Species diversity, from local to global scales, can affect multiple ecosystem functions including maintenance of productivity [31,37], resistance to and recovery from perturbations [38,39], capacity to maintain functional redundancies within an ecosystem [40,41], and stable food web dynamics [42,43]. Although most experimental work linking biodiversity to ecosystem functioning has not distinguished between native and exotic species, and in some cases exotic species perform essential functional roles and ecosystem functions formerly performed by native species [44,45], the focus here is on maintaining native species specifically in recognition of the unpredictable and highly deleterious impacts of some introduced alien species.

Measurements of biodiversity can range from local (alpha diversity) to global (gamma diversity) scales [46] and can span multiple levels of biological organization from species richness and composition, to genetic diversity, to diversity of functional groups. Each biodiversity metric conveys different information about the structural and functional attributes of a particular ecosystem, and collectively they provide important information at different spatial scales. Despite the numerous scales and definitions of diversity, it is clear that, on average, more diverse assemblages support greater ecosystem function [47] and in turn, also provide more ecosystem services [30].

Species richness and composition are critical aspects of an ecosystem's structure. These metrics are also the most commonly measured in ecological surveys allowing them to be compared

Table 2
Quick reference for recommended ecological principles for ecosystem-based MSP.

Principle	Important features	Ecosystem function(s) supported	Considerations for operationalizing
Maintain native species diversity	Species diversity and composition	Productivity	Diversity measures—species, genetic and functional
	Genetic diversity	Resilience (resistance and recovery)	Historic baselines
	Functional redundancy	Food web stability	
Maintain habitat diversity and heterogeneity	Habitat representation	Maintenance of species diversity	Habitats in a range of environmental conditions
	Habitat arrangement	Connectivity	Size of habitats
	Dynamic habitats	Shelter/refuge	Proximity of habitats
		Productivity	Spatial arrangement of habitats
			Historic baselines
Maintain populations of key species	Keystone	Species diversity	Age structure, dispersal, and population demographics
	Foundation	Food web stability	Breeding and aggregation locations
	Basal prey	Resilience	Migration routes
	Top predators	Ecosystem engineering	Historic baselines
Maintain connectivity	Population and species persistence	Species diversity	Scale of ecosystem
	Flow of subsidies	Metapopulation and metacommunity dynamics	Dispersal distance (larval and adult)
			Oceanographic currents/features

across multiple temporal and/or spatial scales to reveal functional attributes of biological communities.

Genetic diversity tends to be measured within populations on smaller spatial scales [48], but there are a growing number of studies that measure genetic diversity and heterogeneity across latitudinal gradients. These large-scale measures of genetic diversity can help identify boundaries of biogeographic regions [49], dispersal patterns of larvae [50], and differential responses to changing climate conditions [51]. Although genetic diversity is important for ecological functioning [52], landscape-scale genetic data are rare, making it difficult to include this kind of diversity in ecosystem-based MSP.

Functional diversity measures the variety of types of organisms that serve different functional roles within a community irrespective of their taxonomic grouping [53,54]. Functional diversity focuses on the guilds of species that are responsible for biological processes within ecosystems [55]. Species redundancy within functional groups can be low in marine communities suggesting that the loss of a single species could result in the loss of an entire functional group [56–58], even in diverse ecosystems [59,60]. The strong positive correlation between species diversity and functional diversity suggests that functional diversity will be maintained if species diversity is maintained [56].

The loss of biodiversity, altered species composition, and subsequent loss of ecosystem functioning have been documented in marine habitats across the globe [61–65]. Together with the documented examples of damage caused by some introduced non-native species [66], these examples highlights the importance of maintaining high native species diversity as an ecological principle that underpins all other management goals and extends beyond traditional conservation goals [30]. Loss or reduction of native species diversity, coupled with changing environmental conditions, can push ecosystems beyond critical thresholds and drastically alter community structure, ecological functioning, and provisioning of services as has been seen in coral reef [67], kelp forest [68,69], and coastal soft-bottom ecosystems [43]. In all of these examples, the type of ecosystem services that could be provided was altered by dramatic changes in species diversity and composition.

2.2.2. Maintain habitat diversity and heterogeneity

Just as maintaining a variety of species can better sustain functioning ecosystems, maintaining habitat diversity—the number of different habitat types within a given area—is a crucially important component of healthy marine ecosystems. Diverse habitats promote species diversity by acting as refugia from competition and predation [70,71], providing multiple sources of prey [72] and settlement substrates [73], supporting species with specialized requirements, and ameliorating environmental stressors [74]. Maintaining habitat heterogeneity—the spatial arrangement and relationships among habitat patches across the seascape—is also critical to ecosystem functioning. Habitat heterogeneity influences connectivity among habitats and facilitates the successful movement of individuals among multiple habitats throughout their lifetime [75,76]. Habitat diversity and heterogeneity are also important for supporting the exchange of organisms and materials among habitats [77–79].

Nevertheless, all habitats are not created equal, nor are they static. For example, upwelling circulation along the eastern margins of the world's ocean basins brings nutrient-rich water from the deep ocean to nearshore surface waters, fueling high levels of primary production that form the base of species-rich and productive nearshore food webs [80,81]. Many animals visit these regions seasonally and form feeding, breeding, and aggregation habitats that only exist for a limited time each year. The development and persistence of these upwelling fronts are essential to the functioning of nearshore marine communities [82,83], and changes to these important habitat-forming features can have significant effects on the survival of adults and successful rearing of young [84,85].

In most ecosystems, increased species diversity is positively correlated with increased habitat diversity [34,86]. Thus, maintaining high habitat diversity and heterogeneity is an important and useful proxy for maintaining species diversity at multiple spatial scales [41]. Because habitat data (e.g., mapping) are relatively easier to collect than species-level data, habitat diversity is often used as a proxy for species diversity [87] for management and conservation planning purposes (e.g., [79]). To maintain the relationship between habitat and species diversity, however, it is necessary to protect habitats of sufficient size, proximity, and numbers so the habitat mix is viable and resilient, allows for individuals to move between habitats (e.g., habitat corridors), and increases the likelihood that all habitats of a given type will not be destroyed during catastrophic events [88,89]. In addition, it is likely that the provision of multiple ecosystem services will be maintained with the protection of multiple habitat types [90].

2.2.3. Maintain key species

Although weak interactions among a large suite of species can have important stabilizing effects on community structure and functioning [91,92], the dynamics of marine ecosystems are often driven by a few key species that have disproportionately strong effects on community structure and function [93]. These key species are essential to marine ecosystem functioning, and fluctuations in their populations can drive high levels of variability in community structure and functioning. Maintaining populations of key species—such as keystone species, foundation species, basal prey species, and top predators—is especially important because there is typically limited functional redundancy of their roles in the community. Such cascading trophic interactions are common in a wide variety of marine ecosystems [94].

Keystone species have community-level effects that are often disproportionate to their biomass [95,96]. For example, in temperate intertidal communities, the seastar *Pisaster ochraceous* maintains high levels of species diversity by consuming the dominant space competitor *Mytilus californianus*, thereby allowing competitively inferior species to persist [97,98]. Predators can also function as keystone species by driving community changes through trophic cascades [99,100]. Sea otters, for instance, promote the presence and persistence of kelp forest habitats around the Aleutian archipelago by consuming herbivorous sea urchins and releasing kelp from intense grazing pressure [69].

Foundation groups or species provide the template from which most additional species interactions and dynamics emerge by creating habitat and refuge for large numbers of other species [101]. Foundation groups or species are dominant structure-forming organisms that create productive and complex habitats, and include mangroves, seagrass beds, salt marshes, oyster beds, and kelp forests, and enhance biodiversity through their facilitative effects [102]. Particularly at the land–sea interface, these foundation species provide such services as coastal protection, erosion control, water catchment, and nutrient retention [103]. Populations of many foundation species have seen massive declines over the last decade [63,104,105], so it is imperative both to recognize the importance of foundation species and the role they play in creating habitat, increasing species diversity, and structuring marine communities around the world [106–108].

Additional key species can be found at either end of the food chain. Basal prey species, such as microbes, certain phytoplankton, macroscopic algae, krill, and small pelagic 'forage' fishes such as anchovies and sardines, form important prey for higher consumers in the food chain and influence the structure and stability of food web dynamics [84,109]. These basal species can have limited redundancy and one species often dominates an entire trophic level [110]. Temporal and spatial variation in primary productivity can alter the type and species composition of basal species, which can have significant negative effects on higher trophic levels [82]. As noted above, top predators also tend to have strong effects on food web dynamics because they often drive trophic cascades in marine ecosystems [99,111]. However, the ecological role of top predators is diminished in many parts of today's ocean because of historical depletion of predator populations (e.g. [64,112]). Top predators may also play an important functional role in connecting distant ecosystems [113] due to their mobility and tendency to move between specific areas [114]. It will be important to continue to document the movement of these species through tagging and tracking programs, such as Tagging of Pacific Pelagics (TOPP, www.topp.org) and Pacific Ocean Shelf Tracking project (POST, http://www.postcoml.org/), so that migration corridors, feeding grounds, and aggregation and breeding areas are accounted for in both the spatial planning process and in ongoing management.

These four types of key species—keystone species, foundation species, basal prey, and top predators—should receive special consideration throughout the MSP process. These species are important drivers of community structure and functioning, and decline of their populations below functional thresholds will result in significant losses of ecosystem services. Because of their disproportionate importance in maintaining ecosystem functions and services, ecosystem-based MSP should aim at maintaining and, where necessary, restoring populations of key species.

2.2.4. *Connectivity*

Connectivity among habitats and populations in marine ecosystems is critical for population and species persistence. Connectivity can occur through the movement of individuals (larvae or adults), nutrients, or materials (e.g., nutrient and detritus) across permeable habitat boundaries. The complex life cycle of most marine organisms involves a pelagic phase (i.e., open populations) in which the movement of individuals is controlled by oceanic currents and eddies and the swimming capability of larvae [115–117]. Across different life histories, dispersal distance may range from less than a meter to hundreds of kilometers [118–120]. Most planktonic larvae have been considered to have long-distance dispersal potential over evolutionary and ecological time scales, but recent evidence for limited movement in coral reef fish and sharp genetic breaks (e.g. [121]) suggest that dispersal can be much shorter than expected [28,122,123]. These recent estimates of short dispersal range suggest that there are effective local retention mechanisms that may provide increased resilience of local populations through increased local reproduction. Recently, for example, a comparison of regional ocean model system (ROMS) modeling of ocean currents in central California and the strength of genetic gradients suggested that local larval retention may be 10–50 times higher in coastal populations than suggested by current models (Galindo et al., in review).

The details of large and small-scale dispersal dynamics throughout a species' life history are critical for maintaining metapopulation and metacommunity dynamics [124]. Individual populations are connected to one another across heterogeneous landscapes by the movement of individuals from one location to another. Due to population and ocean circulation dynamics, some sites may act as larval source populations, while others may be larval sinks that depend entirely on recruitment and migration from other sites for population persistence (see [125] for examples).

Successful recruitment and migration across the landscape is also tightly linked to the quality and suitability of available habitat. Reductions in cohort abundance may be as high as 100% in areas where suitable habitat is unavailable even though larval connectivity is high [73]. In addition, many large marine seascapes—over which spatial planning may be important—span environmental gradients that may exert strong natural selection on populations of larvae that settle in particular areas [126]. Depending on whether populations have strong local retention or, conversely, if they are replaced each generation from a large larval pool, the populations may be locally adapted. The ability of local populations to recover from local perturbations may be limited if locally adapted species become extinct.

The flow of nutrients and other materials between species and habitats is another important aspect of connectivity that contributes important subsidies to distant food webs [127]. The delivery of allochthonous subsidies can increase primary and secondary productivity [109,128], alter predator–prey relationships [129], and change nutrient cycling dynamics [130] in the receiving habitat. Understanding the movement of organisms, nutrients, and materials throughout the marine landscape is necessary to determine the appropriate size, spacing, and location of use areas [131] and requires an understanding of the biology (i.e., larval duration) and physical transport properties of different water masses over time [28]. Recent studies also highlight the importance of connectivity in maintaining the structure and functioning of some ecosystems [132].

2.3. *Overarching guidelines—accounting for context and uncertainty*

While the preceding principles describe structural components that are essential for healthy, functioning marine ecosystems, there are also general, overarching guidelines—the consideration of the influence of context and the pervasiveness of uncertainty—that must also be accounted for in operational decisions of MSP (e.g., use location and distribution; Fig. 1). These guidelines are especially important to address across biogeographic regions and in the face of uncertainties regarding future changes induced by climate and human uses of the marine environment.

2.3.1. *Context*

Contextual factors, such as geomorphology and biogeography, as well as the type, distribution, frequency, and intensity of existing and contemplated ocean uses must be considered when applying the above ecological principles to be able to achieve the operational goals of ecosystem-based MSP (Fig. 1). Ecosystem structure can be visualized as a nested hierarchy, with processes occurring over a range of spatial scales from larger to smaller. For instance, each ocean basin can be subdivided into ecoregions based on oceanographic currents and latitudinal variation in temperature; these ecoregions can be further divided into biogeographic regions that are broadly categorized by different species assemblages and habitat types; and each biogeographic region is made up of multiple types of habitats that contain their own assemblages of species [133]. What is 'natural' for a particular location depends on where it sits within these different hierarchies. For example, the MLPA process in California spans several biogeographic regions, with the result that predicting natural levels of species and habitat diversity at any given location requires knowing which region it is in. Targets and reference points for the creation and assessment of area-based plans will necessarily vary across bioregions.

To account for these nested hierarchies and processes, MSP efforts should explicitly address them from small to large scales. Moreover, management plans should be updated on a periodic basis to assess and address possible changes in native species diversity, habitat diversity and heterogeneity, key species or groups, and demographic connectivity, as discussed above, as well as changes associated with climate change and emerging ocean uses.

2.3.2. *Uncertainty*

All ecosystems and ecosystem processes are characterized by complex interactions and non-linear dynamics that are not fully understood, resulting in uncertainty regarding future responses to perturbations and management interventions. Uncertainty about ecosystem dynamics and responses to current and emerging uses is inherent and should be reduced but is unlikely to ever be eliminated. Ecosystem uncertainty is compounded in important but largely unknown ways as a consequence of interactive effects of multiple stressors in marine ecosystems [134] and by differential vulnerability of diverse habitat types to similar threats [135]. Moreover, future conditions are uncertain, both because of natural environmental variability and because of uncertainty surrounding the consequences of human activities. In particular, the precise effects of climate change on ocean circulation, temperature, wave energy, and acidification are still uncertain and scientists know little about the feedback loops that could enhance or ameliorate these impacts. Variability and uncertainty in ocean ecosystems make it imperative to take a precautionary approach within the planning and governance structure [136], such that the absence of information on the effect of an activity is not interpreted as the absence of impact or harm to the ecosystem [137]. In the face of uncertainty, it is also critical to build redundancies (especially among key species, groups, and drivers of ecosystem structure) and buffer areas into the MSP framework that are akin to creating an insurance policy for environmental changes [34] so that ecosystem functioning and services will be protected (Fig. 1) [10]. Furthermore, uncertainty demands that monitoring of changing climate, ecosystem state, and key ecosystem characteristics be a central component of MSP so that adaptive management can be practiced [138].

3. Application

3.1. *Operationalizing ecological principles and overarching guidelines*

The ecological principles discussed above can be used as a foundation for ecosystem-based MSP to promote a healthy ocean, the delivery of ecosystem services, and sustainable human use of the ocean. These principles can also be used to identify management strategies and build multi-objective solutions to achieve healthy ecological, social, and economic systems (Fig. 1). To create effective management objectives, it will be important to identify the role(s) of these ecological principles in sustaining ecosystem health and human well-being in each management region. Regional differences in ecological systems and ecosystem service values may result in trade-offs among the ecological principles, as well as among ecological, social, and economic principles to meet management objectives. However, defining objectives for each set of principles and examining them together will help to assess where trade-offs are appropriate and how the goals of the planning process can be met.

How each ecological principle is used in the planning process may differ between regions based on the types of data that are available, the spatial resolution of those data, and the ecosystem processes of interest. In all cases, however, the best readily available science should be used for translating ecological principles into operational decisions [139]. Where scientific information is not readily available, managers may rely on data that serve as proxies for the ecological attribute of concern (e.g., assessing connectivity using oceanographic circulation patterns when larval dispersal data are not available) or expert opinion that is supported by the weight of evidence, but should also invest in meaningful monitoring and manage adaptively as new information is gathered.

3.2. *Using ecological principles to guide the development of a marine spatial plan*

There are multiple possible approaches to implement the ecological principles and modifying guidelines presented above. In a spatially explicit planning approach, the first steps should involve identifying existing and future conditions by assessing the vulnerability of species and habitats to activities, the cumulative impacts of multiple activities, local context and uncertainty, and areas where conflicts exist between users and the ecosystem and between multiple users (Fig. 1). Assessments can identify areas where ecosystem health and human well-being may be compromised by the amount or type of activities. Within the planning area, spatial delineations of management measures, where appropriate, should be based on: (1) explicitly identified ecosystem and socioeconomic goals; (2) an assessment of the ranges, types, and intensities of human uses that are compatible with those goals; and (3) use rules that favor compatible uses. The spatial distribution of management measures within each planning region would constitute a marine spatial plan with accompanying management goals and objectives.

The ecological principles identified here can be used in an ecosystem-based MSP implementation framework by guiding the ecological goals and objectives of the process as well as making initial spatial delineations using the following information: (1) populations of native and/or key species, habitats, or connections that must be maintained within a region; (2) the amount of replication that is necessary to maintain populations of native and/or key species and habitat diversity and heterogeneity; (3) the spatial arrangement of areas that would ensure connectivity among populations of native and/or key species, habitats, or subsidies; and (4) adjacent areas are as complementary as possible (e.g., no industrial uses next to protected areas; Fig. 1). These areas would then be compared with social and economic goals to determine the spatial arrangement of human activities.

This kind of comprehensive planning and implementation process, which is based on ecological and socioeconomic principles and objectives, is preferable over a sector-by-sector or activity-by-activity approach for two reasons. First, it addresses the challenge of integrating the many individual spatial planning processes needed for each activity by providing a comprehensive framework within which individual activities can be addressed. Second, it accounts for possible future uses and needs by specifying goals against which new activities can be evaluated. This system could yield explicit criteria and management objectives for identifying the types and combinations of human uses that can occur within different areas based on known or expected compatibility and impacts of different activities on each other and on key ecosystem attributes. It could also focus monitoring efforts, including the design of monitoring protocols and choice of ecological metrics, so that the effectiveness of spatial planning and management schemes can be evaluated over time and adjusted to better achieve management and policy goals (Fig. 1).

4. Discussion

MSP has emerged as a framework for implementing an ecosystem-based, coordinated governance structure in the world's oceans. Maintaining marine ecosystem health and human well-being requires a comprehensive assessment of the vulnerability of marine ecosystems to human activities and how the impacts of those activities can be best partitioned in ocean space. The ultimate goal of ecosystem-based MSP is to distribute human uses in the ocean in a way that allows for existing and emerging cultural, recreational, commercial, and industrial uses, while supporting healthy ecosystems and sustaining the provision of ecosystem services for current and future generations.

Several planning processes and tools already exist to aid planning and implementing ecosystem-based MSP. Feasibility analyses can identify the best spatial placement of activities (e.g., determining possible locations for renewable wind projects; see Massachusetts Ocean Plan, www.mass.gov/ and Coastal Wind Energy for North Carolina's Future, http://www.climate.unc.edu/coastal-wind). Vulnerability analyses integrate spatial data on the distribution of marine habitats using expert assessments of the level of vulnerability of each habitat type to the suite of human activities that occur there [3,135]. Cumulative impact studies quantify the number, map the spatial extent, and assess the frequency of multiple human activities at multiple spatial scales [140]. The combination of vulnerability and cumulative impact maps can inform regional MSP by identifying areas where ecosystem vulnerability and cumulative impact levels meet the objective of maintaining healthy ecosystems or where they are mismatched. Existing and developing decision support tools, such as MARXAN [141] and MarineMap (http://www.marinemap.org/), can be used to visualize how different configurations of use areas can reduce (1) the level of cumulative impacts in any one area, (2) the number of conflicts between users and between users and the ecosystem, and (3) the number of trade-offs that are necessary for each use sector. MarineMap, in particular, can build the ecological goals of a spatial planning project into the program so that it is easy to evaluate whether or not a particular planning scheme meets the ecological goals of the process. Dynamic models will need to be developed that use real-time data to forecast future ecosystem health conditions under different management strategies.

To be effective, ecosystem-based MSP must also satisfy several other objectives. First, it must involve stakeholder participation and cooperation throughout the process. Given the comprehensive nature of ecosystem-based MSP, this goal will be challenging as the number of stakeholder groups could become very large. Second, MSP must also be implemented within a governance framework that: (1) ensures real public accountability, independent decision-making, adaptive management, dependable funding, meaningful public and stakeholder participation, and public transparency; (2) conforms to clear decision-making rules and objectives [139]; and (3) has clearly articulated goals and a means of evaluating whether they are being met for EBM and MSP. Third, a thorough understanding and appreciation of the existing ocean policy, governance, and management structure are also important for ecosystem-based MSP to be successful [11]. In some cases, MSP will fit well into a pre-existing legal, policy, and agency structure; in other cases, adjustments to governance will need to be made (e.g., see [139] for a detailed analysis of California's existing ocean policy, governance, and management framework for implementing ecosystem-based MSP in California and [142] for multiscale governance using examples from the Gulf of Maine). In addition, all ecological and social systems are dynamic such that specific management decisions and tools that emerge from these guiding principles should be modified using an adaptive management process [143,144] that allows for the lessons learned and best available science to be incorporated into operational and governance frameworks in a timely manner [139].

The ecological principles and modifying guidelines proposed here for ecosystem-based MSP combine a number of ecosystem attributes recognized by other area-based planning processes (Table 1), address ecosystem attributes that are most likely to be affected by current and future human uses, and should guide siting and management of human uses. In addition, these principles directly pertain to two of the fundamental goals of MSP—maintenance of healthy ecosystems and continued/restored delivery of ecosystem services. By identifying ecological attributes that are necessary to maintain ecosystem health, and putting them at the forefront, they advance the MSP process by providing a strong scientific foundation that can be coupled with socioeconomic and governance principles to achieve healthy, sustainable ecosystems and human communities.

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