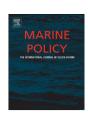
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# Guiding ecological principles for marine spatial planning

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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.

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# 1. Introduction

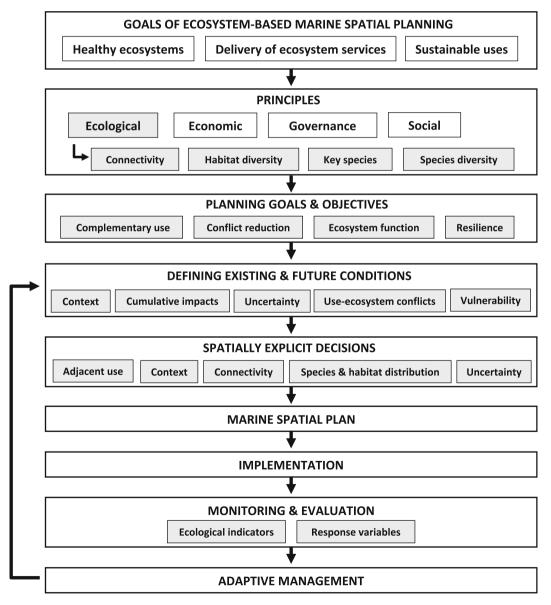
The health of global marine ecosystems is in serious decline, and multiple stressors, including overfishing, pollution, invasive species, coastal development, and climate change, compromise the ability of ocean and coastal ecosystems to support and sustain the goods and services people want and need [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 largescale 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-com plete.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		Habitat heterogeneity			Uniqueness/ rarity	Resilience	Vulnerable life stages	Biological productivity	Natura Iness	Species interactions	Vulnerable habitats	Aggre- gations	Biogeo- chemistry	Bio- geography	Ecosystem integrity	Fitness con- sequences	Proportional importance	Extremes	s Water quality
GBRMP [36] Roberts et al. [34]	х	х	x x		x x	х		х				x			х					
Derous et al.						x		x		x			x				x	x		
Rogers et al. [145]		х		х	х				x											
Crowder and Norse [10]	Х		х	х							х			Х						
Appledoorn [136]	х			Х																X
Convention on biological diversity		Х				Х	х	Х	Х	Х		Х								
Gaydos et al. [146]	х		x				Х				х					x			х	
MLPA [147] Tissot et al. [148]	x x	x x	х	х	х	х	x	х	х	х	х	X			Х	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 ecosystembased 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 ecosystembased 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 Functional redundancy	Resilience (resistance and recovery) Food web stability	Historic baselines			
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)			
		<b>,</b>	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 decisionmaking, 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 preexisting 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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#### References

- [1] POC. Pew Oceans Commission; America's living ocean: charting a course for sea change. A report to the nation. Washington, DC: Pew Trusts; 2003.
- [2] USCOP. US Commission on Ocean Policy; an ocean blueprint for the twentyfirst century. Final report. Washington, DC: USCOP, 2004.
- [3] Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, et al. A global map of human impact on marine ecosystems. Science 2008;319(5865):948–52.
- [4] MEA. Millennium ecosystem assessment. Ecosystems and human wellbeing: synthesis. Washington, DC: Island Press; 2005.
- [5] Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. Human domination of Earth's ecosystems. Science 1997;277(5325):494–9.
- [6] Daily G, Alexander S, Ehrlich P, Goulder L, Lubchenco J, Matson P, et al. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues in Ecology 1997;2:1–18.
- [7] Crowder LB, Osherenko G, Young OR, Airame S, Norse EA, Baron N, et al. Sustainability—resolving mismatches in US ocean governance. Science 2006;313(5787):617–8.
- [8] Turnipseed M, Crowder L, Sagarin R, Roady S. Legal bedrock for rebuilding America's ocean ecosystems. Science 2009;324:183–4.
- [9] McLeod KL, Leslie H, editors. Ecosystem-based management for the oceans. Washington, DC: Island Press; 2009.
- [10] Crowder L, Norse E. Essential ecological insights for marine ecosystembased management and marine spatial planning. Marine Policy 2008;32(5):772–8.
- [11] Gilliland PM, Laffoley D. Key elements and steps in the process of developing ecosystem-based marine spatial planning. Marine Policy 2008;32(5):787–96.
- [12] Ruckelshaus M, Klinger T, Knowlton N, Demaster DR. Marine ecosystem-based management in practice: scientific, and governance challenges. BioScience 2008;58(1):53–63.
- [13] Kappel CV, Halpern BS, Martone RG, Micheli F, Selkoe KA. In the zone comprehensive ocean protection. Issues in Science and Technology 2009;25(3):33–44.
- [14] Halpern BS, McLeod KL, Rosenberg AA, Crowder LB. Managing for cumulative impacts in ecosystem-based management through ocean zoning. Ocean & Coastal Management 2008;51(3):203-11.

- [15] Douvere F. The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 2008;32(5): 762–71
- [16] Ehler C, Douvere F. Marine spatial planning: a step-by-step approach toward ecosystem-based management. Paris, UNESCO: Intergovernmental Oceanographic Commission and Man and the Biosphere Programme; 2009.
- [17] IOPTF. Interim Report of the Interagency Ocean Policy Task Force. Executive Office of the President, 2009. pp. 1–38.
- [18] Boyes SJ, Elliott M, Thomson SM, Atkins S, Gilliland PM. A proposed multiple-use zoning scheme for the Irish Sea. An interpretation of current legislation through the use of GIS-based zonign approaches and effectiveness for the protection of nature conservation interests. Marine Policy 2007;31:287–98.
- [19] Douvere F, Maes F, Vanhulle A, Schrijvers J. The role of marine spatial planning in sea use management: the Belgian case. Marine Policy 2007;31(2):182–91.
- [20] Li HQ. The impacts and implications of the legal framework for sea use planning and management in China. Ocean & Coastal Management 2006;49(9-10):717-26.
- [21] O'Boyle R, Sinclair M, Keizer P, Lee K, Ricard D, Yeats P. Indicators for ecosystem-based management on the Scotian Shelf: bridging the gap between theory and practice. ICES Journal of Marine Science 2005;62(3):598-605.
- [22] Ardron J, Gjerde K, Pullen S, Tilot V. Marine spatial planning in the high seas. Marine Policy 2008;32(5):832–9.
- [23] Day J. The need and practice of monitoring, evaluating and adapting marine planning and management—lessons from the Great Barrier Reef. Marine Policy 2008;32(5):823–31.
- [24] Street MW, Deaton AS, Chappell WS, Mooreside PD. North Carolina habitat protection plan. Morehead City, NC: North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries; 2005 656 pp.
- [25] Olsen E, Gjosaeter H, Rottingen I, Dommasnes A, Fossum P, Sandberg P. The Norwegian ecosystem-based management plan for the Barents Sea. ICES Journal of Marine Science 2007:599–602.
- [26] DFO. Identification of ecologically and biologically significant areas. DFO Can. Sci. Adv. Sec. Ecosyst. Stat. Rep., 2004.
- [27] O'Boyle R, Worcester T. Eastern scotian shelf, Canada. In: McLeod KL, Leslie H, editors. Ecosystem-based management for the oceans. Washington, DC: Island Press; 2009. p. 253–67.
- [28] Cowen RK, Gawarkiewic G, Pineda J, Thorrold SR, Werner FE. Population connectivity in marine systems an overview. Oceanography 2007;20(3): 14–21
- [29] Duffy JE. Why biodiversity is important to the functioning of ecosystems. Frontiers in Ecology and the Environment 2009;7(8):437–44.
- [30] Palumbi SR, Sandifer PA, Allan JD, Beck MW, Fautin DG, Fogarty MJ, et al. Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment 2009;7(4):204–11.
- [31] Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, et al. Impacts of biodiversity loss on ocean ecosystem services. Science 2006;314(5800):787–90.
- [32] Stachowicz JJ, Bruno JF, Duffy JE. Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review of Ecology Evolution and Systematics 2007;38:739–66.
- [33] GBRMPA. Great Barrier Reef Marine Park Zoning Plan. Great Barrier Reef Marine Park Authority, Australian Government, 2003.
- [34] Roberts CM, Andelman S, Branch G, Bustamante RH, Castilla JC, Dugan J, et al. Ecological criteria for evaluating candidate sites for marine reserves. Ecological Applications 2003;13(1):S199-214.
- [35] Derous S, Agardy T, Hillewaert H, Hostens K, Jamieson G, Lieberknecht L, et al. A concept for biological valuation in the marine environment. Oceanologia 2007;49(1):99–128.
- [36] GBRMPA. Biophysical operational principles as recommended by the scientific steering committee for the Representative Areas Program. <a href="http://www.gbrmpa.gov.au/">http://www.gbrmpa.gov.au/</a>, 2002.
- [37] Tilman D, Lehman CL, Thomson KT. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences of the United States of America 1997;94(5): 1857-61
- [38] Leslie HM, Kinzig AP. Resilience science. In: McLeod KL, Leslie H, editors. Ecosystem-based management for the oceans. Washington, DC: Island Press; 2009. p. 55–73.
- [39] Palumbi SR, McLeod KL, Grunbaum D. Ecosystems in action: lessons from marine ecology about recovery, resistance, and reversibility. Bioscience 2008;58(1):33–42.
- [40] Bellwood DR, Hughes TP, Folke C, Nystrom M. Confronting the coral reef crisis. Nature 2004;429(6994):827–33.
- [41] Hewitt JE, Thrush SF, Dayton PD. Habitat variation, species diversity and ecological functioning in a marine system. Journal of Experimental Marine Biology and Ecology 2008;366(1–2):116–22.
- [42] Dulvy NK, Freckleton RP, Polunin NVC. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters 2004;7(5): 410-6
- [43] Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 2007;315(5820):1846–50.

- [44] Sax DF, Gaines SD. Species invasions and extinction: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences of the United States of America 2008;105:11490–7.
- [45] Gribben PE, Wright JT. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology-Progress Series 2006;318:177–85.
- [46] Sala E, Knowlton N. Global marine biodiversity trends. Annual Review of Environment and Resources 2006;31:93–122.
- [47] Naeem S. Expanding scales in biodiversity-based research: challenges and solutions for marine systems. Marine Ecology-Progress Series 2006;311: 273–283.
- [48] Ehlers A, Worm B, Reusch TBH. Importance of genetic diversity in eelgrass Zostera marina for its resilience to global warming. Marine Ecology-Progress Series 2008;355:1–7.
- [49] Bernardi G. Phylogeography and demography of sympatric sister surfperch species, *Embiotoca jacksoni* and *E. lateralis* along the California coast: historical versus ecological factors. Evolution 2005;59(2): 386–94.
- [50] Sotka EE, Palumbi SR. The use of genetic clines to estimate dispersal distances of marine larvae. Ecology 2006;87(5):1094–103.
- [51] Dutton JM, Hofmann GE. Biogeographic variation in Mytilus galloprovincialis heat shock gene expression across the eastern Pacific range. Journal of Experimental Marine Biology and Ecology 2009;376(1):37–42.
- [52] Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. Ecological consequences of genetic diversity. Ecology Letters 2008;11(6):609–23.
- [53] Steneck RS, Dethier MN. A functional-group approach to the structure of algal-dominated communities. Oikos 1994;69(3):476–98.
- [54] Petchey OL, Gaston KJ. Functional diversity: back to basics and looking forward. Ecology Letters 2006;9(6):741–58.
- [55] Walker BH. Biodiversity and ecological redundancy. Conservation Biology 1992;6(1):18–23.
- [56] Micheli F, Halpern BS. Low functional redundancy in coastal marine assemblages. Ecology Letters 2005;8(4):391–400.
- [57] Schiel DR. Rivets or bolts? When single species count in the function of temperate rocky reef communities Journal of Experimental Marine Biology and Ecology 2006;338(2):233–52.
- [58] Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, et al. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 2004;35:557–81.
- [59] Bellwood DR, Hoey AS, Choat JH. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecology Letters 2003;6(4):281–5.
- [60] Bellwood DR, Hughes TP, Hoey AS. Sleeping functional group drives coralreef recovery. Current Biology 2006;16(24):2434–9.
- [61] Piola RF, Johnston EL. Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. Diversity and Distributions 2008;14(2):329–42.
- [62] Thrush SF, Halliday J, Hewitt JE, Lohrer AM. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. Ecological Applications 2008;18(1):12–21.
- [63] Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, et al. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 2006;312(5781):1806–9.
- [64] Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, et al. Historical overfishing and the recent collapse of coastal ecosystems. Science 2001;293(5530):629–38.
- [65] Dulvy NK, Sadovy Y, Reynolds JD. Extinction vulnerability in marine populations. Fish and Fisheries 2003;4(1):25–64.
- [66] Nichols FH, Thompson JK, Schemel LE. Marine Ecology-Progress Series 1990;66(1-2):95-101.
- [67] Hughes TP. Catastrophies, phase-shifts, and large-scale degradation of a Caribbean coral-reef. Science 1994;265(5178):1547–51.
- [68] Springer AM, Estes JA, van Vliet GB, Williams TM, Doak DF, Danner EM, et al. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling?Proceedings of the National Academy of Sciences of the United States of America 2003;100(21):12223–8.
- [69] Estes JA, Palmisano JF. Sea otters—their role in structuring nearshore communities. Science 1974;185(4156):1058–60.
- [70] MacArthur R, Levins R. Limiting similarity, convergence, and divergence of coexisting species. American Naturalist 1967;101(921):377–85.
- [71] Caley MJ, St John J. Refuge availability structures assemblages of tropical reef fishes. Journal of Animal Ecology 1996;65(4):414–28.
- [72] Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA. Habitat associations of estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. Estuaries and Coasts 2006;29(6B):1150-60.
- [73] Steneck RS, Paris CB, Arnold SN, Ablan-Lagman MC, Alcala AC, Butler MJ, et al. Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. Coral Reefs 2009:367-78.
- [74] Graham MH, Vasquez JA, Buschmann AH. Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. Oceanography and Marine Biology 2007;45:39–88.
- [75] Carr MH. Marine protected areas: challenges and opportunities for understanding and conserving coastal marine ecosystems. Environmental Conservation 2000;27(2):106–9.

- [76] Sogard SM. Variability in growth-rates of juvenile fishes in different estuarine habitats. Marine Ecology-Progress Series 1992;85(1–2):35–53.
- [77] Micheli F, Peterson CH. Estuarine vegetated habitats as corridors for predator movements. Conservation Biology 1999;13(4):869–81.
- [78] Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, et al. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 2001;51(8):633–41.
- [79] Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, et al. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conservation Biology 2008;22(4):941–51.
- [80] Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, et al. From wind to whales: trophic links in a coastal upwelling system. Marine Ecology-Progress Series 2005;289:117–30.
- [81] Sakko AL. The influence of the Benguela upwelling system on Namibia's marine biodiversity. Biodiversity and Conservation 1998;7(4):419–33.
- [82] Barth JA, Menge BA, Lubchenco J, Chan F, Bane JM, Kirincich AR, et al. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proceedings of the National Academy of Sciences of the United States of America 2007;104(10):3719–24.
- [83] Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, et al. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proceedings of the National Academy of Sciences of the United States of America 2006;103(34):12799–802.
- [84] Thayer JA, Sydeman WJ. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, Cerorhinca monocerata, in an upwelling system. Marine Ecology-Progress Series 2007;329: 253–65.
- [85] Weise MJ, Costa DP, Kudela RM. Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. Geophysical Research Letters 2006;33(22).
- [86] Williams CB. Area and number of species. Nature 1943;152:264-7.
- [87] Mumby PJ, Green EP, Edwards AJ, Clark CD. The cost-effectiveness of remote sensing for tropical coastal resources assessment and management. Journal of Environmental Management 1999;55(3):157–66.
- [88] Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, et al. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 2002;29(4):436–59.
- [89] Lenihan HS, Peterson CH, Byers JE, Grabowski JH, Thayer GW, Colby DR. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecological Applications 2001;11(3):764–82.
- [90] McLeod E, Salm R, Green A, Almany J. Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment 2009;7(7):362–70.
- [91] Berlow EL. Strong effects of weak interactions in ecological communities. Nature 1999;398(6725):330–4.
- [92] O'Gorman EJ, Emmerson MC. Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences of the United States of America 2009;106(32):13393–8.
- [93] Paine RT. Food webs—linkage, interaction strength and community infrastructure—the 3rd tansley lecture. Journal of Animal Ecology 1980;49(3):667–85.
- [94] Duffy JE. Sea changes: structure and functioning of emerging marine communities. In: Verhoef HA, Morin PJ, editors. Community ecology. Processes, models, and applications. Oxford, UK: Oxford University Press; 2009. p. 95–114.
- [95] Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, et al. Challenges in the quest for keystones. Bioscience 1996;46(8):609–20.
- [96] Soule ME, Estes JA, Miller B, Honnold DL. Strongly interacting species, conservation policy, management, and ethics. Bioscience 2005;55(2): 168–76
- [97] Navarrete SA, Menge BA. Keystone predation and interaction strength: interactive effects of predators on their main prey. Ecological Monographs 1996:66(4):409–29.
- [98] Paine RT. Food web complexity and species diversity. American Naturalist 1966;100(910):65–75.
- [99] Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, et al. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 2002;5(6):785-91.
- [100] Pace ML, Cole JJ, Carpenter SR, Kitchell JF. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 1999;14(12):483–8.
- [101] Dayton PK. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sounds, Antarctica. In: Parker BC, editor. Proceedings of the colloquium on conservation problems in Antarctica. Lawrence, Kansas, USA: Allen Press; 1972
- [102] Bruno JF, Bertness MD. Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gaines SD, Hay ME, editors. Marine community ecology. Sunderland, MA: Sinauer Associates; 2001.
- [103] Barbier EB, Koch EW, Silliman BR, Hacker SD, Wolanski E, Primavera J, et al. Coastal ecosystem-based management with nonlinear ecological functions and values. Science 2008;319(5861):321–3.
- [104] Beck MW, Brumbaugh RD, Carranza A, Coen LD, Defeo O, Lenihan HS, et al. Shellfish at risk: a global assessment of distribution, condition and threats to habitat-forming bivalves. Journal of Shellfish Research 2008;27(4): 989-90.

- [105] Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, et al. A global crisis for seagrass ecosystems. Bioscience 2006;56(12): 987–96.
- [106] Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, et al. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 2009;106(30):12377–81.
- [107] Gilman EL, Ellison J, Duke NC, Field C. Threats to mangroves from climate change and adaptation options: a review. Aquatic Botany 2008;89(2):237–50.
- [108] Soule ME, Estes JA, Berger J, Del Rio CM. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 2003;17(5):1238–50.
- [109] Menge BA, Sanford E, Daley BA, Freidenburg TL, Hudson G, Lubchenco J. Inter-hemispheric comparison of bottom-up effects on community structure: insights revealed using the comparative-experimental approach. Ecological Research 2002;17(1):1–16.
- [110] Bakun A. Wasp-waist populations and marine ecosystem dynamics: navigating the 'predator pit' topographies. Progress in Oceanography 2006;68(2-4):271–88.
- [111] Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, et al. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation 2000;27(2):179–200.
- [112] Myers RA, Worm B. Rapid worldwide depletion of predatory fish communities. Nature 2003;423(6937):280–3.
- [113] McCann KS, Rasmussen JB, Umbanhowar J. The dynamics of spatially coupled food webs. Ecology Letters 2005;8(5):513–23.
- [114] Weng KC, Boustany AM, Pyle P, Anderson SD, Brown A, Block BA. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Marine Biology 2007;152(4):877–94.
- [115] Shanks AL. Pelagic larval duration and dispersal distance revisited. Biological Bulletin 2009;216(3):373–85.
- [116] Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, et al. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 2009: 307–25.
- [117] Cowen RK, Sponaugle S. Larval dispersal and marine population connectivity. Annual Review of Marine Science 2009;1:443–66.
- [118] Siegel DA, Kinlan BP, Gaylord B, Gaines SD. Lagrangian descriptions of marine larval dispersion. Marine Ecology-Progress Series 2003;260: 83–96.
- [119] Kinlan BP, Gaines SD. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 2003;84(8):2007–20.
- [120] Shanks AL, Grantham BA, Carr MH. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 2003;13(1): S69–S159.
- [121] Barber PH, Palumbi SR, Erdmann MV, Moosa MK. Biogeography—a marine Wallace's line?Nature 2000;406(6797):692–3.
- [122] Freiwald J. Movement of temperate reef fishes: implications for their ecology and management. Fish and Fisheries In review, submitted for publication.
- [123] Swearer SE, Caselle JE, Lea DW, Warner RR. Larval retention and recruitment in an island population of a coral-reef fish. Nature 1999;402(6763): 799–802.
- [124] Hastings A, Botsford LW. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences of the United States of America 2006;103(15):6067–72.
- [125] Kritzer JP, Sale PF, editors. Marine metapopulations. Burlington, MA: Elsevier Academic Press; 2006.
- [126] Koehn RK, Newell RIE, Immermann F. Maintenance of an aminopeptidase allele frequency cline by natural-selection. Proceedings of the National Academy of Sciences of the United States of America – Biological Sciences 1980;77(9):5385–9.
- [127] Polis GA, Anderson WB, Holt RD. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 1997;28:289–316.
- [128] Maron JL, Estes JA, Croll DA, Danner EM, Elmendorf SC, Buckelew SL. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecological Monographs 2006;76(1):3–24.
- [129] Sabo JL, Power ME. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 2002;83(11): 3023–36
- [130] Chambers RM, Fourqurean JW, Hollibaugh JT, Vink SM. Importance of terrestrially-derived, particulate phosphorous dynamics in a west-coast estuary. Estuaries 1995;18(3):518–26.
- [131] Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, et al. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 2009:339–51.
- [132] Mumby PJ, Hastings A. The impact of ecosystem connectivity on coral reef resilience. Journal of Applied Ecology 2008;45(3):854–62.
- [133] Groves CR. Drafting a conservation blueprint: a practitioner's guide to planning for biodiversity. Washington, DC: Island Press; 2003.
- [134] Crain CM, Kroeker K, Halpern BS. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 2008;11(12):1304–15.
- [135] Halpern BS, Selkoe KA, Micheli F, Kappel CV. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conservation Biology 2007;21(5):1301–15.

- [136] Appeldoorn RS. Transforming reef fisheries management: application of an ecosystem-based approach in the USA Caribbean. Environmental Conservation 2008;35(3):232–41.
- [137] FAO. Indicators for sustainable development of marine capture fisheries. FAO technical guidelines for responsible fisheries 8. Rome, Italy, 1999.
- [138] Walters CJ, Hilborn R. Adaptive control of fishing systems. Journal of the Fisheries Research Board of Canada 1976;31:145–59.
- [139] Sivas D, Caldwell M. A new vision for California ocean governance: comprehensive ecosystem-based marine zoning. Stanford Environmental Law Journal 2008;27(209):209–70.
- [140] Halpern BS, Kappel CV, Selkoe KA, Micheli F, Ebert C, Kontgis C, et al. Mapping cumulative human impacts to California current marine ecosystems. Conservation Letters 2009;2:138–48.
- [141] Watts ME, Ball IR, Stewart RS, Klein CJ, Wilson K, Steinback C, et al. Marxan with zones: software for optimal conservation based land- and seause zoning. Environmental Modelling & Software 2009;24(12):1513–21.
- [142] Steneck RS, Wilson JA. A fisheries play in an ecosystem theater: challenges of managing ecological and social drivers of marine fisheries at nested spatial scales. Bulletin of Marine Science, in press.

- [143] Rosenberg AA, Mooney-Seus ML, Kiessling I, Mogensen CB, O'Boyle R, Peacey J. Lessons from national-level implementation across the world. In: McLeod KL, Leslie H, editors. Ecosystem-based management for the oceans. Washington, DC: Island Press; 2009. p. 294–313.
- [144] Parma AM, Amarasekare P, Mangel M, Moore J, Murdoch WW, Noonburg E, et al. What can adaptive management do for our fish, forests, food, and biodiversity? Integrative Biology 1998;1(1):16–26.
- [145] Rogers SI, Tasker ML, Earll R, Gubbay S. Ecosystem objectives to support the UK vision for the marine environment. Marine Pollution Bulletin 2007;54:128–44.
- [146] Gaydos JK, Dierauf L, Kirby G, Brosnan D, Gilardi K, Davis GE. Top 10 principles for designing healthy coastal ecosystems like the Salish Sea. EcoHealth 2008;5:460–71.
- [147] DFG. California Marine Life Protection Act, master plan for marine protected areas. Sacramento, CA: Department of Fish and Game; 2008.
- [148] Tissot BN, Walsh WJ, Hixon MA. Hawaiian Islands marine ecosystem case study: ecosystem- and community-based management in Hawaii. Coastal Management 2009;37:255–73.