

The Role of Marine Protected Areas in Providing Ecosystem Services

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INTRODUCTION

Marine ecosystems experience constant change and adaptation processes because they are under the influences of a suite of pressures (Hooper et al., 2012). Human impacts can affect the ecosystem functioning of marine ecosystems and reduce the associated production of goods and services required for human well-being (Cardinale et al., 2012; Mora et al., 2011). For example, major concerns are rising over observed declines in the abundance of particular species as well as reductions in functional diversity and changes in food web structure due to the intensity of some anthropogenic activities (De'ath et al., 2012; Hughes et al., 2010). These changes induce strong modifications of whole ecosystems or some of their components, resulting in loss of function (Graham et al., 2013). Such ecosystem disruptions may affect the flow of ecosystem services (such as food provision) that are vital for human well-being (Carpenter et al., 2006; Chapin et al., 2000; Díaz et al., 2006). As a result, the conservation and/or restoration of marine biodiversity and its derived ecosystem goods and services are major concerns. To this end, marine protected areas (MPAs) are being established worldwide to maintain biodiversity, ecosystem functions, and the flow of ecosystem services (Gaines et al., 2010). MPAs are a specific type of management zone—they may allow some uses, including scuba diving and some types of fishing; may be strictly no-take such as marine reserves; or they may be completely no-access zones where neither extractive nor nonextractive uses are allowed (Day and Dobbs, 2013). Most MPAs include another layer of complexity by combining different levels

of protection within a spatially zoned management scheme. Zones may be dedicated to strict conservation, act as buffer zones that can be used for research, education, or traditional uses, and/or allow nonconsumptive and limited-consumptive uses (Agardy et al., 2003).

Today, MPAs are commonly used around the world as management tools to promote the sustainable use of marine resources (Hargreaves-Allen et al., 2011). In this chapter, we will review the different impacts of MPAs on ecosystem functioning and service production. We will focus especially on the relationship between the effects of MPAs on ecosystem functioning and the benefits provided to people. The livelihoods and well-being of coastal communities rely on ecosystem services produced by marine ecosystems. Thus, it is assumed that MPAs secure human livelihoods and well-being by protecting marine ecosystems and ecosystem services. However, the links between ecological effects of MPAs and services have rarely been explored.

The aims of this synthesis are to (1) identify relationships between the effects of MPAs on ecosystem functioning and service provision; (2) identify knowledge gaps on which future research efforts could focus; and (3) empower marine resource managers to make more informed decisions and maximize the value derived from their natural resource base. We propose that quantification and monitoring of species' functional trait distribution and assemblages' functional diversity are promising approaches for assessing the effects of MPAs on ecosystem functioning and services.

INTRODUCTION TO MARINE PROTECTED AREAS

MPAs are globally important management tools that are expected to (1) control and manage human activities and marine uses; (2) promote the recovery of exploited marine populations; (3) conserve or restore habitats, biodiversity, and food webs; and (4) manage and enhance ecosystem services such as food production, water purification, or recreational activities (Halpern, 2014; Liquete et al., 2013). Most MPAs are implemented to mitigate some of the human-induced modifying forces on marine ecosystems, especially by reducing or removing fishing mortality (Claudet, 2012). Originally, MPAs and especially "no-take" marine reserves were conceived as pragmatic means to eliminate harvest pressure and thereby protect marine depleted and endangered species, habitats, fisheries, and ecosystems, and to provide public enjoyment of the oceans (Mora et al., 2011). Today they are also used as management tools regulating fishing, tourism, and industrial activities. Thanks to different types of zoning, each established according to specific management goals, MPAs can reduce conflict and allow coexistence of different resource uses. Establishment of different-use zones must be combined with the establishment of: easily identifiable borders to reduce possible impacts of incidental intrusions; public information about uses permitted in different zones; and the

participation of local communities and diverse users who contribute to the process (Hargreaves-Allen et al., 2011). Compliance with spatial zoning regulations, such as those within an MPA, depends on whether users understand the regulations designed to ensure the orderly and sustainable use of marine resources. If compliance is good, additional management costs to ensure zoning enforcement will be reduced.

In recent years, MPA research has made several advances. First, empirical data and analyses have shown how MPA effects are driven by different factors such as MPA age, size, fish life history traits, and the level of enforcement (Claudet et al., 2008, 2010; Guidetti et al., 2008). These findings have important implications for MPA design and management. For example, if even young and small MPAs can be effective in increasing fish population density, then old, large, and isolated MPAs may show even greater positive responses (e.g., Edgar et al., 2014). Meanwhile, no positive responses should be expected from MPAs with low levels of enforcement (Guidetti et al., 2008). Second, major advances were made on the numerous indirect ecological effects of protection such as functional diversity and delivery of ecosystem services, which are also time-dependent (Fletcher et al., 2011). Third, the potential socioeconomic benefits of MPAs are now becoming clearer. Studies show, for example, that MPAs can enhance food security, empower local communities (Mascia et al., 2010), and lead to jobs and/or revenue increases in activities linked to MPAs such as fishing and tourism, as well as to the maintenance of traditional activities (McCook et al., 2010; Pascal, 2014), although negative impacts on some users have also been documented (Mascia et al., 2010). Fourth, the general agreement among scientists that MPA networks can optimize conservation and fishery benefits has led to significant advances in network design and evaluation.

Considering these recent findings, it is clear that MPAs can provide different types of benefits. They can ensure the protection and/or the restoration of marine biodiversity that provide multiple ecosystem functions and human benefits. Below we provide a definition and overview of ecosystem services, then review the expected and documented effects of MPAs on the delivery of selected ecosystem services vital for human activities (e.g., fishing and recreational activities) and well-being.

INTRODUCTION TO ECOSYSTEM SERVICES AND THE LINK TO HUMAN WELL-BEING

Ecosystem services are the benefits people derive from nature (Liquete et al., 2013). They are the cornerstones of marine resource systems and are widely used to describe human–nature interactions (Diaz et al., 2011). Thus, ecosystem services support natural ecosystems, livelihoods, and human well-being through direct and indirect processes (Liquete et al., 2013). A conceptual model that represents those different interactions is a cascade linking the

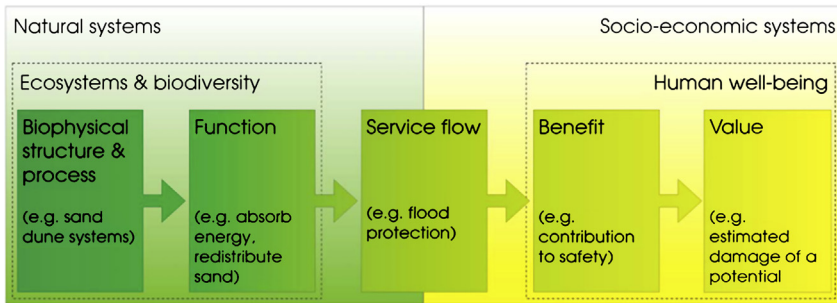


FIGURE 1 The cascade framework showing how natural provision of ecosystem services contributes to human well-being. From *Liquete et al. (2013)*.

biophysical structure and processes with the benefit that people eventually derive (Figure 1). It highlights not only that ecosystems provide services but also that services do not exist in isolation from people's needs (Haines-young and Potschin, 2010).

The Millennium Ecosystem Assessment of 2005 (MA, 2005) classified ecosystem services into four categories: *provisioning services* such as food, water, timber, fiber, genetic resources, and pharmaceuticals; *regulating services* controlling climate, air and water quality, erosion, disease, pests, wastes, and natural hazards; *cultural services* providing recreational, aesthetic, and spiritual benefits; and *supporting services* such as nutrient and water cycling, soil formation, and primary production. According to the MA, approximately 60% of ES are degraded, including capture fisheries.

MPAs are key management tools established to secure the delivery of marine ecosystem services and thus contribute to human well-being (Fletcher et al., 2011). Indeed, improvement in the quality of the natural environment provided by MPAs is expected to strengthen the capacity of coastal ecosystems to produce goods and services for local people, local and nonlocal entrepreneurs, and the global community (TEEB, 2010). From a socioeconomic perspective, MPAs may be seen as public investments in marine ecosystems conservation (Laurans et al., 2013). As such, a basic question is the magnitude of MPAs' contributions to individual and societal well-being. This question has been tackled by cost–benefit analysis.

Alban et al. (2011) synthesized assessments of income and jobs related to the presence of 12 Mediterranean MPAs. A distinction was made between users obtaining commodities (commercial fishers) and recreational users (recreational fishers and scuba divers). Income generated by MPAs was generally high, particularly for commercial fishing and recreational scuba diving. The average yearly money incomes locally generated by uses in MPAs amounted to 710,000 € per MPA (between 48,000 € in Medes Islands and 1,573,000 € in Columbretes) in the case of professional fishing, 551,000 € per MPA (between 16,000 € in Tabarca and 1,099,000 € in Medes Island) in

the case of scuba diving, and 88,000 € per MPA (between 35,000 € in La Graciosa and 211,000 € in Monte da Guia) in the case of recreational fishing (Roncin et al., 2008). These figures should be compared with yearly MPA management costs, which amounted on average to 588,000 € per year per MPA. However, the contribution to different economic sectors varied greatly from place to place. On a relatively remote MPA (Columbretes, Spain), the economic contribution of commercial fishing was dominant. This activity generated nearly 90% of all income provided by the ecosystem use. On an MPA closer to densely populated areas (Medes), incomes generated by commercial fishing amount to only 5% of those generated by scuba diving (Alban et al., 2011). In the Great Barrier Reef Marine Park in Australia, the estimated distribution of economic value between recreational uses and commercial fishing is approximately 4:1 (Stoeckl et al., 2011). However, despite significant improvements in recent years, this type of assessment faces substantial difficulties. First, the limited availability of economic data at a relevant scale frequently hinders a complete assessment of the influence of MPAs on the economy of the neighboring zone (Laurans et al., 2013). Moreover, total value is always underestimated because the measurement of nonmarket values, including nonuse values such as the value of marine biodiversity, is a difficult task. Even assessing the impact of an MPA using some specific market values (e.g., fishery rent) may be problematic due to limited quantitative information on underlying ecological processes (e.g., larval and juvenile spillover from MPAs to fishing grounds) (Pascal and Seidl, 2013); the use of CPUE was suggested as a way to bypass this issue. As a result, the application of cost–benefit analysis to MPAs is generally incomplete (François et al., 2012), providing an assessment of only a part of the net benefits MPAs provide. Below we review the expectations and evidence for MPAs’ contributions to a selected group of ecosystem services.

MARINE PROTECTED AREA EFFECTS ON INDIVIDUAL ECOSYSTEM SERVICES

Review of the literature reveals that MPA establishment is expected to support a suite of services. Here, we provide an overview of the conceptual or empirical basis for such effects (Table 1). As a first step toward establishing a link between ecological change in MPAs and service provision, we also discuss what functional traits of species, functional groups, and/or ecological community attributes underlie MPAs’ effects on services.

Marine Protected Area Effects on Provisioning Services: The Example of Fisheries

MPAs support provisioning services through their effects on fisheries and diversity (Worm et al., 2006). The first anticipated effects of establishing

TABLE 1 Examples of the Effects of MPAs on Ecosystem Services, the Mechanism Underlying Service Provision, and the Functional Traits, Functional Groups, and/or Community Attributes Driving These Effects

Ecosystem Service Category (MA, 2005)	Ecosystem Service	Mechanism by which MPAs Provide Service	Species, Community Attribute, Functional Trait, or Functional Group Underlying Effect	References
Provisioning services	Food	Increased production/stabilization of target species biomass	Large size of target species, recovery of top predators and food web complexity	Goñi et al. (2010)
	Ornamental resources	Increased production/stabilization of ornamental fish biomass	Species diversity	Williams et al. (2009)
	Raw materials	Algal and sand production	Predators controlling herbivory, bioeroders, corallivores	Karnauskas and Babcock (2014)
	Genetic resources	Protection of genetic diversity, adaptation to climate change	Response diversity, genetic diversity	Miller and Ayre (2008)
	Medicinal resources	Protection of molecular diversity	Chemically defended species, biological diversity	Schroder et al. (2004)
Regulating services	Carbon sequestration and climate regulation	Protection of plants and calcifying organisms (e.g., mangroves, sea grass, corals)	Species that have high C sequestration capacity (primary producers, calcifying species, bioconstructors)	Gonzalez-Correa et al. (2007)

Cultural services	Cultural heritage	Maintenance of traditional community-based natural resource management	Charismatic species (e.g., sharks, sea turtles, large mollusks)	Clarke and Jupiter (2010)
	Spiritual and historical heritage	Maintenance of traditional community-based natural resource management	Charismatic habitat (e.g., coral reef, kelp forests)	NA
	Recreational activities	Creation of nature-based eco-tourism opportunities (scenic beauty and emblematic species)	Charismatic species, large species, and habitat-forming species	Rios-Jara et al. (2013)
	Science and education	Creation of opportunities for research and education in placed of reduced human impacts	Biological diversity, complex food webs	Galzin et al. (2004)
Supporting services	Primary production	Protection of primary producers	Primary producers, habitat-forming species	Milazzo et al. (2002)
	Coastal protection	Protection of habitat formers (e.g., corals, sea grasses, mangroves) providing attenuation of wave intensity nature-based	Habitat-forming species	Mumby and Hardone (2010)

[Babcock et al. \(2010\)](#), [Clarke and Jupiter \(2010\)](#), [Galzin et al. \(2004\)](#), [Goñi et al. \(2010\)](#), [González-Correa et al. \(2007\)](#), [Milazzo et al. \(2002\)](#), [Mumby and Harborne \(2010\)](#), [Ríos-Jara et al. \(2013\)](#), [Schroder et al. \(2004\)](#), and [Williams et al. \(2009\)](#).

no-take or limited-take regulations through MPAs can be summarized as follows. First, mortality from fishing is immediately eliminated so that targeted individuals can live longer and attain larger sizes. In the short term, the increase in fish and invertebrate densities and sizes can lead to increases in reproductive output and recruitment (Claudet et al., 2010; Micheli et al., 2012). Possible negative habitat impacts associated with the use of destructive fishing methods also cease, allowing for the recovery of biogenic habitat that in turn positively affects fish recruitment and survival (Mumby and Harborne, 2010). Thus, in the medium to long term, habitat quality is improved, the preharvesting population age and size structure is re-established, and food web complexity increases due to increased diversity and recovery of top predators, which are often major fishery targets (Babcock et al., 2010; McCook et al., 2010; Micheli and Halpern, 2005). Consequently, one of the most commonly described indirect effects of marine reserves involves a trophic cascade, which is classically defined as the indirect effects of apical species in the food web (e.g., carnivores) on basal species (e.g., primary producers), mediated by intermediate consumers (e.g., herbivores) (Babcock et al., 2010).

Fishery effects of protection can only take place if an export of fish individuals occurs over the boundaries of the MPA (“spillover”; McClanahan and Mangi, 2000), and/or if eggs and larvae are exported from the MPA outwards (“seeding”; e.g., Planes et al., 2009). In MPAs with permeable boundaries, spillover can induce increases in catch per unit of effort (CPUE) of target species in surrounding fisheries’ grounds. These increases constitute a yield surplus and fishers’ CPUEs tend to be higher, although often more variable due to seasonal processes underlying spillover (Goñi et al., 2006; McClanahan and Kaunda-Arara, 1996). Spillover can also induce increases in total catch, catch per unit of area, species mean size in catch, and species diversity in catch (Goñi et al., 2010). These increases in turn can lead to increases in fishing effort along the MPA boundaries. For fishers, catch of adult spillover focuses in most cases on the borders of the reserve. The fishers’ behavior in response to the MPA establishment is usually the concentration of effort at the boundaries of the reservation to take advantage of export adults. This mechanism known as “fishing the line” (Roberts et al., 2001) can be interpreted as evidence of a spillover mechanism and becomes so severe in some cases that it may be affecting densities inside the reserve (Halpern et al., 2008). Figure 2 describes the CPUE decreases for lobster fishery from the border of the reserve and thus shows the concentration of effort in this area.

Although this effect has been poorly quantified (Sale et al., 2005), experience shows that the profit generated by the spillover generally has an impact limited to the local fishery and does not seem to significantly increase the densities for large fishing areas. It also has been debated whether the catch from spillover offsets harvest losses due to closure. A recent synthesis by

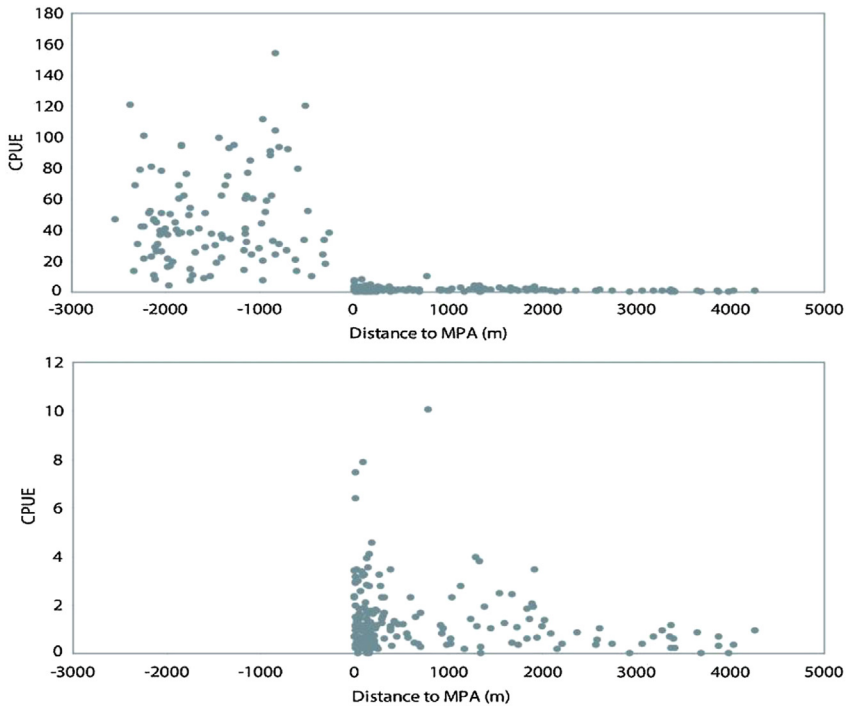


FIGURE 2 Lobster catch per unit effort (CPUE—number of lobsters caught per 600 m of net per day) versus distance from fishing set to the Columbretes Islands Marine Reserve boundary. Positive values are outward the MPA boundaries. Negative values are inward the MPA boundaries. (Upper panel—commercial and experimental data combined; lower panel—commercial fishery data on expanded y-axis scale.) *Adapted from Goñi et al. (2006, 2011).*

Halpern et al. (2010) concluded that even though the spatial extent of the contribution from the MPAs to fisheries is limited (600–1500 m from the MPA edge), in a majority of studies this contribution compensated for the loss of fishing grounds in MPAs. The average magnitude of these effects, however, should be considered with caution because (1) this study pooled very different species—e.g., with different mobility; and (2) studies on spillover focus primarily on species for which some form of spillover is expected.

Studies comparing effects of MPAs on surrounding CPUEs are scarce (Halpern et al., 2010; Harrison et al., 2012; Roberts et al., 2001). Gell et al. (2003) conducted a study selection of nine reserves in several locations with different designs and tested a significant improvement on different species' CPUEs. In their review, the authors quoted two cases of reserves in St Lucia—in Bermuda (Roberts et al., 2003) CPUE for large traps had improved by 46% after five years, and in Nabq (Egypt) the improvement was 66% for the net fishery. It also referred to reserves in Apo (Philippines) with

10-fold increases in longline CPUE after 20 years of protection, with the largest and most stable total catch in the Philippines over a 15-year span. In Tabarca, fishers benefited from a 50%–85% higher CPUE for key species, compared with before closing. Other cases in Mombasa (Kenya) (McClanahan and Mangi, 2000) have the highest catch in the region even with a major effort. However this does not increase the CPUE but only slows its decline. Also in South Africa, Tunley (2009) shows that the reserve has “only” stabilized catch. Other reserves in Chile showed that fishers are benefiting from a CPUE that is 4–10 times superior for a specific bivalve fishery, and in Columbretes (Spain) from a CPUE that is between 6 and 58 times higher for the lobster (Goñi et al., 2006).

Marine Protected Area Effects on Cultural Service: The Example of Recreational Activities

MPAs enhance the development of nonextractive activities, making recreational users perhaps the main beneficiaries of marine conservation (Christie and White, 2007). MPAs provide critical recreational services through nature-based tourism revenue (Balmford et al., 2009). The effects of MPAs stem directly from the fact that the marine environment within an MPA (particularly within a no-take zone) is granted a high level of protection against anthropogenic pressures. Protection in turn is likely to improve the quality of some attributes, such as large charismatic species and/or habitat-forming species that are valuable to visitors (Graham and Nash, 2012). For example, coral reefs are valued as cultural heritage (Hicks et al., 2009). Charismatic habitats (e.g., corals) and species (e.g., reef sharks) serve as focal points for local tourism and ecotourism, thereby enabling residents and visitors to enjoy aesthetic and spiritual values of coral reef ecosystems and seascapes. There are several species, such as the sicklefin lemon shark in French Polynesia and the dusky grouper in the Mediterranean Sea, that increase the recreation/tourism value of tropical and temperate reefs (Clua, 2011; Vandewalle et al., 2007; Guidetti and Micheli, 2011).

Even if, MPAs are expected to be powerful attractors for tourism, quantitative evidence for this benefit remains scarce (Andersson, 2007; Asafu-Adjaye and Tapsuwan, 2008; Depondt and Green, 2006; Harrison, 2007). For example, the relationship between underwater tourism and MPA impacts on some ecological attributes is not well known (Andersson, 2007). There are scientific knowledge gaps and technical difficulties in separating MPA effects on tourism from other context variables such as access and local infrastructure. High costs of studies, late participation by social sciences in MPA science, and effects too weak to be statistically significant have been proposed as reasons for the scarcity of studies of MPA social benefits (Christie et al., 2012; Cinner et al., 2009; Pollnac and Seara, 2010; Sale et al., 2005).

Marine Protected Area Effects on Supporting Services: The Example of Coastal Protection

MPAs provide protection to foundation species such as coral reefs, sea grass, kelps, and mangroves. These species produce physical structures that are natural barriers to waves, hurricanes, typhoons, and elevated sea levels, thereby providing coastal protection to people and critical coastal habitats. Thus, MPAs can contribute to maintaining the ecosystem service of coastal protection through the protection of habitat-forming species and communities (Graham and Nash, 2012). These habitats, when under good ecological conditions, limit the phenomenon of coastal erosion by absorbing high amounts of wave energy and lessening damage from severe weather events (hurricanes, tropical storms, and typhoons) (UNEP-WCMC, 2006) (Kench and Brander, 2006). Coral reefs and mangroves protect against waves by forming barriers along the coastline. Similarly, lagoon areas protected by barrier reefs are generally quiet areas that promote the multiple uses described previously. Several studies show that the reefs act similarly to wave breakers or shallow coasts—this includes a recent meta-analysis of 27 studies conducted in the Atlantic, Pacific, and Indian Oceans revealing that coral reefs provide substantial protection against natural hazards by reducing wave energy by an average of 97% (Ferrario et al., 2014). Reef crests alone dissipate most of this energy (86%). A comparison with artificial structures indicated that coral reefs can provide comparable wave attenuation benefits to artificial defenses, but at lower costs. The median costs of reef restoration projects are in fact an order of magnitude lower than the costs of building artificial breakwaters, indicating that reef conservation and restoration are cost-effective strategies for reducing risk from natural hazards. Finally, an estimated 200 million people receive risk reduction benefits from reefs, or bear hazard mitigation and adaptation costs if reefs are degraded (Ferrario et al., 2014) (it might also be important to highlight the importance of physical processes and low impact of ecological ones for coral reefs).

MARINE PROTECTED AREA EFFECTS ON LONG-TERM ECOSYSTEM FUNCTION AND THE PROVISION OF MULTIPLE SERVICES

Several studies have highlighted the positive effects of MPAs on some aspects of ecosystem function, such as functional diversity and redundancy. MPAs can have positive effects on maintaining specific functional traits, such as large body size, as well as the diversity of functional traits within communities (Micheli and Halpern, 2005; Mouillot et al., 2008). However, few studies have addressed relationships between functional diversity and composition and ecosystem services (Micheli et al., 2014; Raffaelli, 2006). Additional future work directly quantifying ecosystem function and services and investigating

relationships between ecological attributes and service provisioning will be critical for understanding the role of biodiversity protection in maintaining the suite of functions and services provided by marine ecosystems (Menzel et al., 2013; Micheli et al., 2014).

In the next sections, we review work to date exploring these relationships and defining and quantifying functional traits and attributes of marine communities. We propose that broader application of functional frameworks is a key step in linking MPAs and their ecological effects to ecosystem service provision.

The Role of Biodiversity: Expectations from Functional Diversity and Redundancy

The goals of MPAs are increasingly expanding beyond the protection and restoration of a few to the restoration of ecosystem functions and services (e.g., herbivory and maintenance of corals, predatory control of invasive species, recruitment and recovery potential, coastal protection, fisheries, and opportunities for recreation and education). MPAs also aim to maintain long-term ecosystem health and sustain multiple ecosystem functions and services within the context of changing environmental conditions (e.g., UNEP-WCMC, 2008). One suggested approach for tackling this extremely complex and multifaceted sets of goals is to use biodiversity as a target for management and a proxy for the full range of functions and services within an ecosystem (Duffy, 2009; Palumbi et al., 2009). Indeed, a majority of MPAs include biodiversity protection among their goals or anticipated benefits (Pomeroy et al., 2005). Biodiversity conservation goals stem both from a recognition of the existence and option values of species and a growing recognition that biodiversity—the degree of variation in living organisms, at the genetic, population, community, and ecosystem or landscape levels—contributes to the many important ecosystem processes that underlie marine ecosystem health and ecosystem service provision. Therefore, the global trend of declining biodiversity may lead to a similar decline in ecosystem services and human well-being—both in terms of immediate losses in ecosystem services and also in the loss of an ecosystem’s capacity to adapt to environmental changes and sustain the provision of services into the future (Daily, 1997; MA, 2005; Tilman et al., 2006). For example, a study of local experiments, long-term time series, and global fisheries data by Worm et al. (2006) showed that declines in genetic and species diversity in marine systems were associated with decreases in not just the productivity of fisheries, but also in their stability and recovery across different temporal scales.

Most assessments of biodiversity effects on ecosystems have focused on species or genetic diversity and have generally reported positive relationships between biodiversity and ecosystem processes from a range of ecosystems including mudflats (Emmerson et al., 2001), sea grasses (Duffy, 2006), salt marshes (Griffin and Silliman, 2011), kelp forests (Byrnes et al., 2006), and

rocky shores (O'Connor and Crowe, 2005). However, there is an increasing awareness that the nature of the relationship between species diversity and ecosystem processes is highly dependent on the link between species diversity and functional diversity (Micheli and Halpern, 2005). Functional diversity is the variation in functional characteristics represented by the diversity of living organisms, and it is these characteristics that determine the range of ecological roles and species interactions that are present, and thus mediate the relationship between biodiversity, ecosystem functioning, and service provision (Cadotte, 2011; Díaz and Cabido, 2001; Loreau, 1998; McGill et al., 2006). Specifically, biodiversity is expected to promote immediate and long-term ecosystem functioning through patterns of complementarity and redundancy in the functional characteristics it encompasses (Maestre et al., 2012; Walker et al., 1999). Therefore, the protection and restoration of functional diversity is increasingly highlighted as an important principle for management of both marine and terrestrial ecosystems (Chapin et al., 2010; Foley et al., 2010).

Two key reasons underlie the expectation that functional diversity promotes long-term ecosystem health and service provisioning. First, maintaining high levels of functional diversity in an ecosystem allows for the full range of species' ecological roles and interactions to persist and thus for maintenance of multiple ecosystem functions. Both empirical and modeling studies have found that as more ecosystem functions are considered, higher levels of biodiversity are required to sustain all functions simultaneously (Gamfeldt et al., 2008; Hector and Bagchi, 2007; Hensel and Silliman, 2013; Maestre et al., 2012; Zavaleta et al., 2010). Furthermore, in some cases functional diversity, rather than species diversity, may be more important in maintaining ecosystem multifunctionality, since it is the complementarity of species' functional contributions that allows for multiple ecosystem functions to persist (Mouillot et al., 2011). Because many ecosystem services valued by people depend on multiple ecosystem functions (Palumbi et al., 2009), and different ecosystem functions and services may trade off with each other (Bennett et al., 2009; Carpenter et al., 2009), the protection of biodiversity, particularly functional diversity, can serve as a tractable proxy for an ecosystem state that sustains a balance between a range of ecosystem functions, especially when the key drivers and interactions of those functions are not yet well known (Duffy, 2009; Palumbi et al., 2009).

Second, functional diversity may act as a form of insurance for ecosystem functions and services in the face of environmental fluctuations and global environmental change (Bernhardt and Leslie, 2013; Elmqvist et al., 2003; Naeem and Li, 1997). Specifically, functional diversity is expected to promote ecosystem resilience, defined as the ecosystem's capacity to absorb disturbance, reorganize, and maintain its functioning, structure, and feedbacks such that it does not undergo an undesirable phase shift involving the loss of key ecosystem services (Folke et al., 2004). Two aspects of functional diversity underlie this expected link resilience: functional redundancy and response diversity.

Functional redundancy occurs when multiple species contribute similarly to ecosystem functions, such that redundant species may be able to functionally compensate for the decline or loss of one or more species (Naeem and Li, 1997; Walker, 1992, 1995). Therefore, loss of species would not significantly impact the functioning of the ecosystem until the last member of a functionally redundant group is lost. However, the loss of that last member could lead to the complete loss of important ecosystem feedbacks and a complete transformation or shift of the ecosystem to an alternate state (Hughes, 1994). Because of high uncertainty and variability of species' ecological roles, the extent of redundancy, and the vulnerability of functions to environmental changes and human pressures, maintaining high levels of functional diversity and redundancy in natural communities should be a key management goal.

Quantifying and Protecting Functional Diversity and Redundancy in Marine Protected Areas

Quantifying Functional Diversity

Recent reviews of strategies for sustainable management of terrestrial and marine ecosystems have specifically highlighted functional diversity and redundancy as targets for protection or restoration (Chapin et al., 2010; Foley et al., 2010). In order to successfully manage and maintain functional diversity and redundancy in ecosystems, a first step is to develop practical ways to measure and monitor these attributes in the field.

Two approaches have generally been used to quantify functional diversity in ecological communities. The most common method is to assign species to discrete functional groups based on knowledge of species' resource use and life history strategies (Micheli and Halpern, 2005; Simberloff and Dayan, 1991), or by using a hierarchical clustering analysis on a set of measured species traits (Jaksić and Medel, 1990). Functional diversity can then be measured at the level of functional groups: functional-group richness is simply the number of functional groups, while functional-group diversity is usually assessed using the Shannon–Wiener index (H') and incorporates a measure of the relative abundance, or evenness, of the functional groups. Functional redundancy is assessed by calculating species richness or Shannon–Wiener diversity within each functional group. Functional group approaches have a long history in ecology and have provided many insights into species interactions and community structure (Dethier et al., 2003; Simberloff and Dayan, 1991; Steneck and Watling, 1982). However, this method suffers from several problems, arising from the use of discrete groupings to model functional differences that are generally continuous in nature. Most importantly, the threshold for considering functional differences as significant is an arbitrary one, and it is assumed that all pairwise differences between species from different groups are equal in magnitude (Mouchet et al., 2010; Petchey and Gaston, 2002). In some

cases, these problems may compromise the usefulness of functional groups in assessing functional diversity—ecosystem functioning relationships (Wright et al., 2006). On the other hand, particularly in applications of a functional framework to diverse communities, a lack of detailed data on functional traits for all species makes categorical functional classifications, or the use of a mix of categorical and continuous trait values, the only possible approach (Micheli et al., 2014; Stuart-Smith et al., 2013).

To address some of the weaknesses identified in the functional group classification approach and increase the explanatory power of functional diversity for ecosystem function, various trait-based multivariate measures of functional diversity have been developed (Botta-Dukát, 2005; Laliberté and Legendre, 2010; Mason et al., 2005; Mouillot et al., 2013; Petchey and Gaston, 2002; Villéger et al., 2008; Walker et al., 1999). Many of these measures are calculated by first representing species within the community as points in a multivariate functional trait space, and then assessing various aspects of the distribution of species and their relative abundances within this space (Mouillot et al., 2013; Villéger et al., 2008). Unlike the functional group approach, these measures may account for various degrees of functional difference between species. They also allow for different, complementary measures of functional diversity to be assessed, such as the relative abundances of functionally redundant and functionally unique species in the community, or community-wide shifts in specific traits (Mouillot et al., 2008). However, the use of this approach has generally been limited to low-diversity assemblages or subsets of taxa within a community, such as higher taxa that have directly comparable morphological traits (e.g., terrestrial plants, insect families, and fish).

Compared with measures of species diversity, all methods of quantifying functional diversity and redundancy are more data-intensive; they require additional information about each species' functional characteristics in the form of either knowledge about species' basic ecologies or quantitatively measured trait values for each species. The latter is especially time-consuming to obtain and may not be tractable in some species-rich ecosystems such as coral reefs (Micheli et al., 2014). As a result, incorporating functional diversity into assessments of ecosystem health, MPA performance, or MPA design still presents a challenge and has not been widely implemented. Nevertheless, the few studies that have measured functional diversity in the context of MPAs have provided some useful insights into how effective MPAs have been in protecting different aspects of functional diversity.

Spatial Protection of Functional Diversity

Functional diversity has generally not been considered explicitly in the design and location of MPAs. In siting MPAs and MPA networks, areas of high taxonomic diversity (particularly species richness) have usually been targeted as a way to achieve the protection of biodiversity. Because empirical

studies have demonstrated a generally positive relationship between species richness and functional richness, it is often assumed that species richness adequately proxies functional richness for the purposes of management (Foley et al., 2010).

However, the few studies that have examined spatial variation in marine functional diversity have reported spatial mismatches between MPAs and areas of high functional diversity. This incongruence corresponds to a mismatch between hotspots of taxonomic diversity and hotspots of functional diversity that occurs at multiple spatial scales. Regionally, Mouillot et al. (2011) found that existing networks of MPAs in the Mediterranean Sea were spatially congruent with fish species diversity, but failed to cover areas of high functional diversity. At a global scale, Stuart-Smith (2013) reported that areas of high reef fish functional diversity were concentrated in temperate latitudes, in contrast with well-known patterns of species richness that peak in the Tropics. They suggest that the tropical bias for MPA formation may result in failure to protect the functional aspects of biodiversity on a global scale.

Similar mismatches in functional diversity with species diversity and protection efforts have been reported in terrestrial systems (Devictor et al., 2010) and could reflect a more general need to integrate functional diversity into management. One such integrative framework has been developed to prioritize areas for conservation within a series of floodplain water bodies in France. Maire et al. (2013) assessed a combination of fish functional diversity, taxonomic diversity and the diversity of the species' natural heritage and social-economic importance and concluded that downstream areas with high lateral connectivity to the main river channel should be prioritized for protection. A similar integration of spatial patterns of marine functional diversity with other management goals could be useful in improving spatial protection of functional diversity.

Effects of Marine Protected Areas on Functional Diversity

While the limited evidence available suggests that current MPAs fail to provide adequate coverage of areas with high functional diversity, studies addressing the direct effects of MPAs on functional diversity, and in some cases redundancy, have generally found positive effects. Most direct assessments of MPA effects on functional diversity have used functional group approaches to compare functional richness and functional redundancy between MPAs and reference areas, but the emerging use of trait-based multivariate approaches has begun to provide some more detailed insights into the effects of reserves.

In the most spatially extensive assessment of MPA effects on functional diversity, Micheli and Halpern (2005) analyzed a global dataset of reef fishes from 31 different no-take reserve sites, including both temperate and tropical reefs. They reported that in comparison with reference sites, no-take reserves

generally contained more functional groups (higher functional richness) and increased functional redundancy within some groups. Studies of individual MPA systems have reported similarly positive effects of MPAs on functional diversity. In the Bahamas, fish assemblages within a no-take marine reserve contained more functional groups and greater functional redundancy within each group, compared with nearby fished areas (Micheli et al., 2014). In the Mediterranean Sea, MPAs were also associated with higher functional diversity (Villamor and Becerro, 2012) and greater functional redundancy (Stelzenmüller et al., 2009).

Across most of the studied areas, greater functional diversity within MPAs was associated with higher species diversity (Micheli and Halpern, 2005; Micheli et al., 2014; Stelzenmüller et al., 2009). This pattern is often observed at least at low levels of species richness because functional richness is positively related to species richness, although the exact shape of the relationship can vary (Micheli and Halpern, 2005; Petchey and Gaston, 2002). However, opposing or uncorrelated effects of MPAs on species diversity may also be observed when different species increase and decline simultaneously, which is relatively common due to indirect effects of protection on species through competitive and predatory interactions (Micheli and Halpern, 2005). Several reserves from the Micheli and Halpern (2005) analysis were associated with positive effects on functional diversity but negative effects on species diversity, while the Spanish MPA system studied by Villamor and Becerro (2012) reported positive effects on functional diversity but no significant effect on species diversity. Collectively, these studies suggest that though species and functional diversity are generally correlated, functional diversity is more likely to respond positively to protection, and measuring species diversity alone may lead to failure to detect reserve effects on functional diversity.

Trait-based multivariate measures of functional diversity have not yet been widely used to assess the effects of protection measures in either aquatic or terrestrial ecosystems, potentially because they are a newer set of tools that also require a fairly large amount of information. In the context of management, they have generally been applied in assessing ecosystem responses to large-scale environmental and anthropogenic impacts, especially the anthropogenic modification of terrestrial and aquatic habitats (Barragán et al., 2011; Edwards et al., 2014; Helsen et al., 2013; Magnan et al., 2010; Mouchet et al., 2010; Pakeman, 2011). These trait-based approaches are expected to be particularly suitable for assessing shifts in ecological communities for two key reasons. First, trait-based measures of functional diversity are more likely to show predictable shifts with environmental change because each individual species' response to environmental drivers is ultimately determined by its functional traits (i.e., response traits). Second, these trait-based measures are based on species abundances rather than presences or absences, so they are more sensitive to changes in

species assemblages, and could provide advance signals of disturbance in ecosystems ahead of the actual loss of species (Mouillot et al., 2013). Indeed, most of the studies that have applied these measures to assess ecosystem change have reported systematic losses in functional diversity and/or shifts in trait composition consistent with some degree of environmental filtering.

Because global climate change impacts essentially all marine ecosystems (Bernhardt and Leslie, 2013; Halpern et al., 2008), local-scale impacts (e.g., fishing) and management efforts (e.g., MPAs) inevitably co-occur with global-scale environmental changes such as warming and ocean acidification (Crain et al., 2008; Halpern et al., 2008). Therefore, trait-based measures of functional diversity may become increasingly useful for assessing the performance of MPAs in the context of environmental change. The potential value of this approach is illustrated by a recent study of fish functional diversity within a global warming hotspot. Bates et al. (2013) compared species richness and multivariate functional diversity measures between a Tasmanian marine reserve and nearby reference sites over 20 years. They found no significant differences in species richness or overall functional richness between the reserve and reference sites; functional richness increased in both over the study period. However, by comparing the functional trait composition of the fish assemblages, they found that the increase in functional richness within the reserve was partly driven by an increase in large-bodied, carnivorous species that are targeted by fisheries, whereas the increase in functional richness outside the reserve was driven by the colonization of species with warmer affinities. In fact, the degree of invasion of warm-water species was significantly less within the reserve, suggesting that fish communities within the MPA were more resilient to the effects of climate change. In this case, a trait-based multivariate approach was able to detect the interaction between an MPA and a large-scale climate driver, and identify the effect of the MPA on a key function: resilience to climate change. In contrast, a traditional species diversity or functional group classification approach failed to highlight this effect of protection on ecosystem function.

Trait-based functional diversity indices may also be able to provide more specific information about important reserve effects on functional diversity. For example, the integrity and functioning of ecosystems are disproportionately impacted by the contributions of functionally unique species (O’Gorman et al., 2011; Petchey et al., 2008) because functionally unique species, by definition, perform functions with low redundancy. Mouillot et al. (2008) developed and used a trait-based index, the Conservation of Biological Originality (CBO), to examine changes in the prevalence and abundance of functionally unique fish species before and after the establishment of a French MPA. They concluded that the MPA was successful in protecting the most functionally unique members of the fish community: these species were more widely distributed and more abundant after MPA establishment. Unique combinations of functional traits may be crucially important for maintaining ecosystem functioning,

as demonstrated by studies of large parrotfishes in coral reefs of the Great Barrier Reef and Pacific Line Islands (Bellwood et al., 2003).

Results of the studies by Bates et al. and Mouillot et al. suggest that: (1) MPAs can have positive effects on maintaining the diversity of functional traits within communities; and (2) trait-based multivariate measures of functional diversity are a promising approach for assessing reserve effects on functional diversity. More MPA assessments using trait-based multivariate metrics will be needed to determine if these metrics generally provide better insights into ecosystem health and functioning than the less data-intensive traditional approaches based on taxonomic diversity and other community properties such as total abundance, size structure, or species composition, and if any additional information gained is worth allocating more resources for obtaining trait data.

KEY DIRECTIONS AND OPEN QUESTIONS

Our review highlights that empirical evidence for positive effects of MPAs on ecosystem service provision by coastal marine ecosystems is accumulating. However, gaps in knowledge clearly remain. Existing studies are still largely focused on a subset of services, namely provisioning services and to a lesser extent some regulating services. Studies on some regulating, supporting, and even nonmonetary provisioning services (e.g., subsistence fishing), as well as most cultural services (e.g., aesthetic and spiritual values), are still very scarce.

We argue that a possible productive way forward is to apply functional frameworks to assessing the broader effects of MPAs on services, through the links that exist between functional diversity, redundancy, and trait composition and service flows. Developing this research program will require efforts to (1) better link functional trait or functional group assignments to actual ecosystem functioning and service provision, (2) scale up analyses to whole assemblages, and (3) assess the drivers and consequences of temporal variability in functional diversity and trait composition. Such programs would allow better identification of how MPAs can protect existing and/or provide new ecosystem services, as well as identifying which ones are the drivers and correlates. An important point to identify is the extent toward MPA borders at which MPAs still have an effect. It would also enable the clearing out of those ecosystem benefits not affected by MPAs.

A key practical aspect, particularly if the main application aim is to inform management, is to enable and facilitate the acquisition of the additional data needed for functional analyses. Acquisition of morphological and behavioral data through direct collaboration between scientists, MPA managers, and fishers, and through the development of cost-effective monitoring—e.g., through low-cost video systems, publicly available databases, and involvement of diverse users (e.g., through citizen science projects)—are promising avenues for allowing the broader application and testing of functional frameworks to MPA assessments.

To successfully develop scientific frameworks and datasets needed to address the links between MPAs, ecosystem functioning, and ecosystem services, closer collaboration is needed between natural and social scientists on the one hand, and among academics, MPA managers, and users on the other.

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