# How MPAs Enhance the Resilience of Coastal Marine Ecosystems and their Services: A Supplemental Report by the Marine Protected Areas Federal Advisory Committee's Ecosystem Team

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## About This Document

The Marine Protected Areas Federal Advisory Committee (MPA FAC) was charged in January 2018 by the US Departments of Commerce and Interior with identifying benefits of U.S. marine protected areas to marine[i] ecosystems, economies and communities. The MPA FAC was also directed to identify emerging uses and challenges facing federal, state, territorial and tribal MPAs and to make recommendations for sustaining MPA benefits in the face of those challenges. This report was developed by the MPA FAC's *ad hoc* Ecosystems Team (authors listed above) to inform aspects of the Committee's Findings and Recommendations. It was approved as a Supplemental Report by the full MPA FAC on xxx and was submitted by the Committee to the Departments of Commerce and Interior as supplementary material accompanying its official recommendations.

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## Introduction

Marine protected areas (MPAs) play an important role in conservation stewardship and can provide increased protection to coastal populations and infrastructure. The past decade has seen a marked increase in the establishment of MPAs throughout the world (1, 2). This global response has been spurred in part by the International Union for the Conservation of Nature's (IUCN) agreement to establish ten percent of marine waters in MPAs by 2020[1]. The increase also reflects a growing number of scientific studies that have shown how MPAs can achieve a variety of conservation roles. However, these studies also document mixed results in MPA performance (e.g. 3–6). Separately and together, the large number of MPAs around the world are providing scientists with opportunities to synthesize and evaluate what particular conservation goals are

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[1] Formally adopted as Aichi Target 11 by the Convention on Biological Diversity and under the United Nations' Sustainable Development Goal 14 (Life Under Water).

being achieved with MPAs and what attributes of MPA design (e.g., longevity, size) and management (e.g., enforcement, compliance) are responsible for these successes (e.g. 3, 4, 6–10). With this growing body of knowledge, managers and policy makers can now evaluate the design and management of MPAs to determine both how existing MPAs might be adapted to better achieve their goals, and to apply this knowledge to guide ongoing and future efforts to establish new MPAs.

Simultaneous with the growing body of knowledge on MPAs, the goals of MPAs have evolved as well. Of particular importance is the potential role of MPAs in enhancing the resistance and resilience of ecosystems to the impacts of a changing global ocean. There is a growing focus by managers, policy makers, and an interested public in this issue. However, we must note that ecosystem resilience is complex and involves a multitude of ecological processes that underpin a species' and an ecosystem's capacity to persist in its natural state while continuing to produce valuable ecosystem services (e.g., fisheries, eco-tourism, coastal protection, cultural significance). For example, ecosystems are often characterized as coupled social-ecological systems, reflecting the fundamental interactions between humans and non-humans elements of the ecosystem (11). From that recognition emerges the inclusion of resilience of human communities and their economies and how these influence and are influenced by a coupled social-ecological system (e.g. 12). Thus, understanding how MPAs can enhance the resistance and resilience of ecological systems to environmental change requires understanding the concept of ecological resilience, the ecological processes that contribute to it, and how MPAs can, when developed correctly, protect those ecological processes. Here, we focus only on the determinants of the non-human ecological resilience of these systems (referred to as "ecological resilience").


Photo credit: Maya Banks

Here, we first briefly introduce the concept of ecological resilience and the variety of ecological processes that contribute to a population, community or ecosystem's resilience, with special attention to a changing marine environment. We then review the goals of MPAs that contribute to resilience and summarize those attributes of MPAs that have been demonstrated to enhance resilience. Though some recent studies have reviewed design and management attributes of MPAs that underpin their conservation values in the face of a changing climate (e.g. 13, 14), we focus here on their contribution to enhancing a species' or ecosystem's capacity to resist or be resilient to the effects of climate change. In doing so, we conclude with a summary of best practices for managers and policy makers toward this goal of MPAs.

## What is ecological resistance and resilience and why is it important?

The concepts of resistance and resilience in the context of ecological systems (populations, communities, ecosystems) was developed by C.S. Holling (15) and has evolved over time in the literature (16–18). Originally, the *resistance* of a population, community or ecosystem is its capacity to remain intact (i.e. maintain its fundamental taxonomic or *functional structure* and *functional processes*) when subjected to either a non-human or anthropogenic perturbation (e.g., hurricane, epidemic, oil spill). *Ecological resilience* is the capacity of a system to return to its pre-perturbation state (characteristic structure and functions). Currently, resistance is often included as an element of resilience, however we separate them here in order to describe how ecological processes contribute to each. Ecological systems provide fundamental human services. Species populations support economically and culturally important resources (e.g., fisheries, genetic resources, carbon sequestration, protect coastlines from erosion), ecological communities and ecosystems support those species and provide additional services (e.g., primary and net biomass production, habitat, recreation, culture values (19)). Because the well-being and sustainability of human societies and economies depend on these services, ensuring their persistence and productivity in the face of disturbance fundamentally benefits humans.

## What ecological processes contribute to resistance and resilience?

Ecologists have identified a variety of ecological processes that contribute to resistance and resilience depending on whether populations, communities or ecosystems are the target of interest. These processes are synergistic with strong positive feedback among all three levels of ecological organization; increased resistance and resilience of populations increases the resistance and resilience of the communities they constitute, which in turn increases the resistance and resilience of entire ecosystems. Moreover, resistant and resilient ecosystems enhance the resistance and resilience of the communities and populations that comprise them. Whereas this section focuses on ecological processes, it is critical to also recognize that anthropogenic impacts to these ecological traits can lead to evolutionary consequences (e.g., slower growth rates, smaller sizes and younger ages of sexual maturity) that also have ecological consequences, including reduced resistance and resilience to perturbations (20).

Larger *population size*, greater variation in *size and age structure*, greater *genetic diversity*, and spatial *connectivity* among local populations (i.e. *metapopulations*) are all known to enhance the capacity of populations to both resist and rebound from perturbations. For example, larger populations with many adults increases the likelihood that individuals survive a perturbation to more quickly reproduce and replenish themselves. Populations with greater genetic diversity have greater capacity to adapt to changes in environmental conditions. Numerous local populations connected to one another by movement of individuals increase the likelihood that some populations will avoid local perturbations and supply those populations that suffer perturbations with immigrants. More productive populations, those that support large numbers of adults that produce many young, increase the rate at which that population rebounds from a perturbation and contribute to the replenishment of other populations.

Similarly, a variety of processes contribute to the resistance and resilience of ecological communities. Greater *species diversity* and *functional diversity* increase the resistance and

resilience of communities in a number of ways (16, 21–23).The greater the diversity, the more likely a species that enhances resistance or resilience will be present (referred to as the "sampling effect"). For example, keystone predators control prey that can otherwise destabilize a community when their populations become too large. Foundation species like vascular plants and algae create habitat for many species. Increased diversity increases the likelihood that these species occur in a community. Likewise, processes mentioned in the preceding paragraph that increase the resistance and resilience of these ecologically important species, in turn increase the resistance and resilience of the communities they inhabit. Greater species diversity increases the diversity of functional roles of species and the species that contribute to those functions. The presence of primary producers (vascular plants and algae) and planktivores increases the ways and amount of nutrients and carbon incorporated into food webs. Detritivores and herbivores increase the ways and amount of those nutrients and carbon that are available to higher trophic levels. The greater the diversity of functions, the more ways communities can respond to and maintain their fundamental structure and functions (i.e. resist) when subjected to various perturbations. Greater species diversity increases the number of species with similar functional roles. When these species differ in their vulnerability to different perturbations, as one declines, the other persists to compensate for and maintain that function (referred to as "redundancy"). Multiple species that perform similar functions and use resources in different ways increase overall productivity of that functional group (e.g., different species of algae that perform optimally under different light or nutrient conditions). This "complementarity" increases the productivity of a community, which in turn enhances its resistance and resilience to perturbations. Communities with overall *greater biomass and productivity* among the species it comprises, are more likely to resist invasions of non-native species, and like populations, can produce more young and rebound from perturbations more quickly.

Likewise, ecosystems that are large, *productive* and comprised of a *greater diversity of habitat types* support a greater diversity of species and functional processes (e.g., nutrient cycling). They also support larger population sizes of species that require multiple habitat types over their lifetime. Ecosystems often generate resources (energy, nutrients, species) that move to and supply other ecosystems that are deficient in those resources. These subsidies enhance the recipient ecosystem's productivity and diversity, thereby enabling one ecosystem to enhance the resilience of other ecosystems.

## What is the scientific evidence for resilience?

Two very different forms of evidence for ecological resilience emerge from the above description, including the various ecological processes that contribute to it. A robust demonstration of resilience results from the documentation of a population, community or ecosystem resisting or returning to its characteristic structure and functions subsequent to a perturbation. For example, a reef fish population or coral reef returning to its prior population size or relative abundance of coral species, respectively. Such results require a *times series of data that spans long periods* before and after the perturbation. Such observations and demonstrations of resilience are rare. Moreover, to attribute resilience to an MPA requires evidence of differences in resilience in and out of an MPA. Obtaining such data is challenging and costly. Thus, it is not surprising that such rigorous demonstrations that MPAs impart resilience are rare. Alternatively, a less robust

approach is to show that the presence of an MPA protects one or more ecological processes that have been shown to impart resilience, and that these ecological processes are impaired in the absence of the MPA. This requires the non-trivial assumption that the protected ecological processes within an MPA will, in fact, impart resilience to the presumed perturbation. While less robust, observations of protection of ecological processes are far more common, and often applied to infer the role of MPAs in enhancing resistance or resilience.

## How do MPAs enhance resistance and resilience and what attributes of MPAs help to achieve these goals?

Although the literature is rich with modeling studies that provide predicted consequences of MPAs on population, community and ecosystem responses to MPAs, our assessment is focused on *empirical evidence* of the effects of MPAs. Our review was facilitated by other major reviews on the ecological and evolutionary consequences of establishing MPAs (e.g. 13, 14, 24–30). From this review, we identify a variety of ways that MPAs could and do enhance the resilience of populations, communities and ecosystems.

*Population resilience* – One of the most well documented influences of MPAs is the increase in population size (e.g. 31–33) and diversity of size and age classes in a population, especially of larger, older individuals that disproportionately contribute to larval production (e.g. 33). One example of evidence of this population effect enhancing population resilience to a perturbation is the more rapid recovery of an abalone population subjected to a hypoxia event within an MPA compared to harvested populations outside the MPA (34). The greater number of mature abalone that survived the hypoxia event allowed those individuals to more rapidly replenish and recover the population within the MPA as well as nearby populations outside the MPA.


Photo credit: Arturo Hernandez
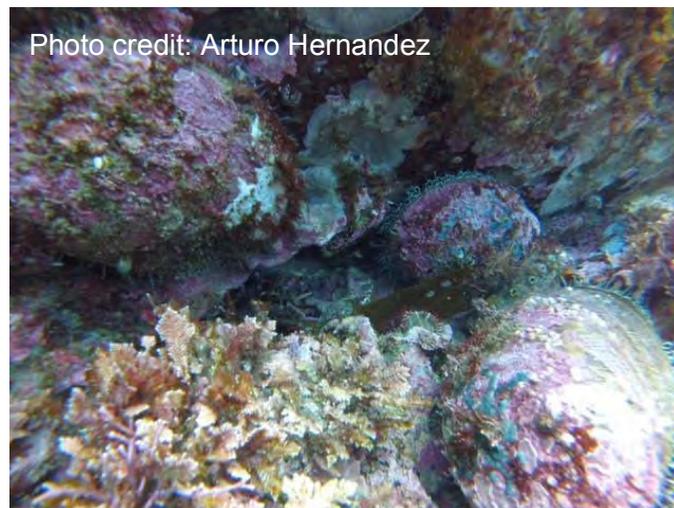
Other examples of direct evidence of increased population resilience include MPAs that are no-take (34, 35) and networked (36). Other studies provide evidence for MPA effects on the various ecological processes shown to enhance population resilience. Both small (10) and larger (37–39), older (10, 40) and those that incorporate multiple ecosystems (41, 42), are among the design features that can increase the size of populations. Of management actions, no-take reserves significantly increased population responses (34, 38, 49–56, 40, 42–48), and greater than MPAs that allowed partial take (10, 37, 57–59). In addition, strong enforcement (10, 31, 43, 46, 47, 59) and compliance (5, 31) were required for greater population responses. Larger (38)or no-take (34, 35, 63–65, 44, 45, 48, 49, 51, 60–62) MPAs exhibit broader size structure.  Larger (38), or

networked (31) MPAs with multiple ecosystems (66) exhibit greater biomass and larval production. Fewer examples indicate that partial take MPAs (e.g., 57) increase biomass and larval production as well as no-take MPAs (10, 34, 63, 67, 68, 40, 42, 44, 45, 47, 48, 52, 57). Genetic diversity of a population has also been found to increase (69) within a large and networked (39) MPA.

*Community resilience* – Direct evidence of community resilience has been observed in MPAs (33, 70), especially with multiple ecosystems (39, 71) or no-take reserves (45, 54, 57, 58, 62, 72–75) that are well enforced (75). Like those studies that have documented increases in the abundance of particular species, the overall abundance of multiple species has also been observed in many instances. Design attributes associated with these increases in multiple species include either small (10) or large (38,


Photo credit: NOAA

76), and older (10, 47, 53, 76) MPAs that contain multiple ecosystems (41, 71). Management criteria that increase assemblage-wide abundance include both partial take (10, 77, 78) and no-take reserves (10, 30, 79–81, 44, 53, 57, 60, 65, 72, 77, 78), with strong enforcement (6, 10) and compliance (44). Similarly, overall biomass among species increases in either small (77, 78) and larger (4) older (4) MPAs with isolated habitat (4) and multiple ecosystems (66, 67, 82). Though this response can occur in partial take (77, 78) MPAs, it is particularly evident in no-take reserves (4, 10, 80, 83–85, 40, 44, 60, 65, 67, 72, 77, 78) with strong enforcement (4, 6, 10, 83). Increased productivity of multiple species is observed in larger MPAs (86).

As described above, increased taxonomic and functional diversity are known to be central to the resistance and resilience of ecological communities. Taxonomic diversity have been shown to increase within (33) and adjacent to (63) MPAs and numerous studies indicate that this increase occurs predominantly in no-take marine reserves (4, 10, 75, 83, 87–92, 39, 53, 58, 60, 63, 65, 72, 74). The increases in taxonomic diversity are more prevalent in larger (4, 38, 39), older (4, 53, 76), networked (39) MPAs that include multiple ecosystems (42, 67) and habitats are isolated (4) to limit movement out of the MPA. In addition to no-take, increases are most notable in well enforced MPAs (4, 75, 83, 88) with documented compliance (88). Functional diversity can increase in an MPA (33, 63, 93), especially older (57) MPAs with multiple ecosystems (67, 71, 82). Functional diversity increases within (43, 45, 75, 80, 83, 89, 94, 95, 51, 54, 57, 62, 65, 67, 72, 74) and adjacent to (63, 75, 83) no-take MPAs with documented enforcement.

*Ecosystem resilience* – Direct and indirect evidence of enhanced population and community resilience attributed to MPAs as described above underpin the broader resilience of ecosystems. For example, increased population resilience of species that play ecologically significant roles can contribute to the resilience of the ecosystems they inhabit. Increased resilience of important

habitat-forming species that enhance local biodiversity, or higher trophic levels that control lower trophic levels can translate into greater resilience of ecosystems (see case studies). Increased biodiversity is known to enhance ecosystem resilience in many ways and one common consequence of MPAs is to increase local biodiversity (see above). Ecosystem connectivity, the movement of species from one ecosystem to another, can be especially important to the resilience of ecosystems and their services (see case studies). Some of these mechanisms of resilience can also enhance the likelihood of resilience of ecosystem services and the local human communities that rely upon those services (e.g. local fisheries 5, 63, 96, 97). However, such consequences are not always the case (e.g. 3, 98–101) and are dependent on the design (e.g., inclusion of deep reef habitat as refuge from climate effects) and management (e.g., strong community compliance) of MPAs and their relationships with coastal human communities and their uses of coastal ecosystem services (e.g. 5, 97, 102, 103).

## Conclusions

The scientific literature review reveals two important conclusions with respect to the contributions of MPAs for increasing the resistance and resilience of MPAs to environmental and ecological perturbations.

First, there is growing evidence for the enhancement of resistance and resilience of populations, communities and ecosystems by MPAs. However, as expected, direct observations of resilience are few, and the bulk of evidence involves the enhancement of those ecological processes known to enhance resistance and resilience. Greater support for studies that monitor populations, communities and ecosystems in and out of MPAs over time to evaluate their responses to perturbations will provide us with more direct evidence and greatly advance our understanding of whether and how MPAs support resilience to various forms of environmental and ecological perturbations.

Second, those MPAs that exhibit the highest likelihood of enhancing resistance and resilience are well-enforced, older, larger, no-take reserves that include multiple ecosystems, and are part of an ecologically-based MPA network. Thus, to enhance the resistance and resilience of existing MPAs to perturbations, including those perturbations associated with a changing climate, MPAs should be evaluated against these design and management criteria. Adapting existing MPAs and designing future MPAs using these criteria should greatly enhance the contribution of MPAs for the long-term protection of species, the biodiversity they constitute, and the ecological communities and ecosystems that support that biodiversity. However, it is understood that management decisions involving the development of MPAs are not taken with such a narrow view and must take other aspects for human communities into account including aspects such as economics and cultural values.

# Case Studies

## 1) No-take reserves enhance ecosystem resistance to invasive species

Two good examples of how no-take MPAs enhance ecosystem resistance to invasive species come from kelp forest ecosystems on opposite sides of the Pacific Ocean. Climate change has increased the intrusion of warm tropical waters down the eastern coast of Tasmania, bringing large numbers of an invasive sea urchin larvae and extending the distribution of the species (54, 62). The local lobster fishery there has reduced the size of lobsters along the coast except in reserves that prevent their take. Only large lobster can consume and control the invasive sea urchins. In areas outside the reserves, where large lobsters are rare, the invasive sea urchins have deforested reefs. The loss of kelp forest threatened the multimillion dollar abalone fishery sustained by kelp forests. Within reserves, kelp forests remain intact demonstrating the critical importance of protecting predators that influence the entire state and productivity of the ecosystem.



Photo credit:Scott Ling

In the North American kelp forests on the Northern Channel Islands of southern California, an invasive alga is displacing kelp forests, including the giant kelp and other algae that form the foundation of the forest ecosystem and the many species that inhabit it (104). Spiny lobster and the California sheephead both feed on sea urchins. In their combined presence, sea urchin numbers are depressed and native algae are abundant. Outside of MPAs, where spiny lobster and the California sheephead are both fished, the resulting loss of predators led to a large number of sea urchins that have greatly reduced the abundance of both the native and the invasive algae. In an adjacent older no-take reserve (since 1978) where both the lobster and California sheephead are abundant, sea urchins are at moderate abundance and native algae are abundant, collectively limiting the invasion of the invasive alga. In the adjacent more recently created reserve (2003), lobster and California sheephead are only at moderate abundance, urchins are at moderate abundance, native algae are less abundant, and the invasive alga is abundant. Thus, only when both predators are
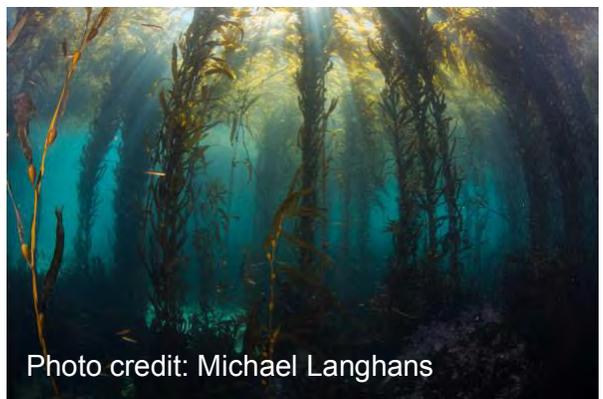


Photo credit: Michael Langhans



Photo credit: Michael Langhans

abundant in the no-take reserve is the kelp forest intact and resistant to the invasive alga, especially over time as the effects of the MPA begin to manifest in the ecology of the protected area.

## 2) Protecting nursery habitat for herbivorous fishes enhances coral reef resilience

When coral reefs are damaged by hurricanes, bleaching events, diseases, or outbreaks of the crown-of-thorns sea star, macroalgae can quickly grow on the surface of the dead coral to cover the reef and prevent future growth or larval recruitment of corals. In these instances, coral reefs can persist in these algae-dominated stable states for decades. In conjunction with sea urchins, herbivorous fishes (e.g., parrotfishes) play a key role in consuming algae and allowing corals to recover. The juveniles of herbivorous reef fishes often inhabit inshore mangrove forests and



Photo credit: NOAA

seagrass beds before migrating to offshore coral reefs where they feed on algae (71). When these inshore nursery habitats are destroyed by coastal development, land-based pollution and sedimentation, aquaculture or other anthropogenic perturbations, the capacity for herbivorous fishes to graze algae and facilitate the recovery of coral reefs is undermined (66). Consequently, MPAs that protect these nursery habitats are critical to the resilience of nearby coral reef ecosystems (41, 67).

# 3) Management failures undermine the role of MPAs for resilient fisheries and communities
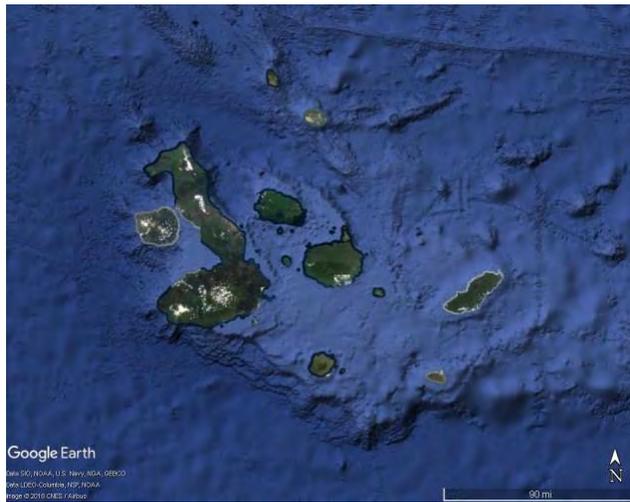




Created in 1998, the Galapagos Marine Reserve (GMR) extends 40 nautical miles from, and encompasses, the entire Galapagos archipelago (133,000 km2). It is one of the largest multi-use marine protected areas in the world and is comprises fishing, conservation and tourism zones. Six percent of the GMR is designated solely for conservation, and another 11% is designated for tourism, in which extractive activities (e.g. fishing) are banned (Jones 2013). Goals of the GMR include (i) biodiversity protection that helps support a growing ecotourism industry, (ii) restoration and sustainability of depleted coastal commercial fisheries (largely sea cucumber, lobsters, and grouper), and (iii) to provide an alternative tourism-based fishery to these depleted commercial fisheries, all of which are central to a sustainable and resilient economy for local communities. However, shortcomings in many of the management attributes identified in our analysis have prevented any realization of the commercial (102) and recreational (99) fisheries goals, thereby undermining any resiliency of these fisheries and the communities they support. A governance structure that has failed to both instill a community-wide recognition for the importance of protecting biodiversity and to enforce prohibited fishing in conservation areas, resulted in civil unrest and poor compliance, including continued illegal fishing activities (98, 102). The GMR provides an excellent example of how

inadequate and inconsistent management and community support can prevent the ability of MPAs to impart resiliency for fisheries and to benefit the communities they support.

## 4) Protecting coastal wetlands supports resilient coastal communities

In 2012, when Hurricane Sandy made landfall in the Northeastern USA, coastal communities suffered devastating losses from coastal flooding, destroying destroyed structures and disrupting livelihoods. However, communities inland of protected coastal marshes in Barnegat Bay, New Jersey (see map) experienced an estimated $82 million reduction in losses (8.5% of total damage). This economic benefit reflects the $235 million reduction in losses attributed to protection by coastal marshes across the 11 states impacted by Hurricane Sandy. Moreover, the diminished losses evidenced by Hurricane Sandy reflect the ongoing protection provided for coastal communities and their economies by coastal wetlands in this region (105). Historically, coastal wetlands extended across most of the coastline of Barnegat Bay. In 1960, after much of these wetlands were lost to urban development, the Edwin B. Forsythe National Wildlife Refuge was established to protect the remaining coastal marshes as habitat for birds as part of an important Atlantic flyway. Narayan et al. (105) found that in addition to preserving critical habitat for migratory birds, coastal wetlands saved millions of dollars by enhancing the resistance of coastal communities to flood damage. Protected wetlands are one example of the value in protecting coastal ecosystems (wetlands, seagrasses, mangrove forests, coral reefs) for resistant and resilient shorelines, coastal communities and their economies (e.g., 106).
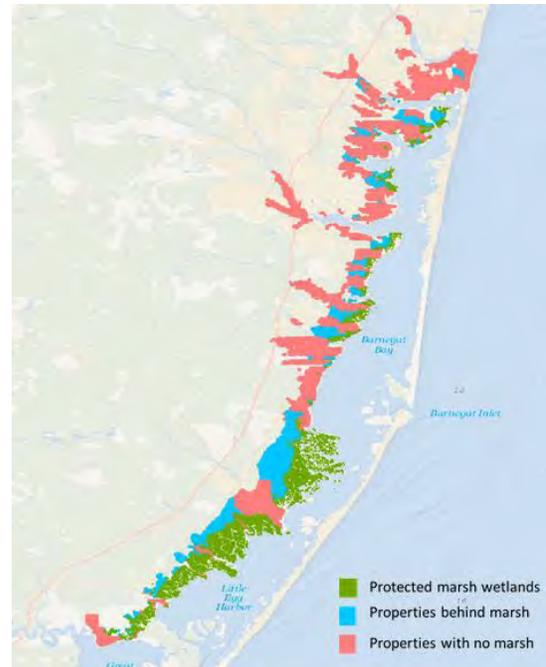
## Definitions

**Functional processes** include the ecological functions of a species (e.g., habitat-forming, keystone predator), communities (e.g., primary production,

**Marine Protected Area** Executive Order 13158 defines MPA as"[a]ny area of the marine environment that has been reserved by Federal, State, territorial, tribal or local laws or regulations to provide lasting protection for part or all of the natural and cultural resources therein.

**Metapopulations** are collections of spatially discrete local populations that are connected to one another by the movement of individuals among them. Local populations that contribute to replenishment of other local populations are referred to as "sources", whereas those that receive individuals but do not contribute individuals to other populations are referred to as "sinks".

**Population structure** is the relative number of individuals of different sizes, ages or sex in a population. Community structure is the particular species (their taxonomic identity) or functional roles (e.g., algae, herbivores, predators) that constitute a community and their relative abundances. Ecosystem structure includes both the community structure and the types and relative abundance of geological (e.g., rock, sand) and oceanographic features and conditions (physical and chemical).

**Resilience** is the ability of an ecosystem or community to absorb, recover from, and more successfully adapt to adverse events such as extreme weather or long-term changing environmental conditions, such as sea level rise.

## Acknowledgements

# Supplemental Material

**Table 1**. Summary of the literature review to evaluate MPA design and management attributes that influence their likelihood of enhancing the resilience of marine **populations**. Columns represent those ecological features (e.g., population size, community diversity) that are known to enhance resilience. Rows represent design (e.g., MPA size, network) and management (e.g., level of protection, enforcement) attributes. Numbers in the table identify articles cited in the text and listed in the Literature Cited section that have demonstrated those MPA design and management attributes to influence the mechanisms of resilience identified in the columns.

| | MPA goals (ecological) | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Population* | | | | | | |
| | size (abundance, density) | size structure | biomass/ larval production | genetic diversity | regulation (reduced variation) | productivity | resilience |
| **MPA attribute** | | | | | | | |
| MPA presence | (26, 31–33) | (33) | (33) | (26, 69) | | | |
| *Design attributes* | | | | | | | |
| size (small) | (10) | | | | | | |
| size (large) | (26, 37–39) | (38) | (38) | (39) | | | |
| habitat isolation (MPA isolated by sand, depth) | | | | | | | |
| individual vs. network | | | (31) | (39) | | | (36) |
| longevity | (10, 40) | | (5) | | | | |
| connectivity (multiple ecosystems within MPA) | (41, 42) | | (66) | | | (42) | |
| smaller buffer zone | | | | | | | |
| *Management attributes* | | | | | | | |
| partial take | (10, 37) | | (57) | | | | |

| | MPA goals (ecological) | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Population* | | | | | | |
| | size (abundance, density) | size structure | biomass/ larval production | genetic diversity | regulation (reduced variation) | productivity | resilience |
| no take | (10, 25, 45–54, 27, 55–59, 34, 37, 38, 40, 42–44) | (25, 34, 62–65, 107, 35, 44, 45, 48, 49, 51, 60, 61) | (5, 10, 52, 57, 63, 67, 68, 25, 27, 34, 40, 44, 45, 47, 48) | | | | (26, 34, 35) |
| enforcement | (10, 31, 43, 46, 47, 59) | | (46, 47) | | | | |
| compliance | (31) | | (5) | | | | |
| human impact outside of MPA | | | (5) | | | | |
| **Global MPA attribute** | | | | | | | |
| Comprehensive (what areas lack representation?) | | | | | | | |
| Placed in populated areas (areas of high need) | | | | | | | |

**Table 2**. Summary of the literature review to evaluate MPA design and management attributes that influence their likelihood of enhancing the resilience of marine **communities**. Columns represent those ecological features (e.g., population size, community diversity) that are known to enhance resilience. Rows represent design (e.g., MPA size, network) and management (e.g., level of protection, enforcement) attributes. Numbers in the table identify articles cited in the text and listed in the Literature Cited section that have demonstrated those MPA design and management attributes to influence the mechanisms of resilience identified in the columns.

| | MPA goals (ecological) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Community* | | | | | | | |
| | species (taxonomic) diversity | species abundance/ density (fish assemblages) | functional diversity/ trophic levels | Larval export and recruitment | biomass | Juvenile and adult spillover | productivity | resilience |
| **MPA attribute** | | | | | | | | |
| MPA presence | (26, 33, 63) | | (26, 33, 63, 93) | | | (14, 26, 108, 109) | | (33, 70) |
| *Design attributes* | | | | | | | | |
| size (small) | | (10) | | (110) | (77, 78) | | | |
| size (large) | (4, 27, 38, 39) | (38, 76) | | | (4, 27) | (27, 55) | (27, 86) | |
| habitat isolation (MPA isolated by sand, depth) | (4) | | | (91) | (4) | | | |
| individual vs. network | (39) | | | (36, 39, 56) | | | | |
| longevity | (4, 53, 76) | (10, 47, 53, 76) | (57) | | (4) | | | |
| connectivity (multiple ecosystems within MPA) | (27, 42, 67) | (41, 71) | (67, 71, 82) | (27, 67) | (27, 66, 67, 82) | | | (39, 71) |
| smaller buffer zone | | (76) | | (27, 111) | | (27) | | |
| *Management attributes* | | | | | | | | |
| partial take | | (10, 77, 78) | | | (77, 78) | | | |

| | MPA goals (ecological) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Community* | | | | | | | |
| | species (taxonomic) diversity | species abundance/ density (fish assemblages) | functional diversity/ trophic levels | Larval export and recruitment | biomass | Juvenile and adult spillover | productivity | resilience |
| no take | (4, 10, 74, 75, 83, 87, 88, 90–92, 27, 39, 53, 58, 60, 63, 65, 72) | (10, 24, 77–81, 25, 30, 44, 53, 57, 60, 65, 72) | (24, 25, 67, 72, 74, 75, 80, 83, 84, 89, 94, 95, 28, 43, 45, 51, 54, 62, 63, 65) | (56, 94) | (4, 10, 77, 78, 80, 83–85, 24, 25, 40, 44, 60, 65, 67, 72) | (27, 28, 46, 64, 68, 91, 107) | | (45, 54, 57, 58, 62, 72–75) |
| enforcement | (4, 75, 83, 88) | (10) | (75, 83) | | (4, 6, 10, 83) | | | (75) |
| compliance | (88) | (44) | | | | | | |
| human impact outside of MPA | (9) | | (9) | | | | | |
| **Global MPA attribute** | | | | | | | | |
| Comprehensive (what areas lack representation?) | (88) | | | | | | | |
| Placed in populated areas (areas of high need) | (27, 88) | | | (92) | | | | |

**Table 3**. Summary of the literature review to evaluate MPA design and management attributes that influence their likelihood of enhancing the resilience of marine **ecosystems**. Columns represent those ecological features (e.g., population size, community diversity) that are known to enhance resilience. Rows represent design (e.g., MPA size, network) and management (e.g., level of protection, enforcement) attributes. Numbers in the table identify articles cited in the text and listed in the Literature Cited section that have demonstrated those MPA design and management attributes to influence the mechanisms of resilience identified in the columns.

| | MPA goals (ecological) | | |
| --- | --- | --- | --- |
| | *Ecosystem* | | |
| | protect habitat diversity | productivity | resilience |
| **MPA attribute** | | | |
| MPA presence | | | |
| *Design attributes* | | | |
| size (small) | | | |
| size (large) | | | |
| habitat isolation (MPA isolated by sand, depth) | | | |
| individual vs. network | (91) | | |
| longevity | | | |
| connectivity (multiple ecosystems within MPA) | (27) | | (27) |
| smaller buffer zone | | | |
| *Management attributes* | | | |
| partial take | | | |
| no take | | | (44) |
| enforcement | | | |
| compliance | | | |
| human impact outside of MPA | | | |
| **Global MPA attribute** | | | |
| Comprehensive (what areas lack representation?) | | | |
| Placed in populated areas (areas of high need) | | | (27, 112) |

# Literature Cited

1.	Watson, J. E. M., Dudley, N., Segan, D. B. & Hockings, M. The performance and potential of protected areas. *Nature* **515,** 67 (2014).
2.	Lubchenco, J. & Grorud-Colvert, K. Making Waves: The science and politics of ocean protection. Mature science reveals opportunities for policy progress. *Science (80-. ).* **350,** 382–383 (2015).
3.	McClanahan, T. R., Marnane, M. J., Cinner, J. E. & Kiene, W. E. A Comparison of Marine Protected Areas and Alternative Approaches to Coral-Reef Management. *Curr. Biol.* **16,** 1408–1413 (2006).
4.	Edgar, G. J. *et al.* Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506,** 216–20 (2014).
5.	Cinner, J. E. *et al.* Bright spots among the world's coral reefs. *Nature* **535,** 416–419 (2016).
6.	Gill, D. A. *et al.* Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543,** 665–669 (2017).
7.	Sale, P. F. *et al.* Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.* **20,** 74–80 (2005).
8.	Mora, C. *et al.* Coral reefs and the global network of Marine Protected Areas. *Science (80-. ).* **312,** 1750–1751 (2006).
9.	Mora, C. *et al.* Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol.* **9,** (2011).
10.	Giakoumi, S. *et al.* Ecological effects of full and partial protection in the crowded Mediterranean Sea: a regional meta-analysis. *Sci. Rep.* **7,** 1–12 (2017).
11.	Ostrom, E. A General Framework for Analyzing Sustainability of Social-Ecological Systems. *Science (80-. ).* **325,** 419–422 (2009).
12.	Walker B., Holling C. S., Carpenter S. R., K. A. Resilience, Adaptability and Transformability in Social–ecological Systems. *Ecol. Soc.* **9,** (2004).
13.	McLeod, E., Salm, R., Green, A. & Almany, J. Designing marine protected area networks to address the impacts of climate change. *Front. Ecol. Environ.* **7,** 362–370 (2009).
14.	Carr, M. H. *et al.* The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **27,** 6–29 (2017).
15.	Holling, C. S. Resilience and Stability of Ecological Systems. *Annu. Rev. Ecol. Syst.* **4,** 1–23 (1973).
16.	Berkes, F. & Folke, C. *Linking Social and Ecological Systems: Management practices and social mechanisms for building resilience.* (Cambridge University Press, 1998).
17.	Folke, C. *et al.* Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annu. Rev. Ecol. Evol. Syst.* **35,** 557–581 (2004).
18.	O'Leary, J. K. *et al.* The Resilience of Marine Ecosystems to Climatic Disturbances. *Bioscience* **67,** 208–220 (2017).
19.	Millennium Ecosystem Assessment. *Ecosystems and Human Well-Being: Synthesis.* (2005).
20.	Palkovacs, E. P., Moritsch, M. M., Contolini, G. M. & Pelletier, F. Ecology of harvest-driven trait changes and implications for ecosystem management. *Front. Ecol. Environ.* **16,** 20–28 (2018).
21.	Stachowicz, J. J., Bruno, J. F. & Duffy, J. E. Understanding the Effects of Marine Biodiversity on Communities and Ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **38,** 739–766 (2007).
22.	Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80,** 1455–1474 (1999).
23.	Loreau, M. *et al.* Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science (80-. ).* **294,** 804 LP-808 (2001).
24.	Graham, N. A. J. *et al.* Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol.*

*Environ.* **11,** 541–548 (2013).

25. Gell, F. R. & Roberts, C. M. Benefits beyond boundaries: The fishery effects of marine reserves. *Trends Ecol. Evol.* **18,** 448–455 (2003).

26. Baskett, M. L. & Barnett, L. A. K. The Ecological and Evolutionary Consequences of Marine Reserves. *Annu. Rev. Ecol. Evol. Syst.* **46,** 49–73 (2015).

27. Green, A. L. *et al.* Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation. *Coast. Manag.* **42,** 143–159 (2014).

28. Bernhardt, J. R. & Leslie, H. M. Resilience to Climate Change in Coastal Marine Ecosystems. *Ann. Rev. Mar. Sci.* **5,** 371–392 (2013).

29. Costello, M. J. & Ballantine, B. Biodiversity conservation should focus on no-take Marine Reserves. *Trends Ecol. Evol.* **30,** 507–509 (2015).

30. Palumbi, S. R. Marine reserves and ocean neighborhoods: The Spatial Scale of Marine Populations and Their Management. *Annu. Rev. Environ. Resour.* **29,** 31–68 (2004).

31. Rossiter, J. S. & Levine, A. What makes a 'successful' marine protected area? The unique context of Hawaii's fish replenishment areas. *Mar. Policy* **44,** 196–203 (2014).

32. Munroe, D. M., Klinck, J. M., Hofmann, E. E. & Powell, E. N. A modelling study of the role of marine protected areas in metapopulation genetic connectivity in Delaware Bay oysters. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **24,** 645–666 (2014).

33. Bates, A. E. *et al.* Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Chang.* **4,** 62–67 (2014).

34. Micheli, F. *et al.* Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One* **7,** (2012).

35. Dunlop, E. S., Baskett, M. L., Heino, M. & Dieckmann, U. Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evol. Appl.* **2,** 371–393 (2009).

36. Almany, G. R. *et al.* Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr. Biol.* **23,** 626–630 (2013).

37. Pieraccini, M., Coppa, S. & De Lucia, G. A. Beyond marine paper parks? Regulation theory to assess and address environmental non-compliance. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **27,** 177–196 (2017).

38. Edgar, G. J. & Barrett, N. S. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J. Exp. Mar. Bio. Ecol.* **242,** 107–144 (1999).

39. Almany, G. R. *et al.* Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* **28,** 339–351 (2009).

40. Abesamis, R. A. & Russ, G. R. Density-dependent spillover from a marine reserve: Long-term evidence. *Ecol. Appl.* **15,** 1798–1812 (2005).

41. Olds, A. D., Connolly, R. M., Pitt, K. A. & Maxwell, P. S. Habitat connectivity improves reserve performance. *Conserv. Lett.* **5,** 56–63 (2012).

42. Olds, A. D., Albert, S., Maxwell, P. S., Pitt, K. A. & Connolly, R. M. Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific. *Glob. Ecol. Biogeogr.* **22,** 1040–1049 (2013).

43. Galasso, N. M. *et al.* Fish-seastar facilitation leads to algal forest restoration on protected rocky reefs. *Sci. Rep.* **5,** 1–9 (2015).

44. McCook, L. J. *et al.* Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proc. Natl. Acad. Sci.* **107,** 18278–18285 (2010).

45. Hamilton, S. L. & Caselle, J. E. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proc. R. Soc. B Biol. Sci.* **282,** 20141817–20141817 (2014).

46. Evans, R. D. & Russ, G. R. Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **14,** 505–519 (2004).

47. Guidetti, P. & Sala, E. Community-wide effects of marine reserves in the Mediterranean Sea. *Mar.*

*Ecol. Prog. Ser.* **335,** 43–56 (2007).

48. Willis, T. J., Millar, R. B. & Babcock, R. C. Protection of exploited fish in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol.* **40,** 214–227 (2003).

49. Davidson, R. J. Changes in population parameters and behaviour of blue cod (*Parapercis colias* ; Pinguipedidae) in Long Island-Kokomohua Marine Reserve , Marlborough Sounds , New Zealand. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **11,** 417–435 (2001).

50. Rowe, S. Movement and harvesting mortality of American lobsters (Homarus americanus) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Can. J. Fish. Aquat. Sci.* **58,** 1336–1346 (2001).

51. Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W. & Willis, T. J. Changes in community structure in temperate marine reserves. *Mar. Ecol. Prog. Ser.* **189,** 125–134 (1999).

52. Halpern, B. S. & Warner, R. R. Marine reserves have rapid and long lasting effects. *Ecol. Lett.* **5,** 361–366 (2002).

53. Claudet, J., Pelletier, D., Jouvenel, J. Y., Bachet, F. & Galzin, R. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biol. Conserv.* **130,** 349–369 (2006).

54. Ling, S. D. & Johnson, C. R. Marine reserves reduce risk of climate-driven phase shift by reinstating size-and habitat-specific trophic interactions. *Ecol. Appl.* **22,** 1232–1245 (2012).

55. Halpern, B. S., Lester, S. E. & Kellner, J. B. Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.* **36,** 268–276 (2009).

56. Harrison, H. B. *et al.* Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* **22,** 1023–1028 (2012).

57. Caselle, J. E., Davis, K. & Marks, L. M. Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA. *Ecol. Lett.* **21,** 43–53 (2018).

58. Lamb, J. B., Williamson, D. H., Russ, G. R. & Willis, B. L. Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. *Ecology* **96,** 2555–2567 (2015).

59. Jupiter, S. D., Weeks, R., Jenkins, A. P., Egli, D. P. & Cakacaka, A. Effects of a single intensive harvest event on fish populations inside a customary marine closure. *Coral Reefs* **31,** 321–334 (2012).

60. Lester, S. E. *et al.* Biological effects within no-take marine reserves: A global synthesis. *Mar. Ecol. Prog. Ser.* **384,** 33–46 (2009).

61. Faunce, C. H., Lorenz, J. J., Ley, J. A. & Serafy, J. E. Size structure of gray snapper (Lutjanus griseus) within a mangrove 'no-take' sanctuary. *Bull. Mar. Sci.* **70,** 211–216 (2002).

62. Ling, S. D., Johnson, C. R., Frusher, S. D. & Ridgway, K. R. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proc. Natl. Acad. Sci.* **106,** 22341–22345 (2009).

63. Stelzenmüller V., Maynou F., M. P. Patterns of species and functional diversity around a coastal marine reserve: a fisheries perspective. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **19,** 554–565 (2008).

64. Roberts, C. M., Bohnsack, J. A., Gell, F. R., Hawkins, J. P. & Goodridge, R. Effects of Marine Reserves on Adjacent Fisheries. *Science (80-. ).* **294,** 1920–3 (2001).

65. Halpern, B. S. The Impact of Marine Reserves : Do Reserves Work and Does Reserve Size Matter? *Ecol. Appl.* **13,** S117–S137 (2014).

66. Mumby, P. J. *et al.* Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427,** 533 (2004).

67. Olds, A. D., Pitt, K. A., Maxwell, P. S. & Connolly, R. M. Synergistic effects of reserves and connectivity on ecological resilience. *J. Appl. Ecol.* **49,** 1195–1203 (2012).

68. Alcala, A. C., Russ, G. R., Maypa, A. P. & Calumpong, H. P. A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. *Can. J. Fish. Aquat. Sci.* **62,** 98–108 (2005).

69.    Pérez-Ruzafa, Á., González-Wangüemert, M., Lenfant, P., Marcos, C. & García-Charton, J. A. Effects of fishing protection on the genetic structure of fish populations. *Biol. Conserv.* **129,** 244–255 (2006).

70.    Mellin, C., Aaron Macneil, M., Cheal, A. J., Emslie, M. J. & Julian Caley, M. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* **19,** 629–637 (2016).

71.    Adam, T. C. *et al.* Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. *PLoS One* **6,** (2011).

72.    Sala, E. & Giakoumi, S. No-take marine reserves are the most effective protected areas in the ocean. *ICES J. Mar. Sci.* (2017). doi:10.1093/icesjms/fsx059

73.    Lamb, J. B. *et al.* Reserves as tools for alleviating impacts of marine disease. *Philos. Trans. R. Soc. B Biol. Sci.* **371,** 20150210 (2016).

74.    Wing, S. R. & Jack, L. Marine reserve networks conserve biodiversity by stabilizing communities and maintaining food web structure. *Ecosphere* **4,** 1–14 (2013).

75.    Raymundo, L. J., Halford, A. R., Maypa, A. P. & Kerr, A. M. Functionally diverse reef-fish communities ameliorate coral disease. *Proc. Natl. Acad. Sci.* **107,** 17067–17070 (2010).

76.    Claudet, J. *et al.* Marine reserves: Size and age do matter. *Ecol. Lett.* **11,** 481–489 (2008).

77.    Sciberras, M. *et al.* Evaluating the relative conservation value of fully and partially protected marine areas. *Fish Fish.* **16,** 58–77 (2015).

78.    Sciberras, M., Jenkins, S. R., Kaiser, M. J., Hawkins, S. J. & Pullin, A. S. Evaluating the biological effectiveness of fully and partially protected marine areas. *Environ. Evid.* **2,** 1–31 (2013).

79.    Lester, S. E. & Halpern, B. S. Biological responses in marine no-take reserves versus partially protected areas. *Mar. Ecol. Prog. Ser.* **367,** 49–56 (2008).

80.    Stockwell, B., Jadloc, C. R. L., Abesamis, R. A., Alcala, A. C. & Russ, G. R. Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Mar. Ecol. Prog. Ser.* **389,** 1–15 (2009).

81.    Alcala, A. C. & Russ, G. R. A direct test of the effects of protective management on a tropical marine reserve. *J. Cons. int. Explor.* **46,** 40–47 (1990).

82.    Mumby, P. J. Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. *Biol. Conserv.* **128,** 215–222 (2006).

83.    Guidetti, P. *et al.* Large-scale assessment of mediterranean marine protected areas effects on fish assemblages. *PLoS One* **9,** (2014).

84.    Caselle, J. E., Rassweiler, A., Hamilton, S. L. & Warner, R. R. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Sci. Rep.* **5,** 1–14 (2015).

85.    Ban, N. C., McDougall, C., Beck, M., Salomon, A. K. & Cripps, K. Applying empirical estimates of marine protected area effectiveness to assess conservation plans in British Columbia, Canada. *Biol. Conserv.* **180,** 134–148 (2014).

86.    Rhodes, K. L., McIlwain, J., Joseph, E. & Nemeth, R. S. Reproductive movement, residency and fisheries vulnerability of brown-marbled grouper, Epinephelus fuscoguttatus (Forsskål, 1775). *Coral Reefs* **31,** 443–453 (2012).

87.    Côté, I. M., Mosqueira, I. & Reynolds, J. D. Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis. *J. Fish Biol.* **59,** 178–189 (2001).

88.    Edgar, G. J. Marine protected areas need accountability not wasted dollars. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **27,** 4–9 (2017).

89.    Behrens, M. D. & Lafferty, K. D. Effects of marine reserves and urchin disease on southern Californian rocky reef communities. *Mar. Ecol. Prog. Ser.* **279,** 11 (2004).

90.    Russ, G. R. & Alcala, A. C. Enhanced biodiversity beyond marine reserve boundaries : The cup spillith over Linked references are available on JSTOR for this article : Enhanced biodiversity beyond marine reserve boundaries : The cup spillith over. **21,** 241–250 (2016).

91.    Jones, G. P. *et al.* Larval retention and connectivity among populations of corals and reef fishes:

History, advances and challenges. *Coral Reefs* **28,** 307–325 (2009).

92. Salm, R. V., Done, T. & McLeod, E. in *Coral Reefs and Climate Change: Science and Management* (eds. Phinney, J., Hoegh-Guldberg, O., Kleypas, J., Skirving, W. & Strong, A.) 207–222 (American Geophysical Union, 2006).

93. Villamor, A. & Becerro, M. A. Species, trophic, and functional diversity in marine protected and non-protected areas. *J. Sea Res.* **73,** 109–116 (2012).

94. Mumby, P. J. *et al.* Trophic cascade facilitates coral recruitment in a marine reserve. *Proc. Natl. Acad. Sci.* **104,** 8362–8367 (2007).

95. Shears, N. T. & Babcock, R. C. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132,** 131–142 (2002).

96. Cabigas, R. B., Manzano, L. L. & Nobukazu, N. Success and Failure of Marine Protected Area Management Affecting the Fish Catch by Adjacent Fishermen in Sarangani Bay, Mindanao, Philippines. *South Pacific Stud.* **33,** 1–24 (2012).

97. Ban, N. C. *et al.* Social and ecological effectiveness of large marine protected areas. *Glob. Environ. Chang.* **43,** 82–91 (2017).

98. Jones, P. J. S. A governance analysis of the Galápagos Marine Reserve. *Mar. Policy* **41,** 65–71 (2013).

99. Schuhbauer, A. & Koch, V. Assessment of recreational fishery in the galapagos marine reserve: Failures and opportunities. *Fish. Res.* **144,** 103–110 (2013).

100. Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D. & Wilson, S. K. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518,** 94–97 (2015).

101. Christie, P. Marine Protected Areas as Biological Successes and Social Failures in Southeast Asia. *Am. Fish. Soc.* **42,** 155–164 (2004).

102. Hearn, A. The rocky path to sustainable fisheries management and conservation in the Galápagos Marine Reserve. *Ocean Coast. Manag.* **51,** 567–574 (2008).

103. Cinner, J. E., Fuentes, M. M. P. B. & Randriamahazo, H. Exploring Social Resilience in Madagascar ' s Marine Protected Areas. *Ecol. Soc.* **14,** (2009).

104. Caselle, J. E., Davis, K. & Marks, L. M. Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA. *Ecol. Lett.* **21,** 43–53 (2017).

105. Narayan, S. *et al.* The Value of Coastal Wetlands for Flood Damage Reduction in the Northeastern USA. *Sci. Rep.* **7,** 1–12 (2017).

106. Beck, M. W. *et al.* The global flood protection savings provided by coral reefs. *Nat. Commun.* **9,** 2186 (2018).

107. Gaines, S. D., White, C., Carr, M. H. & Palumbi, S. R. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci.* **107,** 18286–18293 (2010).

108. Forcada, A., Bayle-Sempere, J. T., Valle, C. & Sánchez-Jerez, P. Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Mar. Environ. Res.* **66,** 536–547 (2008).

109. Christie, M. R. *et al.* Larval connectivity in an effective network of marine protected areas. *PLoS One* **5,** 1–8 (2010).

110. Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S. & Jones, G. P. Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. *Science (80-. ).* **316,** 742–744 (2007).

111. Shanks, A. L., Grantham, B. A. & Carr, M. H. Propagule Dispersal Distance and the Size and Spacing of Marine Reserves Author ( s ): Alan L . Shanks , Brian A . Grantham and Mark H . Carr Source : Ecological Applications , Vol . 13 , No . 1 , Supplement : The Science of Marine Reserves Published by : **13,** (2016).

112. McLeod, E. *et al.* Integrating Climate and Ocean Change Vulnerability into Conservation Planning. *Coast. Manag.* **40,** 651–672 (2012).

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i For the purpose of our current MPA FAC charge, the term "marine" includes ocean, coastal, estuarine and Great Lakes ecosystems throughout the United States.