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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Executive Summary

In the face of growing demands on marine ecosystem services and a changing global climate, **our Marine Protected Area Federal Advisory Committee (MPAFAC) *ad hoc* Ecosystem Resilience Team sought to determine the ecological benefits of, and the most important design features for, ecologically resilient Marine Protected areas. This charge required our team to determine** (i) whether marine protected areas (MPAs) impart or enhance the resistance or resilience of species populations, communities, and ecosystems to natural or human-caused disturbances, and (ii) if so, what design features and management approaches contribute to those effects. To evaluate these, we conducted a global scale review of the peer-reviewed literature and synthesized this information as a Supplementary Report accompanying MPAFAC's Findings and Recommendations on Sustaining MPA Benefits in a Changing Ocean. We

clarify what ecological resilience is, what ecological mechanisms contribute to it (e.g., increased population sizes, greater species diversity, habitat protection, intact species interactions), and the evidence required to attribute resistance and resilience to MPAs. We examined which of several design criteria (e.g., size, isolation, longevity) and management approaches (e.g., level of protection, enforcement, compliance for MPAs) were thought to **provide maximum** resilience **benefits**. Our review included over 100 peer-reviewed publications. In addition, we provide four case studies that exemplify both the success and failure of MPAs to achieve this goal. **The scientific literature review reveals two important conclusions.**

- **First, regarding ecological benefits: 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.**
- **Second, regarding desired designed features: 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.**

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 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.

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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).

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

Figure 1. Human communities benefit greatly from and are highly reliant on a diversity of services only made available by marine ecosystems.

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 a pink abalone, *Haliotis corrugata*, 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

Figure 2. Larger populations of pink abalone (Haliotis corrugata) in reseres off Baja California exhibit greater resilience to hypoxia events.

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, 40, 42–56), and greater than MPAs that allowed partial take (10, 37, 57–59). In addition, strong enforcement (10, 31, 51, 54, 55, 59) and compliance (5, 31) were required for greater population responses. Larger (38) or no-take (34, 35, 43, 45, 52, 53, 56, 60–65) 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, 40, 42, 46, 52, 53, 55–57, 60, 67, 68). Genetic diversity of a population has also been found to increase (69) within a large and networked (39) MPA.

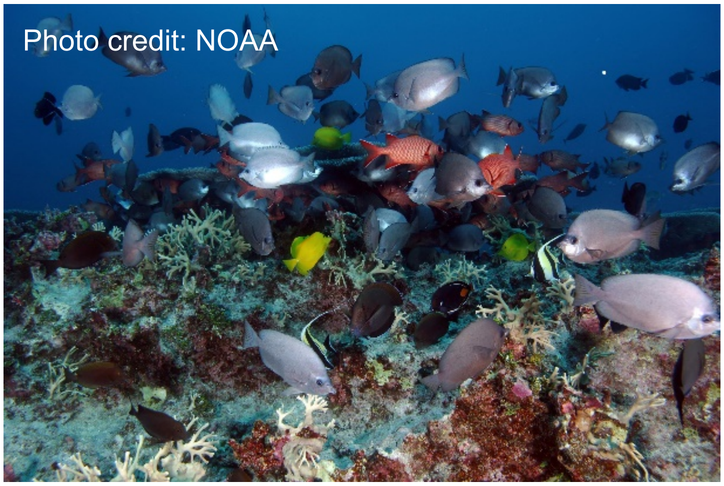

Figure 3. Species rich communities within marine protected areas are more resistant and resilient to natural and human-caused disturbances.

Community resilience – Direct evidence of community resilience has been observed in MPAs (33, 70), especially with multiple ecosystems (39, 71) or no-take reserves (48, 53, 57, 58, 65, 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, 76), and older (10, 47, 55, 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, 47, 52, 57, 62, 63, 72, 77–81), with strong enforcement (6, 10) and compliance (52). 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, 40, 52, 62, 63, 67, 72, 77, 78, 80, 83–85) 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 (60) MPAs and numerous studies indicate that this increase occurs predominantly in no-take marine reserves (4, 10, 39, 47, 58, 60, 62, 63, 72, 74, 75, 83, 87–92). The increases in taxonomic diversity are more prevalent in larger (4, 38, 39), older (4, 47, 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, 60, 93), especially older (57) MPAs with multiple ecosystems (67, 71, 82). Functional diversity increases within (45, 48, 51, 53, 57, 62, 65, 67, 72, 74, 75, 80, 83, 89, 94, 95) and adjacent to (60, 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, 60, 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, delivering large numbers of larvae of an invasive sea urchin, *Centrostephanus rodgersii*, and extending the distribution of the species (48, 65). The local lobster, *Jasus edwardsii*, 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.

Figure 4. Large lobster protected in marine reserves on the coast of Tasmania control invasive sea urchins that otherwise wipeout kelp forests and the species (e.g., abalone) that depend on them.

In the North American kelp forests on the Northern Channel Islands of southern California, an invasive alga, *Sargassum horneri*, is displacing kelp forests, including the giant kelp, *Macrocystis pyrifera*, and other algae that form the foundation of the forest ecosystem and the many species that inhabit it (57). Spiny lobster, *Panulirus interruptus*, and the California sheephead, *Semicossyphus pulcher*, both feed on purple sea urchins, *Strongylocentrotus purpuratus*. 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

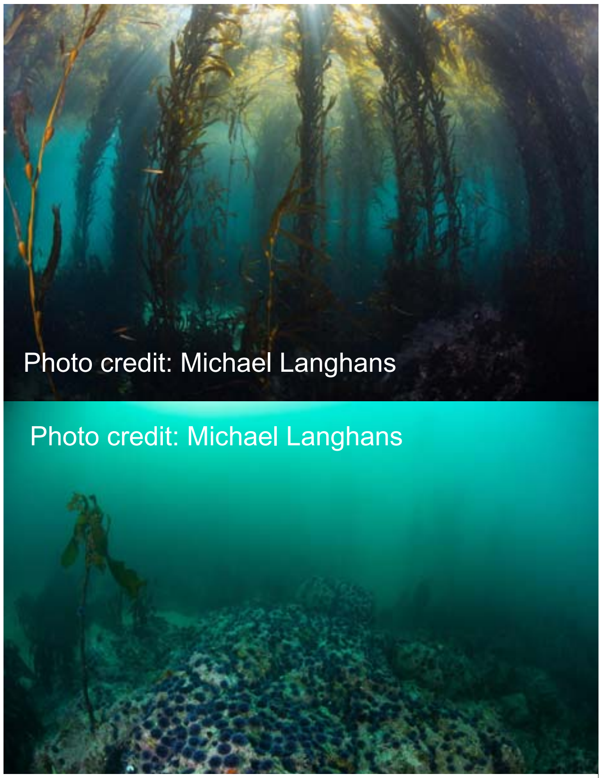

Figure 5. Alternative states of forested reefs and "urchin barrens" along the coast of California.

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 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, *Acanthaster planci*, 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 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).

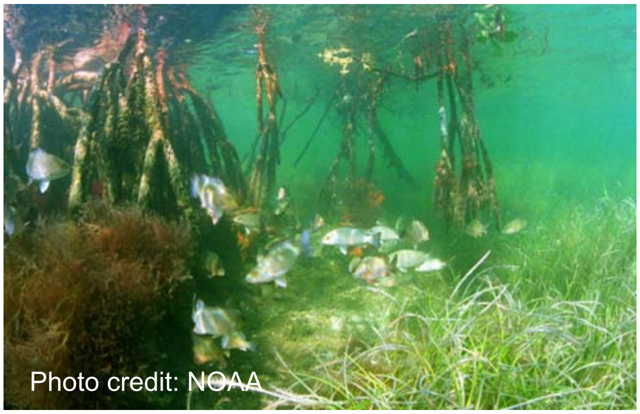
Photo credit: NOAA

Figure 6. MPAs that include mangroves and seagrass beds protect critical nursery habitat for young coral reef fishes of ecological and economic importance.

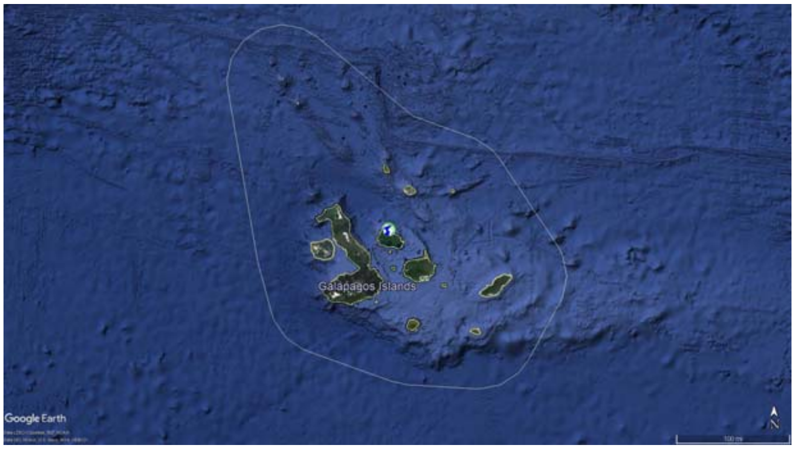

Figure 7. Galapagos Marine Reserve. White line indicates boundary of the reserve.

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

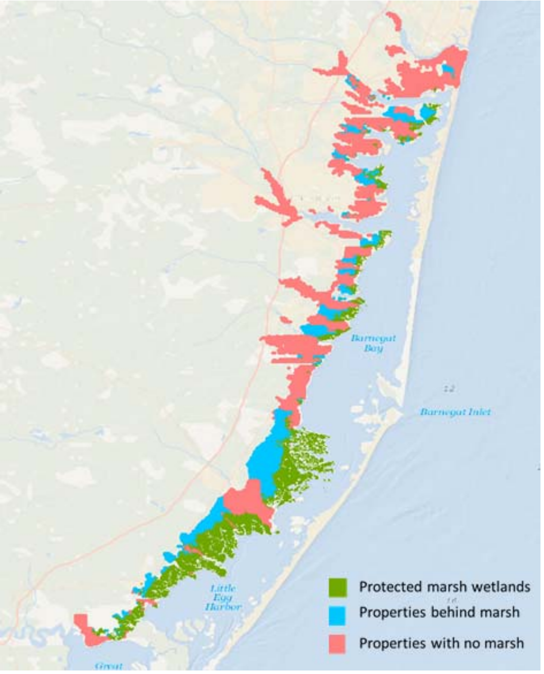

Figure 8. Association of human communites that resisted impact of Hurricane Sandy with protected coastal wetlands.

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 (104). 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. (104) 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 (105).

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 recover from and more successfully adapt to adverse events.

Resistance is the capacity of a population, community or ecosystem not to change in its fundamental structural and functional traits (e.g., taxonomic and functional composition of species, trophic structure, productivity, nutrient cycling).

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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, 27, 34, 37, 38, 40, 42–59)	(25, 34, 35, 43, 45, 52, 53, 56, 60–65, 106)	(5, 10, 25, 27, 34, 40, 46, 52, 53, 55–57, 60, 67, 68)				(26, 34, 35)
enforcement	(10, 31, 51, 54, 55, 59)		(54, 55)				
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, 60)		(26, 33, 60, 93)			(14, 26, 107, 108)		(33, 70)
Design attributes								
size (small)		(10)		(109)	(77, 78)			
size (large)	(4, 27, 38, 39)	(38, 76)			(4, 27)	(27, 49)	(27, 86)	
habitat isolation (MPA isolated by sand, depth)	(4)			(90)	(4)			
individual vs. network	(39)			(36, 39, 50)				
longevity	(4, 47, 76)	(10, 47, 55, 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, 110)		(27)		
Management attributes								

	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
partial take		(10, 77, 78)			(77, 78)			
no take	(4, 10, 27, 39, 47, 58, 62, 63, 72, 74, 75, 83, 87, 88, 90–92)	(10, 24, 25, 30, 47, 52, 57, 62, 63, 72, 77, 78, 80, 81)	(24, 25, 28, 45, 48, 51, 53, 60, 62, 65, 67, 72, 74, 75, 80, 83, 84, 89, 94)	(50, 94)	(4, 10, 24, 25, 40, 52, 62, 63, 67, 72, 77, 78, 80, 83–85)	(27, 28, 54, 61, 68, 90, 106)		(48, 53, 57, 58, 65, 72–75)
enforcement	(4, 75, 83, 88)	(10)	(75, 83)		(4, 6, 10, 83)			(75)
compliance	(88)	(52)						
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)			(91)				

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	(90)		
longevity			
connectivity (multiple ecosystems within MPA)	(27)		(27)
smaller buffer zone			
Management attributes			
partial take			
no take			(52)
enforcement			
compliance			
human impact outside of MPA			
Global MPA attribute			
Comprehensive (what areas lack representation?)			
Placed in populated areas (areas of high need)			(27, 111)

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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.