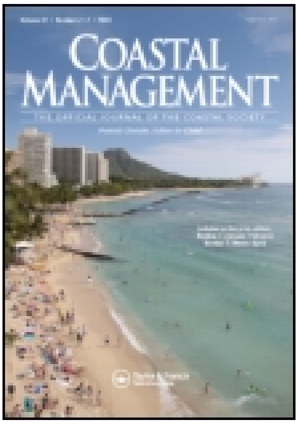

Coastal Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ucmg20

Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation

Alison L. Green [a] , Leanne Fernandes [b] , Glenn Almany [c] , Rene Abesamis [d] , Elizabeth McLeod [e] , Porfirio M. Aliño [f] , Alan T. White [g] , Rod Salm [g] , John Tanzer [h] & Robert L. Pressey [i]

[a] Indo-Pacific Division , The Nature Conservancy , West End , Queensland , Australia

[b] Earth to Ocean Consulting , Townsville , Queensland , Australia

[c] Laboratoire d'Excellence “CORAIL,” USR 3278 CNRS-EPHE CRIOBE , Perpignan , France

[d] Silliman University , Negros Oriental , Philippines

[e] Indo-Pacific Division , The Nature Conservancy , Austin , Texas , USA

[f] University of the Philippines , Manila , Philippines

[g] Indo-Pacific Division , The Nature Conservancy , Honolulu , Hawaii , USA

[h] World Wildlife Fund , Gland , Switzerland

[i] ARC Centre of Excellence for Coral Reef Studies , Townsville , Queensland , Australia

Published online: 12 Feb 2014.

Coastal Management, 42:143–159, 2014

ISSN: 0892-0753 print / 1521-0421 online
DOI: 10.1080/08920753.2014.877763

Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation

ALISON L. GREEN,[1] LEANNE FERNANDES,[2] GLENN ALMANY,[3] RENE ABESAMIS,[4] ELIZABETH McLEOD,[5] PORFIRIO M. ALIÑO,[6] ALAN T. WHITE,[7] ROD SALM,[7] JOHN TANZER,[8] AND ROBERT L. PRESSEY[9]

[1]Indo-Pacific Division, The Nature Conservancy, West End, Queensland, Australia
[2]Earth to Ocean Consulting, Townsville, Queensland, Australia
[3]Laboratoire d'Excellence "CORAIL," USR 3278 CNRS-EPHE CRIOBE, Perpignan, France
[4]Silliman University, Negros Oriental, Philippines
[5]Indo-Pacific Division, The Nature Conservancy, Austin, Texas, USA
[6]University of the Philippines, Manila, Philippines
[7]Indo-Pacific Division, The Nature Conservancy, Honolulu, Hawaii, USA
[8]World Wildlife Fund, Gland, Switzerland
[9]ARC Centre of Excellence for Coral Reef Studies, Townsville, Queensland, Australia

Overfishing and habitat destruction due to local and global threats are undermining fisheries, biodiversity, and the long-term sustainability of tropical marine ecosystems worldwide, including in the Coral Triangle. Well-designed and effectively managed marine reserve networks can reduce local threats, and contribute to achieving multiple objectives regarding fisheries management, biodiversity conservation and adaptation to changes in climate and ocean chemistry. Previous studies provided advice regarding ecological guidelines for designing marine reserves to achieve one or two of these objectives. While there are many similarities in these guidelines, there are key differences that provide conflicting advice. Thus, there is a need to provide integrated guidelines for practitioners who wish to design marine reserves to achieve all three objectives simultaneously. Scientific advances regarding fish connectivity and recovery rates, and climate and ocean change vulnerability, also necessitate refining advice for marine reserve design. Here we review ecological considerations for marine reserve design, and provide guidelines to achieve all three objectives simultaneously regarding: habitat representation; risk spreading; protecting critical, special and unique areas; reserve size, spacing, location, and duration; protecting climate resilient areas; and minimizing and avoiding threats. In addition to applying ecological guidelines, reserves must be designed to address social and governance considerations, and be integrated within broader fisheries and coastal management regimes.

Address correspondence to Alison L. Green, The Nature Conservancy, 245 Riverside Drive, West End, Queensland, Australia 4101. E-mail: agreen@tnc.org

Keywords coral reefs, ecological guidelines, marine protected area design, tropical marine ecosystems

Introduction

Overfishing, degradation, and loss of key habitats (e.g., coral reefs, seagrass beds, and mangrove forests) due to local and global threats are undermining fisheries production, food security, livelihoods, biodiversity, and the long-term sustainability of tropical marine ecosystems worldwide (Hoegh-Guldberg et al. 2009; Bell, Johnson, and Hobday 2011; Pandolfi et al. 2011). This will result in escalating hardship and economic instability in the Coral Triangle and other regions, where fisheries provide important ecosystem goods and services for coastal communities (Hoegh-Guldberg et al. 2009; Willmann and Kelleher 2010; Foale et al. 2013).

Marine reserves (defined here as areas of ocean that are protected from all extractive and destructive activities) can be an effective tool for reducing local threats, and can contribute to fisheries management and biodiversity conservation in the face of climate change (Russ 2002; Lester et al. 2009; McLeod et al. 2009). The benefits of marine reserves include increases in the diversity, density, biomass, body size, and reproductive potential of many species (particularly fisheries species) within their boundaries (Lester et al. 2009). Marine reserves also provide significant conservation and fisheries benefits to other reserves and fished areas through the export of eggs, larvae, and adults (Halpern, Lester, and Kellner 2010; Harrison et al. 2012; Hamilton et al. 2013).

Marine reserve networks are collections of individual reserves that are ecologically connected (Dudley 2008; IUCN-WCPA 2008). Such networks can deliver additional benefits through mutual replenishment of individual reserves (e.g., Harrison et al. 2012), which facilitates recovery after disturbance (McLeod et al. 2009).

The design and effective management of ecological networks of marine reserves is critical to maximize their benefits to fisheries management, biodiversity conservation, and climate change adaptation (Walmsley and White 2003; McLeod et al. 2009; Gaines et al. 2010). Existing ecological guidelines for designing marine reserve networks have focused on achieving either fisheries (e.g., Fogarty and Botsford 2007), biodiversity (e.g., Almany et al. 2009) or climate change (e.g., McLeod et al. 2012) objectives independently, or fisheries and biodiversity (Roberts et al. 2003; Gaines et al. 2010) or biodiversity and climate change (McLeod et al. 2009) objectives combined. While there are many similarities among guidelines for achieving different objectives, there are some key differences, particularly regarding marine reserve size and duration of protection (i.e., permanent, long or short term, or periodic closures). Consequently, marine reserves designed to maximize fisheries benefits are seldom designed to maximize their contribution to protecting the full range of biodiversity in the face of climate change (e.g., Hamilton, Potuku, and Montambault 2011). While networks designed to maximize biodiversity conservation and climate change adaptation are seldom designed to maximize fisheries benefits (i.e., fisheries issues are often addressed by avoiding conflicting use with marine reserves, rather than by maximizing production in fished areas: Klein et al. 2010; Grantham et al. 2013). Thus an integrated set of marine reserve guidelines is needed for practitioners who wish to maximize benefits for all three objectives simultaneously.

Recent studies have also provided fresh insights into connectivity, vulnerability, and recovery rates of coral reef and coastal pelagic fish species, and climate and ocean change vulnerability of tropical marine ecosystems (Jones et al. 2009; McLeod et al. 2012; Hutchings et al. 2012). These studies necessitate a review of ecological guidelines for marine reserve network design, particularly regarding their configuration (size, shape, spacing, and location) and duration of protection.

Here, we review ecological considerations for designing marine reserve networks to achieve fisheries, biodiversity, and climate change objectives, and provide specific guidelines (summarized in Table 1) regarding how they can be used to achieve all three objectives simultaneously in tropical marine ecosystems. These guidelines are intended to contribute to larger planning processes that include implementing marine reserves networks to complement human uses and values, and align with local legal, political, and institutional requirements (Knight and Cowling 2007; Christie et al. 2009a). While these guidelines were developed to support marine protected area (MPA) network design in the Coral Triangle (White et al. 2014; Walton et al. 2014; Weeks et al. 2014), they can be applied to tropical marine ecosystems worldwide.

Ecological Considerations and Guidelines for Marine Reserve Design

Habitat Representation

Different species use different habitats, thus protection of all species (including focal species) and maintenance of the health, integrity, and resilience of the ecosystem can be achieved if adequate examples of each major habitat (including each type of coral reef, mangrove, and seagrass community) are protected within marine reserves (Salm, Done, and McLeod 2006; McLeod et al. 2009; Gaines et al. 2010). Where focal species include key fisheries species, functional groups important for maintaining ecological resilience to local and global threats (e.g., herbivores), and rare and threatened species.

To determine how much of each habitat to protect, it is important to consider that a population can only be maintained if it produces sufficient eggs and larvae to sustain itself (Botsford, Hastings, and Gaines 2001; Botsford et al. 2009a). This threshold is unknown for most marine populations (Botsford et al. 2009a). Thus, fisheries ecologists have expressed it as a fraction of unfished stock levels, and examined empirical evidence to determine a general safe value of that parameter (Botsford et al. 2009a). Meta-analyses suggest that keeping this threshold above ∼35% of unfished stock levels ensures adequate replacement over a range of species (Botsford, Hastings, and Gaines 2001; Fogarty and Botsford 2007; FAO 2011).

To approximate the level of protection of this threshold, ∼35% of the habitats used by focal species should be protected in marine reserves (Fogarty and Botsford 2007), where habitat protection is a proxy for protecting fisheries stocks. While lesser levels of habitat protection (but not less than 10%) may be sufficient in areas with low fishing pressure (Botsford, Hastings, and Gaines 2001; Botsford et al. 2009b), higher levels (40%) are required where fishing pressure is high to protect species with lower reproductive output or delayed maturation (e.g., sharks and some groupers: Fogarty and Botsford 2007). Higher levels of habitat protection may also be required in areas vulnerable to severe disturbances (e.g., typhoons) and climate change impacts (e.g., Allison et al. 2003).

Therefore, to maximize benefits to fisheries management and biodiversity conservation in the face of climate change, marine reserves should encompass at least 20–40% of each major habitat. The recommended percentage will vary, based on fishing pressure and whether there is effective fisheries management in place outside reserves. If fishing pressure is high and the only protection offered to fisheries species is in marine reserves, then the proportion of each major habitat in reserves should be ≥30%. If effective fisheries

Table 1
Ecological guidelines for designing marine reserve networks for fisheries management, biodiversity conservation, and climate change adaptation

Category	Ecological guidelines
Habitat Representation	Represent 20–40% of each major habitat (i.e., each type of coral reef, mangrove, and seagrass community) in marine reserves, depending on fishing pressure and if effective fisheries management is in place outside reserves.
Risk Spreading	Replicate protection of each major habitat within at least three widely separated marine reserves.
Protecting Critical, Special and Unique Areas	Protect critical areas (e.g., FSAs, nursery, nesting, breeding, and feeding areas) in the life history of focal species (including key fisheries species, herbivores and rare and threatened species e.g., turtles, dugong and cetaceans) in permanent or seasonal marine reserves.
	Protect special or unique areas (e.g., isolated habitats with unique assemblages and populations, important habitats for endemic species, and highly diverse areas) in marine reserves.
Incorporating Connectivity	Apply minimum and variable sizes (e.g., 0.5–1 km and 5–20 km across) to marine reserves, depending on focal species for protection, how far they move, and if other effective management is in place outside reserves.
	Space marine reserves 1–15 km apart, with smaller reserves closer together.
	Protect key habitats used by focal species throughout their lives (e.g., for home ranges, nursery areas and FSAs) in marine reserves, and ensure reserves are spaced to allow for movements among them (e.g., ontogenetic habitat shifts, spawning migrations).
	Include whole ecological units (e.g., offshore reefs) in marine reserves.
	Use compact marine reserve shapes (e.g., squares) rather than elongated ones.
	Locate more marine reserves upstream if there is a strong, consistent, unidirectional current.
	Protect spatially isolated areas or populations (e.g., remote atolls separated by >20 kilometers from similar habitats) in marine reserves.
Allowing Time for Recovery	Ensure marine reserves are in place for the long-term (20–40 years), preferably permanently.
	Short term (<5 years) or periodically harvested marine reserves should be used in addition to, rather than instead of, long-term or permanent reserves.

(Continued on next page)

Table 1
Ecological guidelines for designing marine reserve networks for fisheries management, biodiversity conservation, and climate change adaptation *(Continued)*

Category	Ecological guidelines
Adapting to Changes in Climate and Ocean Chemistry	Protect refugia in marine reserves where habitats and species are likely to be more resistant or resilient to climate and ocean change including: • Areas where habitats and species are known to have withstood environmental changes (or extremes) in the past (e.g., coral communities that appear more resilient to high SSTs); • Areas with historically variable SSTs and ocean carbonate chemistry, where habitats and species are more likely to withstand changes in those parameters in future; and • Areas adjacent to low-lying inland areas without infrastructure that coastal habitats (e.g., mangroves, tidal marshes and turtle nesting beaches) can expand into as sea levels rise.
Minimizing and Avoiding Local Threats	Avoid placing marine reserves in areas that have been, or are likely to be, impacted by local threats (e.g., land based runoff) that cannot be managed effectively. Place marine reserves in areas that have not been, or are less likely to be, impacted by local threats including: • Areas where threats (e.g., overfishing or destructive fishing) can be managed effectively; and • Areas within or adjacent to other effectively managed marine or terrestrial areas. Integrate marine reserves within broader spatial planning and management regimes (e.g., large multiple-use MPAs, EAF, EBM, and ICM).

management is in place outside reserves, or if fishing pressure is low, then a lesser level of protection (20%) is needed. These recommendations are supported by empirical studies that show that 20–30% habitat protection in marine reserves can achieve fisheries objectives in areas with different levels of fishing pressure (e.g., Russ et al. 2008; Russ and Alcala 2010), which is also the minimum level of habitat protection recommended by IUCN-WCPA (2008).

Risk Spreading

Large-scale disturbances can have serious impacts on tropical marine ecosystems (e.g., coral bleaching and major storms: West and Salm 2003; Villanoy et al. 2012). Since it is difficult to predict with certainty which areas are most likely to be affected by these and other disturbances (e.g., ship groundings, oil spills), it is important to protect at least three examples of each major habitat in marine reserves and spread them out to reduce the chance that all examples will be adversely impacted by the same disturbance (Salm, Done, and

McLeod 2006; McLeod et al. 2009; see *Spacing*). Thus if one example of a major habitat is severely damaged, others may remain to provide the larvae required to replenish the affected area. Since variations in communities and species within major habitats are often poorly understood, habitat replication also increases the likelihood that examples of each are represented within the marine reserve network (McLeod et al. 2009; Gaines et al. 2010).

Protecting Critical, Special, and Unique Areas

Fish spawning aggregations (FSAs) and associated migratory corridors and staging areas (where fish aggregate prior to and after spawning) are spatially and temporally predictable and concentrate reproductively active fish in a manner that enhances their vulnerability to overfishing (Sadovy and Domeier 2005; Domeier 2012; Rhodes et al. 2012). Some fisheries species and herbivores (e.g., groupers and rabbitfishes) travel long distances to form FSAs for relatively short periods of time (days or weeks: Domeier 2012). For these species, such gatherings are the only opportunities to reproduce, and they are crucial to population maintenance. Some fisheries and herbivorous species (e.g., snappers and parrotfishes) also group together in feeding or resting areas, or nursery areas where juveniles use different habitats than adults (e.g., Nagelkerken et al. 2001). Therefore, it is important to protect the range of habitats that species use throughout their lives in marine reserves (particularly areas used during critical life history phases: Adams et al. 2011; Gaines et al. 2010; Rhodes et al. 2012), and to ensure that reserves protecting each of these areas are spaced to allow for movements of focal species among them (see *Incorporating Connectivity)*.

If the temporal and spatial location of these areas is known, they should be protected in permanent or seasonal marine reserves (Gaines et al. 2010; Rhodes et al. 2012). If the location of these areas is unknown, or the scale of movement is too large to include in individual marine reserves, they can be protected within a network of marine reserves in combination with other management approaches (e.g., seasonal capture and sales restrictions during the spawning season: Sadovy and Domeier 2005; Rhodes et al. 2012).

Rare and threatened species also aggregate and use habitats that are crucial to the maintenance of their populations (e.g., sea turtle nesting areas, dugong feeding areas, cetacean migratory corridors, and calving grounds). These areas should be protected in permanent or seasonal marine reserves (e.g., DPW 2013) in combination with other management approaches (e.g., hunting regulations and restrictions on the use of nets in cetacean migratory corridors).

Other special and/or unique sites should also be included in marine reserves to ensure that all examples of biodiversity and ecosystem processes are protected. They include: isolated habitats that often have unique assemblages and populations, habitats that are important for endemic species, and areas that are highly diverse (Jones, Srinivasan, and Almany 2007; McLeod et al. 2009).

Incorporating Connectivity

Connectivity, the demographic linking of local populations through the dispersal of individuals as larvae, juveniles, or adults (Jones et al. 2009), is a key ecological factor to consider in marine reserve design, since it has important implications for the persistence of metapopulations and their recovery from disturbance (Botsford, Micheli, and Hastings 2003; Almany et al. 2009; McCook et al. 2009). Most coral reef and coastal pelagic fish species have a bipartite life cycle where larvae are pelagic before settling out of the plankton and forming an association with coral reefs. These species vary greatly in how far they move during their life history phases (Palumbi 2004), although larvae of most species have the potential to move much longer distances (10s–100s of kilometers: Almany et al. 2009; Jones et al. 2009) than adults and juveniles that tend to be more sedentary (with home ranges <1 m to a few kilometers: Russ 2002). Exceptions include coral reef species where adults and juveniles exhibit large-scale (10s–100s of kilometers) ontogenetic shifts in habitat use (i.e., among coral reef, mangrove and seagrass habitats; e.g., Nagelkerken et al. 2001) or migrations to FSAs (e.g., Rhodes et al., 2012), and pelagic species that migrate very large distances (100s to 1,000s of kilometers: Palumbi 2004).

When adults and juveniles leave a marine reserve, they become vulnerable to fishing (Kramer and Chapman 1999; Gaines et al. 2010). However, larvae leaving a reserve can generally disperse without elevated risk because of their small size and limited exposure to the fishery (Gaines et al. 2010). Thus movement patterns of coral reef and coastal pelagic fish species at each stage in their life cycle is an important consideration in designing the configuration of marine reserve networks (e.g., Kramer and Chapman 1999; Botsford, Micheli, and Hastings 2003; Palumbi 2004). Where movement patterns of focal species are known, this information can be used to refine reserve size, shape, spacing and location (e.g., IUCN-WCPA 2008) to maximize benefits to both fisheries and conservation (Palumbi 2004; Jones, Srinivasan, and Almany 2007; Gaines et al. 2010).

Size and Shape. For marine reserves to protect biodiversity and contribute to fisheries enhancement outside their boundaries, they must be able to sustain fisheries species within their boundaries throughout their juvenile and adult life history phases (Palumbi 2004; IUCN-WCPA 2008; Gaines et al. 2010). This allows for the maintenance of spawning stock, by allowing individuals to grow to maturity, increase in biomass and reproductive potential, and contribute to stock recruitment and regeneration (Russ 2002).

Marine reserve size should therefore be determined by the rate of export of adults and juveniles ("spillover") to fished areas (Gaines et al. 2010). While spillover directly benefits adjacent fisheries, if the reserve is too small, excess spillover may reduce the density of protected biomass within the reserve (Kramer and Chapman 1999; Botsford, Micheli, and Hastings 2003; Gaines et al. 2010).

This tradeoff has led to divergent recommendations regarding the size of marine reserves based on the need to achieve different objectives. For example, from a biodiversity and climate change perspective, moderate to large reserves (e.g., 4–20 km across) are recommended, because they enhance population persistence by increasing the protection of larger populations of more species (Shanks, Grantham, and Carr 2003; McLeod et al. 2009; Gaines et al. 2010). In contrast, smaller reserves (0.5–1 km across) have been recommended for fisheries management, since they allow for the export of more adults and larvae to fished areas, leading to potential increases in recruitment and stock replenishment (Jones, Srinivasan, and Almany 2007; Lester et al. 2009; Harrison et al. 2012). Such small reserves are common in the Coral Triangle, where they have provided benefits for some species (e.g., Russ and Alcala 2010; Hamilton, Potuku, and Montambault 2011).

Where movement patterns of focal species are known, they can be used to refine marine reserve size. Some species (e.g., some groupers, surgeonfishes, and parrotfishes) have small home ranges (Figure 1) and can be protected within small marine reserves (<0.5 to 1 km across), while others are more wide ranging (e.g., bumphead parrotfish and humphead wrasse) and require medium to large marine reserves (5–10 or 10–20 km across). Some species move across very large distances and require even larger marine reserves (10s to 100s of kilometers across) including some snappers, emperors, jacks, and most sharks. Since pelagic fishes (e.g., tuna and oceanic sharks) can migrate over 1,000s of kilometers,

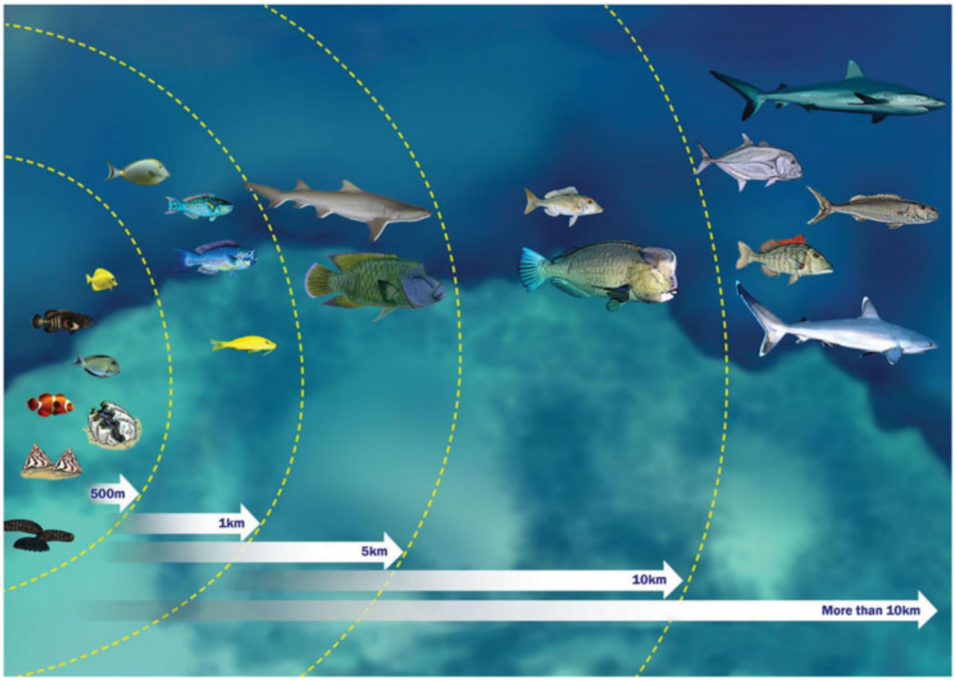

Figure 1. Different species have home ranges of different sizes (modified from Maypa 2012), so they need different sized marine reserves. To maintain healthy populations of focal species, marine reserves should be larger than their home ranges.

marine reserves are likely to have limited utility for these species. Species whose ranges are larger than the size of the reserve will only be afforded partial protection. However, reserves can provide benefits for these species if they protect locations where individuals aggregate and become vulnerable to fishing mortality (e.g., FSAs).

Optimal reserve size will also depend on the level of resource use and the efficacy of other management tools. Where fishing pressure is high and there is no additional effective fisheries management in place, networks of both small (0.5–1 km across) and moderate to large (5–20 km across) marine reserves will be required to achieve both biodiversity and fisheries objectives. However if additional effective management is in place for wide ranging species outside reserves, then networks of small marine reserves can contribute to achieving both conservation and fisheries objectives (provided that a sufficiently large proportion of the meta-population is protected overall: see *Habitat Representation*).

Larval dispersal also has implications for marine reserve size, since the larger the reserve, the more likely larvae will settle within their natal reserve and the population will be self-sustaining. However, even small reserves can provide recruitment benefits within and close to their boundaries, because self-recruitment is common in many coral reef fish species (Jones, Srinivasan, and Almany 2007).

It is important to note that these recommendations regarding minimum reserve size must be applied to the specific habitats that focal species use, rather than the overall size of the reserve (which may include other habitats). For example, for coral reef species, minimum size recommendations apply to the specific coral reef habitats that they use (e.g., for their home ranges), rather than other habitat types (e.g., open ocean, seagrass beds).

In places where marine reserve boundaries are extensively fished, compact reserve shapes (e.g., squares or circles rather than elongated ones) should also be used to minimize edge effects and maintain the integrity of the interior of reserves (Carr et al. 2003; McLeod et al. 2009). Similar benefits can be achieved by including whole ecological units (e.g., offshore reefs) in marine reserves (McLeod et al. 2009).

Spacing. Benefits for biodiversity conservation, fisheries management, and climate change adaptation are all increased by placing reserves within mutually replenishing networks, with spacing such that reserves are connected to one another through larval dispersal while maximizing recruitment subsidy to fished areas (Botsford, Hastings, and Gaines 2001; 2003, Botsford et al. 2009b; Almany et al. 2009; McLeod et al. 2009).

Several studies conducted on a variety of coral reef fish species and in different locations provide similar estimates of the relationship between distance and the magnitude of larval dispersal. Across species and locations, the average larva disperses between 5 and 15 km from its parents; some larvae disperse up to 35 km, and a few may disperse several hundred kilometers, resulting in reduced levels of connectivity between widely separated populations or reserves (reviewed in Jones et al. 2009). At the same time, self-recruitment, even to small areas of habitat (diameters of 0.5–0.9 km), is common and occurs consistently through time (although its magnitude varies).

The magnitude of dispersal (i.e., the amount of larvae reaching a particular site) declines with distance from the source population. Thus as the distance between reserves increases, the amount of larvae they exchange (larval connectivity) decreases. In order for the populations inside a reserve to persist through time, the amount of larvae reaching them must result in recruitment that equals or exceeds mortality (sustaining dispersal: Jones et al. 2009). While lesser levels of dispersal may play an important role in helping populations recover after disturbance (seeding dispersal), they are insufficient to sustain populations over time.

An important consideration regarding recommendations for spacing between reserves is the relationship between reserve size and larval dispersal. Large reserves produce more larvae than small reserves, because they protect larger populations and contain more breeding adults (Palumbi 2004; Jones, Srinivasan, and Almany 2007). Because small reserves produce fewer larvae, the proportion of larvae reaching a site at a given distance declines with the size of the source population. So the smaller reserves are, the closer they should be (Jones et al. 2009).

Reserves spaced between 1 and 15 km should therefore maximize connectivity between reserves, and between reserves and non-reserve areas, to ensure the persistence of reserve populations and contribute to the replenishment of fished populations. Reserve spacing toward the upper end of this range also will also assist with *Risk Spreading*.

Location. A common recommendation is to protect larval "source" populations (e.g., Almany et al. 2009), which can consistently provide larvae to other populations. In practice, identifying source populations is difficult and typically relies on fine scale oceanographic modeling (e.g., Bode and Armsworth 2006). Furthermore, larval dispersal studies indicate that delivery of larvae from one site to another is likely to vary over time, such that a location might act as a source in one year, but not another (Jones et al. 2009). Consequently, marine reserves should be located based on other considerations (i.e., key habitats and fish movements among and within them: see *Size and Shape; Spacing*; and *Protecting Critical,* *Special and Unique Areas*). However since currents are likely to influence dispersal to some degree, if there is a strong, consistent, unidirectional current, a greater number of marine reserves should be located upstream (McLeod et al. 2009).

Another consideration is isolated populations (e.g., remote atolls) that are largely self-replenishing and have high conservation value where they harbor endemic species and/or unique assemblages (Jones, Srinivasan, and Almany 2007). Low connectivity with other areas makes these locations less resilient to disturbance, so protecting a large portion of their area may be necessary to ensure population persistence (Almany et al. 2009). Pinsky et al. (2012) suggest that populations or locations separated from their nearest neighbor by more than twice the standard deviation of larval dispersal would be largely reliant on self-recruitment for replenishment. In this context, and given the data so far obtained from dispersal studies (Jones et al. 2009), conservatively, a location or population 20–30 km from its nearest neighbor should be considered isolated and afforded greater protection.

Allowing Time for Recovery

Coral reef fish species differ in their vulnerability to fishing and recovery rates in marine reserves, depending on their life history and ecological characteristics, fishing intensity, and the size of the remaining population (Jennings 2000; Hutchings et al. 2012). In the Coral Triangle, species in lower trophic groups that have smaller maximum sizes, faster growth rates, shorter life spans, and faster maturation rates tend to recover more quickly than species in higher trophic groups that have larger maximum sizes, slower growth rates, longer life spans, and slower maturation rates. For example, in the Philippines, populations of planktivores (e.g., fusiliers) and some herbivores (e.g., parrotfishes) recovered in <5–10 years when protected from overfishing in marine reserves, while predators (e.g., groupers) took much longer (20–40 years: Stockwell et al. 2009; Russ and Alcala 2010). Faster recovery rates have been recorded in marine reserves in areas where fishing pressure is lower (e.g., Great Barrier Reef and Papua New Guinea: Russ et al. 2008; Hamilton, Potuku, and Montambault 2011), while longer recovery rates have been recorded in other heavily fished areas (e.g., Kenya: McClanahan et al. 2007).

Therefore, long-term protection in marine reserves allows the full range of species and habitats to recover, and maintain, ecosystem health and associated fishery benefits (IUCN-WCPA 2008). While benefits can be realized for some species in the short term (<5 years), especially in areas with low fishing pressure (Russ et al. 2008; Hamilton, Potuku, and Montambault 2011), long-term protection allows all species the opportunity to grow to maturity, increase in biomass and contribute more, and more robust, eggs and larvae for population replenishment (Russ and Alcala 2004; Hart 2006; Kaplan, Hart, and Botsford 2010). Permanent protection helps maintain these benefits over the long-term (Russ and Alcala 2004; Hart 2006; Kaplan, Hart, and Botsford 2010).

In some Coral Triangle countries (e.g., Papua New Guinea and Solomon Islands), short-term or periodically harvested marine reserves are the most common form of traditional marine resource management (e.g., Foale and Manele 2004). These reserves can help address particular fisheries management needs where stocks need to be protected or restored (e.g., FSAs), or where communities wish to stockpile resources for feasts or close areas to fishing for cultural reasons (e.g., Foale and Manele 2004).

While short-term or periodic reserves also may function as a partial insurance factor by enhancing overall ecosystem resilience against catastrophes (Allison et al. 2003), the benefits of improved ecosystem health and increased biomass of species are quickly lost when the reserves revert to open access unless fisheries are managed carefully to ensure that the amount harvested is less than the amount built-up during protection (Jupiter et al. 2012). Therefore, while these closures may provide short-term benefits for some species and communities, they are usually less useful for conserving biodiversity or building resilience where the aim is to build and maintain healthy, natural communities and sustain ecosystem services (Jupiter et al. 2012).

Marine reserves should therefore be in place for the long-term (20–40 years), preferably permanently. Short-term or periodic reserves should be used in addition to, rather than instead of, long-term or permanent reserves.

Adapting to Changes in Climate and Ocean Chemistry

Changes in climate and ocean chemistry represent a serious and increasing threat to tropical marine ecosystems (Burke et al. 2011). Of particular concern is the increasing frequency and severity of mass coral bleaching primarily due to increasing sea-surface temperatures (SSTs), inundation of coastal habitats (e.g., mangroves, tidal wetlands and turtle nesting areas) due to sea-level rise, and weakening of calcareous skeletons of corals and other organisms due to ocean acidification (Hoegh-Guldberg, Mumby, and Hooten 2007; Lovelock and Ellison 2007; Pandolfi et al. 2011).

The effects of these changes on habitats and species vary based on different internal (e.g., genetic) and external (e.g., environmental) factors, which results in varying degrees of resilience (West and Salm 2003). Scientists hypothesize that areas where habitats and species are likely to be more resistant or resilient to climate and ocean change include: areas where habitats and species are known to have withstood environmental changes (or extremes) in the past (e.g., coral communities that appear more resilient to high SSTs); areas with historically variable SSTs and ocean carbonate chemistry, where habitats and species are more likely to withstand changes in those parameters in future; and areas adjacent to low-lying inland areas without infrastructure that coastal habitats can expand into as sea levels rise (West and Salm 2003; Salm, Done, and McLeod 2006; McLeod et al. 2009, 2012). Such potential climate change refugia should be protected within marine reserves, because they are likely to be important for maintaining biodiversity in the face of climate change (West and Salm 2003; Salm, Done, and McLeod 2006; McLeod et al. 2009, 2012). They are also likely to provide fisheries benefits, since habitat loss is a major threat to tropical coastal fisheries in the face of climate and ocean change (Bell, Johnson, and Hobday 2011).

Minimizing and Avoiding Local Threats

Tropical marine ecosystems have been seriously degraded by local threats in the Coral Triangle and other regions worldwide, particularly by unsustainable marine resource use (e.g., overfishing), destructive activities (e.g., blast fishing, trawling), coastal development, and pollution (Burke et al. 2011). These threats decrease ecosystem health and productivity, adversely affect many species (including focal species), and severely undermine the long-term sustainability of marine resources and the ecosystem services they provide (Cesar, Burke, and Pet-Soude 2003; Hoegh-Guldberg et al. 2009; Burke et al. 2011). Such threats can also decrease ecosystem resilience to other stressors, including climate change (Salm, Done, and McLeod 2006). Therefore, it is important to minimize or avoid these threats in marine reserves, and prioritize areas for protection that are more likely to contribute to ecosystem health, fisheries productivity, and resilience to climate change.

Local threats that originate within reserve boundaries (e.g., overfishing, destructive activities) can be managed within reserves, although effective management remains one of the greatest challenges facing marine conservation and management worldwide, including in the Coral Triangle (White et al. 2014). Other threats that originate beyond reserve boundaries (e.g., runoff of sediments and nutrients from land) must be addressed by integrating marine reserves within broader management frameworks (Salm, Done, and McLeod 2006; see below).

To optimize protection of areas that are less likely to be exposed to local threats and therefore likely to contribute more to biodiversity conservation, fisheries management and climate change adaptation: avoid placing marine reserves in areas that have been, or are likely to be, impacted by local threats that cannot be managed effectively (e.g., land based pollution); place marine reserves in areas that have not been, or are less likely to be, impacted by local threats including areas where threats (e.g., overfishing and destructive fishing) can be managed effectively, and areas within or adjacent to other effectively managed marine or terrestrial areas (Russ and Alcala 2004; IUCN-WCPA 2008).

Integration within Broader Management Frameworks

Well-designed and effectively managed marine reserves can play an important role in fisheries management, biodiversity conservation and climate change adaptation. However, to maximize their contribution to achieving these objectives, reserves must be embedded within broader management frameworks that address all threats to ensure the long-term sustainability of marine resources and the ecosystem benefits they provide (Salm, Done, and McLeod 2006; Christie et al. 2009b).

Where possible, all of the ecosystem (or as large an area as possible) should be included within a multiple-use MPA that includes, but is not limited to, marine reserves; so different types of protection in different zones can offer synergistic benefits to achieve multiple objectives simultaneously (Salm, Done, and McLeod 2006; FAO 2011). Marine reserves should also be embedded within broader management frameworks (Salm, Done, and McLeod 2006; Jones, Srinivasan, and Almany 2007). For example, fisheries objectives can be addressed more effectively if reserves are integrated within an Ecosystem Approach to Fisheries (EAF: FAO 2011). Reserves should also be integrated within broader spatial planning (e.g., Alvarez-Romero et al. 2011) and management regimes (e.g., Ecosystem Based Management or EBM, and Integrated Coastal Management or ICM) that address multiple threats including those arising from land (White, Eisma-Osorio, and Green 2005; Salm, Done, and McLeod 2006; Christie et al. 2009b).

Summary

Well-designed and effectively managed marine reserves can reduce local threats and maximize their contribution to achieving multiple objectives regarding fisheries management, biodiversity conservation, and climate change adaptation. Previously, ecological guidelines for marine reserve design provided advice for achieving one or two of these objectives independently. While many similarities exist in the guidelines provided for different objectives, key differences have resulted in conflicting advice (particularly regarding marine reserve size and duration of protection). Thus, there is a need to provide integrated guidelines for practitioners who wish to design marine reserves to achieve all three objectives simultaneously. Recent scientific advances also necessitate refining advice for marine reserve design.

Here we provide, for the first time, an integrated set of ecological guidelines (Table 1) that practitioners can use to design marine reserve networks to maximize benefits for fisheries management, biodiversity conservation and climate change adaptation simultaneously. Implementing these guidelines will also provide a more robust approach to achieving each objective. For example, protecting climate resilient areas to achieve biodiversity conservation by maintaining critical habitats, also benefits fisheries management since habitat loss is a major threat to coastal fisheries in the face of climate and ocean change. Improved fisheries management also benefits climate change adaptation, through the protection of key fisheries species that play a critical role in maintaining ecosystem resilience (e.g., herbivores).

Field practitioners are already applying these guidelines (Table 1) to the design of the Coral Triangle MPA System (Walton et al. 2014) and individual MPA networks within the Coral Triangle (e.g., Tun Mustapha Park, Malaysia: Weeks et al. 2014) and beyond. Since each of these guidelines are important for designing marine reserve networks to achieve all three objectives, full application of the guidelines will maximize the benefits for fisheries management, biodiversity conservation and climate change adaptation. These guidelines will also provide additional benefits for tourism management, since they will ensure that healthy ecosystems and populations of charismatic species of value to the tourism industry are maintained (e.g., sharks, large reef fishes, and turtles).

In practice, it is often difficult to apply ecological guidelines due to information gaps (particularly regarding identifying climate resilient areas) and socioeconomic, cultural, and political considerations (e.g., McCay and Jones 2011). Therefore these guidelines must contribute to larger planning processes that include identifying and prioritising high priority information needs, and designing marine reserves networks to achieve ecological outcomes while complementing human uses and values, and aligning with local legal, political, and institutional requirements (Knight and Cowling 2007; Christie et al. 2009a). Well-defined guidelines, such as those in Table 1, can provide a foundation for reserve design against which tradeoffs between ecological and other factors can be evaluated.

When required to compromise in the application of these guidelines, practitioners should prioritize applying ecological guidelines regarding representation and replication of major habitats and minimizing and avoiding local threats, since application of these guidelines increases the likelihood of protecting the range of species, habitats, and processes of importance, and of ensuring against the impacts of unpredictable disturbances. In addition, guidelines regarding protecting critical, special, and unique areas and the size, spacing, location, and duration of marine reserves can add significant benefits for achieving all three objectives. Since climate change impacts are likely to increase in frequency and severity, it will also be increasingly important to identify and protect refugia that have the best chance of surviving in the long term.

To ensure the long-term sustainability of tropical marine ecosystems and the ecosystem services they provide, marine reserves should be integrated within broader spatial planning and management frameworks that address all threats. Adaptive management systems should also be used that allow practitioners to refine the design as more information becomes available or as the ecological and social context changes (Wet and Salm 2003; IUCN-WCPA 2008).

Acknowledgments

The authors are grateful to A. Maypa, P. Lokani, J. Jompa, A. Soemodinoto, M. Knight, H. Possingham and R. Pomeroy who contributed to previous documents, and A. Maypa, S. Atkinson and M. Gombos for Figure 1.

Funding

This article is a synthesis of several documents developed with support from the U.S. Agency for International Development of the United States Government (USAID) funded Coral Triangle Support Partnership (CTSP). CTSP is a consortium led by the Word Wildlife Fund, the Nature Conservancy and Conservation International. Funding was made possible by the generous support of the American people through USAID Project Number: GCP LWA Award # LAG-A-00-99-00048-00. The contents are the responsibility of the authors and do not necessarily reflect the views of USAID.

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