Biophysical Principles for Designing a Network of Replenishment Zones for the Mesoamerican Reef System

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EXECUTIVE SUMMARY

The Mesoamerican Reef System (MAR) is one of the largest coral reef ecosystems in the world, which supports unique biodiversity and provides critical ecosystem goods and services to nearly two million people. These ecosystems, and the goods and services they provide, are in decline due to a combination of local (habitat destruction, unsustainable fishing practices, rapid tourism growth, invasive species and pollution) and global threats (changes in climate and ocean chemistry).

Replenishment Zones (RZs: areas of ocean protected from all extractive and destructive activities) can reduce local threats and be powerful tools for fisheries management, biodiversity conservation and adaptation to changes in climate and ocean chemistry, but only if they are well designed and managed. To date, each of the four countries with jurisdiction over the MAR (Belize, Guatemala, Honduras and Mexico) have used different approaches to design and implement their own networks of Marine Protected Areas (MPAs), including RZs. So far more than 50% of the MAR is protected within MPAs, but only 5.03% is within RZs (*Appendix II*).

Since the MAR is one large, ecologically connected system, a more coordinated regional approach to designing a network of RZs is required. Scientists and managers are now working towards designing and implementing a network of RZs throughout the MAR, which will build on the networks already being established in each country. As the first step in this process, we've used the best available science to develop 13 biophysical design principles for the MAR (Table 1), which aim to maximize biological objectives, by taking into account key biological and physical processes in the region.

These principles relate to seven categories regarding: habitat representation; risk spreading; protecting critical, special and unique areas; incorporating connectivity; allowing time for recovery; adapting to changes in climate and ocean chemistry; and minimizing and avoiding local threats. A scientific rationale for each principle is also provided, along with explanatory notes and research priorities for refining the principles further in future (particularly regarding understanding more about larval connectivity, changes in climate and ocean chemistry and the ecology of focal species, and the implications for designing networks of RZs).

These biophysical design principles are intended to contribute to larger planning processes that will include integrating RZs within broader planning and management regimes, and implementing RZs to complement human uses and values and align with local legal, political, and institutional requirements.

Table 1. Biophysical principles for designing a network of Replenishment Zones (RZs) for the Mesoamerican Reef System, including the scientific rationale and explanatory notes for each principle, as well as some research priorities.
Where focal species include key fisheries species, functional groups that are importantfor maintaining ecological resilienceto local and global threats, and rare and threatened species.

Category	Biophysical Design Principle	Scientific Rationale, Explanatory Notes and Research Priorities
Habitat Representation	1. Represent 20-30% of each major habitat type (e.g. coral reefs, mangroves) in RZs.	Different species use different habitats (e.g. different types of coral reefs, mangrove forests and seagrass beds), so each major habitat type should be protected. Percent habitat representation in each country should be based on fishing pressure, whether there is effective fisheries management in place outside RZs, and the condition of the resources. Percent habitat representation should also consider the vulnerability, diversity or rarity of each habitat, and the ecosystem services it provides. A research priority for the region is to define a common list of major habitat types and quantify their representation in the current network of RZs.
Risk Spreading	2. Protect at least three replicates of each major habitat in RZs in each ecologically distinct region of the MAR.	Large scale disturbances (e.g. coral bleaching and major storms) can cause serious impacts on major habitat types (see *Habitat Representation*), and it is difficult to predict which areas are most likely to be affected. Protecting examples of major habitat types in widely separated RZs reduces the chance that they will all be impacted by the same disturbance, so damaged areas may be replenished by larvae from unaffected areas. There are at least five ecologically distinct regions in the MAR, which differ in terms of their environment and associated species. Therefore, principles of habitat representation and replication need to be applied within each of these regions to ensure adequate protection of all species.

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Table 1. *[continues]*

Category	Biophysical Design Principle	Scientific Rationale, Explanatory Notes and Research Priorities
Protecting Critical, Special and Unique Areas	3. Protect areas of importance during the entire life cycle of focal species (e.g. spawning or nursery areas), sites with high endemism, sites with high abundance of rare and/or threatened species, healthy areas and areas with high habitat complexity in RZs.	Some focal fisheries species concentrate in areas that are critically important for their population maintenance (e.g. nursery and spawning areas), and protecting these areas can yield significant benefits for fisheries and biodiversity conservation. These areas should be protected in permanent or seasonal RZs, in combination with other management approaches (e.g. temporal closures during spawning season). Some rare and threatened species aggregate and use habitats that are crucial to their population maintenance (e.g. feeding or breeding areas for sea turtles, crocodiles, manatees, cetaceans and whale sharks); while some areas have unique geological features (e.g. blue holes), assemblages and populations (e.g. endemic species), high habitat or species diversity, or are particularly healthy and resilient. These areas should be protected in permanent or seasonal RZs in combination with other management approaches (e.g. hunting regulations and restrictions on the use of nets in cetacean migratory corridors).
Incorporating connectivity	4. Consider movement patterns of adults and juveniles of focal species when determining the size of RZs.	RZs must be large enough to sustain focal fisheries species within their boundaries during their adult and juvenile life history phases. Different species move different distances as adults and juveniles (e.g. for home ranges, ontogenetic habitat shifts and spawning migrations). RZs should be more than twice the size of the home range of adults and juveniles of focal species for protection (in specific habitats in all directions). Therefore, larger RZs can benefit a larger number of focal species. Species whose movement patterns are larger than the size of RZs will only be afforded partial protection, so RZs must be integrated with other fisheries management tools to manage wide ranging species. Research priorities include developing a list of focal species for the MAR, and conducting empirical studies of movement patterns of focal species required to refine this approach in the region.
	5. Ensure RZs are close enough to allow for the movement of focal species between habitats used throughout their life cycle.	Some species use different habitats throughout their lives (e.g. for home ranges, nursery and spawning areas). All habitats used by juveniles and adults of focal species should be protected within individual RZs. Where ontogenetic movements or spawning migrations cover long distances, different habitats used by focal species can be protected within multiple smaller RZs, provided that the location of these RZs allows for movements of focal species among protected habitats.
	6. RZs should include, where possible, entire ecological units (e.g. whole reefs or mangrove forests).	The protection of entire ecological units minimizes the threat of fishing mortality and helps maintain the integrity of RZs, since many species are likely to stay within their preferred habitat type.

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Table 1. *[continues]*

Category	Biophysical Design Principle	Scientific Rationale, Explanatory Notes and Research Priorities
Incorporating connectivity *[finishes]*	7. Design RZs using compact shapes rather than elongated ones.	Compact shapes (e.g. squares) minimize edge effects by limiting the spillover of adults and juveniles more than other shapes (e.g. long thin rectangles), which helps maintain the integrity of the RZ. Therefore, compact shapes should be used whenever possible, except when protecting naturally elongated habitats (e.g. long narrow reefs).
	8. Design a network of RZs to maintain larval connectivity within and among RZs, and to maximize dispersal to fishing areas.	Larval dispersal plays a key role in ensuring that populations persist through time, and is an important consideration for designing RZs. Further research is needed in the MAR to: review the best available information on connectivity for the region; assess the potential of combining different types of connectivity data to inform marine spatial planning; and use region specific larval dispersal data to design a network of RZs for the MAR.
Allowing Time for Recovery	9. RZs should be in place permanently to allow for the population recovery of all focal species, and to enhance fisheries production in the long term.	Populations of focal species recover at different rates in RZs depending on their life history characteristics, trophic level and many other factors (e.g. habitat quality and the size of the remaining population). Recovery of all focal species on the MAR is likely to take decades (>20-40 years). Therefore, long term protection in RZs (>20-40 years) is required for all species to grow to maturity, increase in biomass and contribute more robust eggs and larvae to replenish populations, enhance adjacent fisheries, and maintain ecosystem health and resilience. Permanent protection and strict enforcement of RZs will ensure that these benefits are maintained in the long-term. Short-term (<5 years) or periodically harvested RZs are not recommended as they only provide limited benefits for some species in the short term. These benefits are quickly lost once these areas are reopened to fishing unless they are managed very carefully (which is seldom the case). Therefore, they have limited benefits for conserving biodiversity, fisheries enhancement or building ecosystem health or resilience. So, if they are used, they should be used in addition to, not instead of, permanent RZs. Long term monitoring (>20-40 years) is required to understand more about recovery rates of focal species within RZs on the MAR.
	10. Seasonal RZs can be used to protect focal species during critical life stages (e.g. in spawning and nursery areas).	Seasonal closures can be used to protect critical areas at critical times (e.g. spawning or nursery areas), which can be very important to protect or restore populations of focal fisheries species (see *Protecting Critical, Special and Unique Areas*).

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Table 1. *[ends]*

Category	Biophysical Design Principle	Scientific Rationale, Explanatory Notes and Research Priorities
Adapting to Changes in Climate and Ocean Chemistry	11. Address threats from rising sea temperatures and sea levels, and changes in ocean chemistry, by: a. Increasing percent habitat representation. b. Spreading the risk. c. Increasing protection of key species that increase ecosystem resilience (e.g. parrotfish).	Changes in climate (e.g. from rising sea temperatures and sea levels) and ocean chemistry represent a serious and increasing threat to tropical marine ecosystems on the MAR. Since patterns of observed coral bleaching events and projected stress are highly spatially and temporally variable, we can't identify areas that are likely to be more resistant or resilient to these events at present. Furthermore, there is still a lot of uncertainty regarding how organisms will respond to these changes, and further research is required to identify habitats and species that are more likely to survive so they can be prioritized for protection. Meanwhile, protecting an increased percentage of each habitat type (see *Habitat Representation*), multiple examples of each major habitat type in widely separated RZs (see *Risk Spreading*), and species such as parrotfishes that play a critical role in maintaining ecosystem resilience will increase the chances that some examples of each habitat type and associated species will survive. Further research is required to improve our ability to identify resistant and resilient areas in the MAR for protection in RZs, including assessing predictive models, and conducting more detailed field surveys and analyses of bleaching events to refine and validate the models. This principle should be revised as more information becomes available.
	12. Prioritize the protection of coastal habitats (e.g. mangrove forests and turtle nesting beaches) that have greater probability of surviving sea level rise.	Complex models are required to identify coastal habitats (e.g. mangrove forests and turtle nesting beaches) that may be more likely to survive sea level rise, which are not currently available for the MAR. In the absence of these models, coastal habitats for protection can be evaluated in terms of how likely they are to survive sea level rise based on factors such as if they have room to move to higher ground.
Minimizing and Avoiding Local Threats	13. Prioritize placing RZs where there are, or are more likely to be, low levels of threats now and in future.	Marine ecosystems have been degraded by local threats in the MAR (including from habitat destruction, unsustainable fishing practices, rapid tourism growth and unsustainable practices, invasive species and pollution), which have adversely affected many species. This has led to a decline in ecosystem health, productivity and resilience to climate change, severely undermining the long-term sustainability of marine resources and the ecosystem services they provide. Therefore, it is important to: avoid placing RZs where ecosystems have been, or are more likely to be, degraded by local threats that can't be managed effectively (e.g. river runoff with unnaturally high levels of sediments and nutrients, and pollutants such as pesticides); and prioritize placing RZs where there are, or are more likely to be, healthy ecosystems and low levels of threats (e.g. areas influenced by healthy river systems with natural levels of sediment and nutrients and no pollutants).

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INTRODUCTION

The Mesoamerican Reef System

The Mesoamerican Reef System (MAR) is the longest coral reef ecosystem in the Western Hemisphere, supporting unique biodiversity (Roberts *et al*. 2002) and spanning more than 1,000 km along the coasts of Belize, Guatemala, Honduras and Mexico (Kramer *et al*. 2015: Figure 1).

The MAR is constituted by waters that belong to distinct environmental regimes. The region includes at least five distinct ecological areas (Chollett *et al*. 2012b), ranging from warm, clear waters offshore, to turbid inshore areas around bays and cold areas subjected to upwelling in the north of the ecoregion (Chollett *et al*. 2012b). The Mexican portion of the MAR is devoid of aboveground rivers, while in the southern portion, rivers represent important environmental features. This mosaic of environments influences the organisms that inhabit each region, and translates into different biological communities even within the same habitat type. Albeit formed by ecologically distinct areas, the MAR is a highly connected system, with strong currents bringing larvae and runoff from the south of the ecoregion towards the north (Cowen *et al*. 2006, Paris and Chérubin 2008, Soto *et al*. 2009).

The MAR is a priority ecoregion (Olson and Dinerstein 2002) that supports local economies and culturally rich livelihoods of its nearly two million inhabitants in Belize, Guatemala, Honduras and Mexico (Kramer *et al*. 2015) by providing food, income through fisheries and tourism, and coastal protection.

Fisheries are socially and economically central to all four countries in the MAR:

- In Belize, the fishing industry is very important for the economy of the country, contributing 5% to Belize's Gross Domestic Product (GDP) in 2003 (FAO 2015). Fisheries exports represented US$106.8M in 2004, with farmed shrimp being the main product, followed by lobster and conch for 60% of the total value of the country's capture fisheries sector (which was US$10.8 million in 2010: Wade *et al*. 2011 in Foley 2012). Foley (2012) reported that the fisheries sector employed 2,400 registered fishers and an additional 15,000 people in processing and exporting roles, which comprised ~5% of the Belizean population.[1] The contribution of coral reefs and mangroves to Belize's fishing industry, through the provision of habitats for almost all commercially caught species, has been estimated to be US$14 to 16 million per year (Cooper *et al* 2008).
- Even though the Caribbean coast of Guatemala is relatively small, there were more than 3,700 artisanal fishers in 2003 (FAO 2005b). Fishing activities benefit more than 34 communities directly and 100,655 people that live on the coast (Heyman and Granados-Dieseldorff 2012). Based on extrapolations from fishers' interviews, Heyman and Granados-Dieseldorff (2012) reported a total of 5.6 million pounds of artisanal fishery landings for 1998 on the Caribbean coast of Guatemala, with an approximate value of US$3.8M. Finfish is the most important fishery in this area by effort, comprising 84% of the boats (FAO 2005b).
- In Honduras, fishing and aquaculture contributed 6.2% to the national economy in 2015 (BCH 2016) and 24.4% to the primary sector in 2013 (FAO 2015), mostly associated with the lobster fishery. This is the most important fishery both in terms of effort (e.g. it comprised 59% of the industrial fisheries fleet in 2010-2012: Chollett *et al*. 2016a) and profit, producing about US$180.3M per year for the period 2000-2010 (FAO 2015) and US$51.8M for the 2014-2015 season alone (BCH 2016). Artisanal fisheries on the north shore of Honduras employ about 10,000 fishers, which mostly target reef finfish (Box and Canty 2010).
- According to Cordero-Sosa and Ramírez-González (2011), in Quintana Roo, Mexico, the focal fisheries are lobster (50.5%), being the most important fishery, followed by scale (37.1%), shrimp (6.6%), shark (2.9%) and conch (2.8%). In 2013, the fishery supported 25 co-operatives with more than 2,200 associated fishermen (Bobadilla 2014). Although significant in terms of livelihoods, other activities (e.g. tourism, commerce) are the most important economic activities in the state, and fishing contributed just 0.06% of the GDP in 2010 (Bobadilla 2014).

In Belize, tourism is the single largest contributor to the nation's economy, with tourism expenditure representing 24% of the US$1.5 billion GDP (Kramer *et al*. 2015). While in Mexico, Quintana Roo depends mostly on tourism, receiving more than 60% of Mexico's tourism (CONABIO 2012 in Lucas *et al*. 2012), employing 34% of the 668,482 people of working age in the State (HRI

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[1] Belize's population in 2014 was 351,706 (World Bank Database, http://data.worldbank.org/indicator/SP.POP.TOTL)

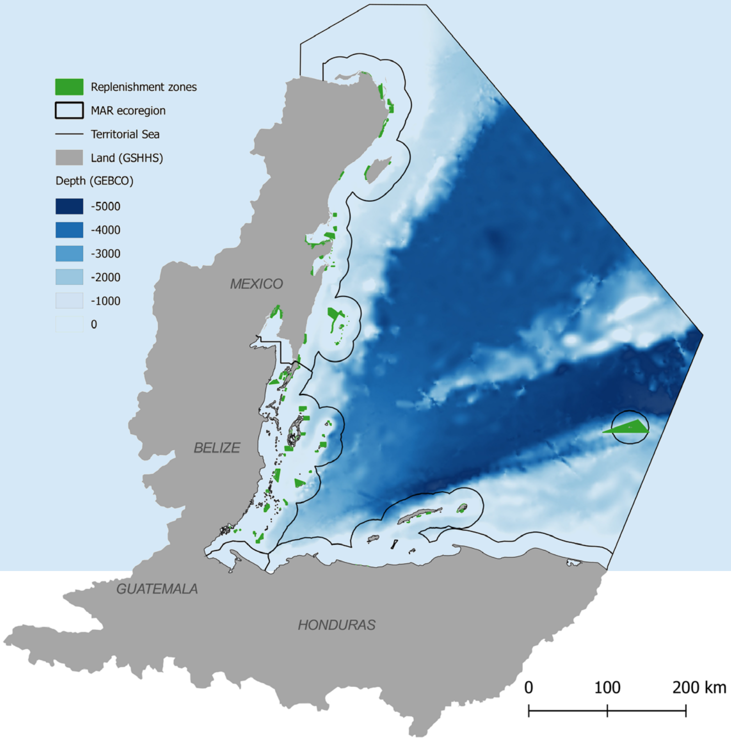

Figure 1. Where: replenishment zones coverage data is discribed in *Appendix II*; the coastline is from the Global, Self-Consistent, Hierarchical, High-resolution Shoreline (GSHHS) dataset; and bathymetry is from the General Bathymetric Charts of the Ocean (GEBCO) dataset.

2012) and contributing up to 85% of the GDP in 2010 (Bobadilla 2014). Cancun alone receives an average of ~22 million visits per year (Lucas *et al*. 2012). In Honduras, the tourism industry is growing, particularly activities related to coastal and beach relaxation and enjoyment. Income from tourism increased by 14.8% in 2014 compared with 2013, representing 7.8% of the country's GDP (IHT 2015). In 2014, tourist activities brought more than 2M tourists to Honduras (including cruise ship visitors), employed about 210,000 people and generated US$698M (IHT 2015). The Caribbean coast of Guatemala, including Livingston, Punta de Manabique and Sarstoon are visited by national and international tourists who arrive in an occasional and sporadic way. Difficulties in transportation and lack of infrastructure may be one of the reasons for the small number of visitors to this area (Boix 2009).

Coral reefs and mangroves also provide vulnerable coastal communities with natural protection against storm surges, hurricanes and erosion, by absorbing and dissipating wave energy (Dalberg 2016). In Belize, they provide protection for 40% of the population, and this ecosystem service is valued at between US$270 and 390 million per year. The combined value of this protection, in terms of avoided damage to coastal properties alone, is estimated at between US$231 and 347 million per year (Cooper *et al*. 2008). In addition, using the social cost of carbon (which estimates the economic damage associated with increased carbon dioxide emissions), the total annual value of carbon sequestration by coastal mangrove forests in Belize is over US$39 million (Dalberg 2016).

Unfortunately, the health of coastal ecosystems has been declining in the MAR due to the combined effects of local (habitat destruction, unsustainable fishing practices, rapid tourism growth, invasive species and pollution) and global threats (particularly rising sea temperatures causing mass coral bleaching: Kramer *et al*. 2015). The overall health condition of the MAR's reefs is now considered "fair" with low but slowly increasing coral cover (~16-18%), high and increasing dominance of fleshy macroalgae, low abundances of the herbivorous sea urchin *Diadema antillarum*, and low abundances of focal fisheries species (snappers and groupers) and herbivorous fishes (parrotfishes) that are important for ecosys-

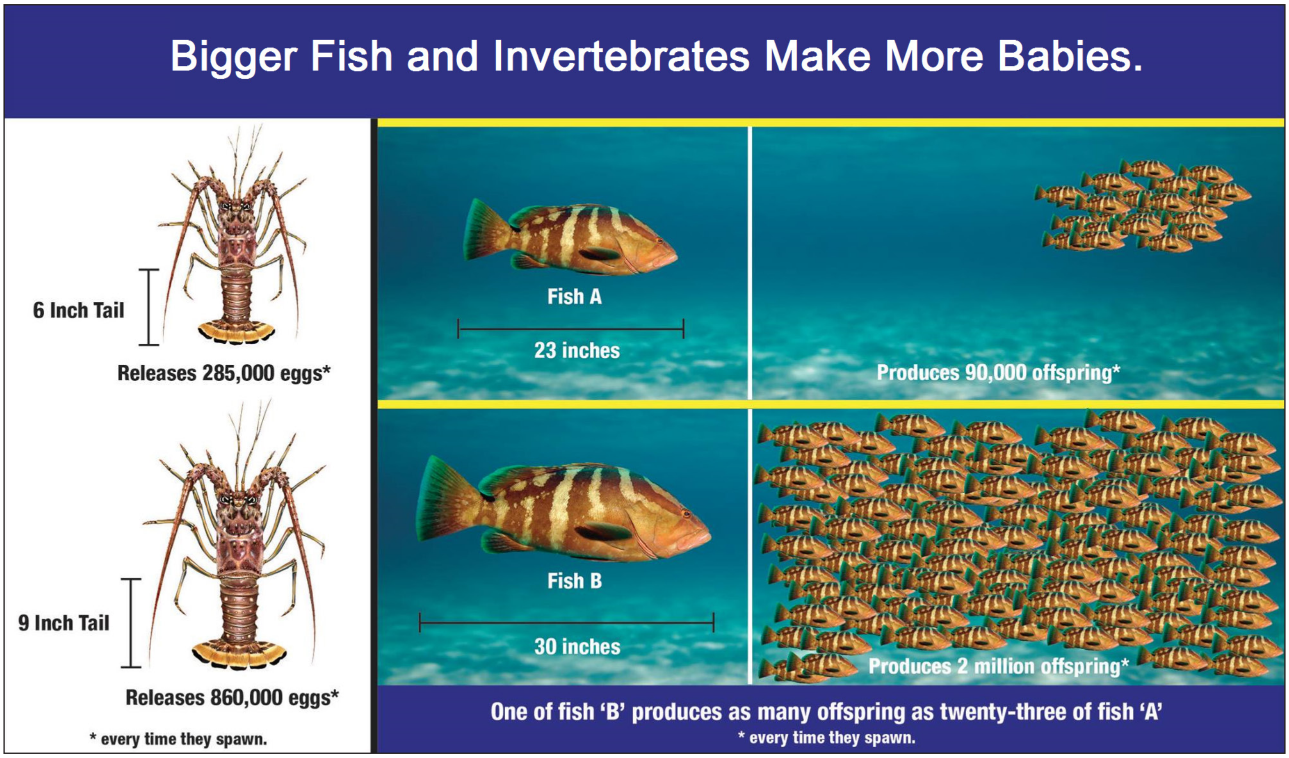

Figure 2. Replenishment zones allow fisheries species to grow larger and produce more offspring, enhancing fisheries in adjacent areas. [Poster modified from "The Bahamas Protected MPA Infographic Series 2017", wich was based on fecundity calculations for Nassau grouper (Sadovy and Eklund 1999) and Caribbean spiny lobster (Fonseca-Larios y Briones-Fourzan 1998)].

tem resilience (Kramer *et al*. 2015). Iconic species such as large groupers are now rare, and mainly only found in replenishment zones (Kramer *et al*. 2015). Mangrove (Hirales-Cota *et al*. 2010, Chen *et al*. 2013) and seagrass ecosystems (Short *et al*. 2006), which are important nursery areas (Heck *et al*. 2003, Mumby *et al*. 2004), also show signs of degradation throughout the region.

It is also likely that this decline in the health of ecosystems on the MAR has led to a decline in their ability to maintain biodiversity and provide ecosystems goods and services for people (e.g. see Moberg and Folke 1999). Fisheries are also showing signs of overexploitation and decline. Overfishing of marine resources beyond the capacity of the system to maintain natural and economically productive levels, has resulted in the severe depletion of resource populations and localized extinctions in some cases (Gorrez 2005). Furthermore, although they are a main source of income in the region, lobster catches in Quintana Roo and Belize have shown steady declines since the 80s, highlighting the need for better resource management (FAO 2005a, Sosa-Cordero 2011, Fowley 2012). The same has occurred with conch landings in Belize, which have dropped from about 800 Ton in 1970 to 230 Ton in 2000 (Catarci 2004). Nassau grouper, once the most desirable target species in the region, is now endangered (Sadovy 2010) and some known spawning aggregations have been extirpated (Aguilar-Perera 2006).

Urgent action is required to reverse this decline in coastal ecosystems and the goods and services they provide on the MAR.

The Benefits of Replenishment Zones

Replenishment Zones[2] (RZs) are areas of ocean that are protected from all extractive and destructive activities, which can be effective tools for addressing local and global threats, enhancing fisheries yields, protecting biodiversity, improving resilience of marine populations and ecosystems, and adapting to changes in climate and ocean chemistry (Green *et al*. 2014a, b). This is because they allow marine species (especially focal fisheries species) to live longer, grow larger and increase their reproductive potential, contributing more to population recovery within RZs and enhancing fisheries in adjacent areas through the spillover of adults, juveniles and larvae (Figure. 2).

However, the degree to which RZs can contribute to enhancing fisheries yield depends on how well the fishery is managed beyond their boundaries (reviewed in Botsford *et al*. 2014). Where a fishery is well managed (e.g. at or below Maximum Sustainable Yield), adding RZs may diminish yield because the fishable area is decreased. Conversely, in areas like the MAR where there is overfishing and populations of focal fisheries species have declined (Kramer *et al*. 2015), RZs can play an important role in enhancing fisheries yields (Botsford *et al*. 2014). However, RZs can only be effective fisheries management tools if they are well designed and effectively managed (Green *et al*. 2014a).

Designing a network of RZs will produce larger fisheries and conservation benefits for the MAR than establishing multiple RZs independently. This is because an interacting network capitalizes on the ability of larvae and adults to move between habitat patches to help marine resources thrive even if fisheries resources outside the network are being depleted or if some of the individual RZs have been disturbed (Hastings and Botsford 2003, 2006).

Existing Replenishment Zones

Each of the four MAR countries have protected more than 20% of their territorial seas in MPAs, with 34,462.37 km^2 of the marine area within MAR territorial waters being protected (*Appendix II*). However only 9.66% of the marine area is under full protection in RZs (Figure 1, *Appendix II*). Effective management of these areas also remains a challenge, due to several factors including difficulties with compliance and enforcement, possibly due to the lack of involvement of fishers during the design process and concerns by fishers that they will not have equitable access to the benefits of RZs (Velez *et al*. 2014, Moreno *et al*. 2016).

Research comparing RZs and areas open to fishing in the MAR has shown that RZs have larger fish biomass (Polunin and Roberts 1993, Newman *et al*. 2006, Huntington *et al*. 2010, McClanahan *et al*. 2011,) and abundance of apex predators such as reef sharks (Newman *et al*. 2006, Bond *et al*. 2012). For example, long term monitoring has shown that some protected areas have 10 times more biomass of fisheries species (snapper and grouper) than areas with no protection (Kramer *et al*. 2015). Gear fisheries restrictions (bans on spearfishing) are also helping to ensure that some areas have more, large groupers (Kramer *et al*. 2015).

However, in some parts of the region, the positive effects of protection are small and eas-

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[2] Also known as no-take areas, marine reserves, fish refugia and core zones in Marine Protected Areas.

ily confounded by environmental drivers (Huntington *et al*. 2010), and they have not translated into measurable recovery of coral cover (McClanahan *et al*. 2011). This moderate response has been attributed to several design, ecological and compliance factors (McClanahan *et al*. 2011). For example, the RZs assessed might be too small or the recovery time too short to translate into measurable ecological benefits. On the other hand, environmental disturbances could override the benefits of protection, and the presence of complex food webs could hinder simple cascading responses. The lack of a large response could also be related to insufficient compliance (McClanahan *et al*. 2011).

This research shows that RZs can be important management tools on the MAR if they are well designed and managed, and combined with other fisheries management tools to complement and improve their effectiveness (Kramer *et al*. 2015). Therefore, there is an urgent need to increase the level of protection within RZs on the MAR, and to combine them more effectively with other fisheries management tools.

Previously, each of the four countries in the MAR has been designing and implementing networks of Marine Protected Areas independently, which include RZs. Each country has used a different approach, and their networks are in different stages of development (Figure. 1, *Appendix II*):

- Belize has committed to expanding RZs to include at least 10% of all major habitat types. The goal of the expansion is to meet the combined needs of conservation and restoration of biodiversity and fisheries, ecological integrity and ecosystem services and climate change resilience, while ensuring benefits to the livelihoods of people. A draft proposal for the expansion has been developed through spatial planning and analysis (using MARXAN and guiding principles), development of a decision support tool, and participatory stakeholder consultation (Cruz *et al*. 2016). The initiative also includes demonstration of benefits of RZs to stakeholders, a national communications campaign, and a national plan addressing economic alternatives and fisheries diversification. Currently the network of functional RZs in Belize covers 3.09% of territorial waters.
- Honduras has an initiative to include 20% of their fishable waters in RZs to meet the combined needs of conservation and restoration of biodiversity, and to sustain fisheries. This national initiative has been promoted among the different sectors lead by the fisheries authorities. The current RZs have been declared by fishermen initiatives with endorsement by local fisheries authorities. Ongoing efforts to expand and declare more RZs along the north coast should include applying biophysical design principles combined with input and participation from local fishermen and support from local authorities. Currently there are no official estimates of fishable area for the country, but the present network of RZs covers 2.46% of Honduras's territorial waters within the MAR ecoregion.
- In 2012, the first two fully-protected RZs were established in Guatemala in Graciosa Bay through an agreement (signed by CONAP and the fishing communities) for five years. These RZs are located inside the Wildlife Refuge Punta de Manabique. This was an important step for Guatemala because the communities pushed for the protection of these areas. The Fisheries Department (DIPESCA) published a fishing ban through a ministerial agreement in 2016, establishing these areas as RZs for another five years. Currently this network of RZs protects 0.14% of the Atlantic (MAR) territorial waters of the country.
- Mexico has committed to protecting 10% of coastal and marine areas at a national level as part of the Aichi Biodiversity targets. In the

Mexican MAR, the multi-sectorial Kanan Kay Alliance is working to establish an effective network of RZs that protect 20% of the territorial waters of the State of Quintana Roo, to allow for the recovery of artisanal fisheries and conservation of the Mesoamerican Reef. Currently the network of functional RZs in Mexico covers 3.97% of territorial waters.

Using Biophysical Principles to Design a Network of Replenishment Zones

Since the MAR is one large, ecologically connected system, a coordinated regional approach to designing a network of RZs is now required. This is necessary to protect all ecologically distinct areas in the MAR within a network of RZs, and to address ecological processes (such as connectivity: Paris and Chérubin 2008) and threats (such as overfishing and climate change: Burke *et al*. 2011) that cross jurisdictional boundaries.

Scientists and managers are now working towards designing and implementing a network RZs for the entire region, which will build on the networks already being established in each country. As the first step in this process, 37 scientists and managers from the four countries (see Appendix I) convened in Cancun (July 12-15, 2016) to use the best available science to develop biophysical design principles for the MAR (Zepeda *et al*. 2016). The aim of these design principles is to maximize benefits for fisheries, conservation, and climate change objectives by taking into account key biological and physical processes in the region (e.g. see Fernandes *et al*. 2005, Green *et al*. 2009).

To do this, we started with global reviews and principles regarding how to design networks of RZs in tropical marine ecosystems to maximise the benefits for fisheries management and biodiversity conservation in the face of climate change (Abesamis *et al*. 2014, Green *et al*. 2014a, b). We then went through each principle and adapted or refined the approach to suit the biophysical environment in the MAR while considering the best available information for the region.

Here we present, for the first time, biophysical design principles for enhancing fisheries, conserving biodiversity and adapting to changes in climate and ocean chemistry throughout the MAR. If applied, these principles 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. large reef fishes and sea turtles: Green *et al*. 2014a).

These biophysical principles for designing a network of RZs in the MAR should be applied using the precautionary approach and best available information, and they may require adaptation or refinement as more information becomes available or if the situation changes (e.g. due to climate change).

These principles are also intended to contribute to a larger planning process that will include implementing RZs in ways that will complement human uses and values, and align with local legal, political, and institutional requirements (see Green *et al*. 2014a). This will require another process to identify socioeconomic and governance design principles, which will aim to maximize the benefits and minimize the costs to communities and other stakeholders (e.g. see Fernandes *et al*. 2005, Green *et al*. 2009).

Furthermore, to maximize their benefits for fisheries enhancement, biodiversity protection and climate change adaption, RZs must be embedded within broader planning and management frameworks that will address all threats to ensure the long-term sustainability of marine resources and the ecosystem benefits they provide (Salm *et al*. 2006, Christie *et al*. 2009b: see *Discussion*).

Figure 3. Focal fisheries species (from Brumbaugh 2014): spiny lobster, queen conch and Nassau grouper.

BIOPHYSICAL PRINCIPLES FOR DESIGNING A NETWORK OF REPLENISHMENT ZONES FOR THE MESOAMERICAN REEF SYSTEM

Here we provide 13 biophysical design principles (Table 1) which, when used collectively, will maximise the ecological benefits of a network of RZs to enhance fisheries, conserve biodiversity and adapt to changes in climate and ocean chemistry in the Mesoamerican Reef System (MAR). These principles relate to seven categories regarding: habitat representation; risk spreading; protecting critical, special and unique areas; incorporating connectivity; allowing time for recovery; adapting to changes in climate and ocean chemistry; and minimising and avoiding local threats.

We also provide the scientific rationale for each principle, based on recent reviews and guidelines regarding how to design networks of RZs in tropical marine ecosystems to maximise the benefits for fisheries management and biodiversity conservation in the face of climate change (e.g. Abesamis *et al*. 2014, Green *et al*. 2014a, b). Where the design principles for the MAR are based on the ecology of focal species, these include: key fisheries species such as the Nassau grouper (*Epinephelus striatus*), spiny lobsters (*Panulirus argus*) and queen conch (*Lobatus gigas*) (Figure 3); functional groups that are important for maintaining ecological resilience to local and global threats (e.g. herbivorous fishes such as parrotfishes); and rare and threatened species (e.g. sea turtles, manatees and cetaceans).

There are often information gaps and socio-economic, cultural, political and other reasons that can prevent the full application of all these principles. When required to comprise, we recommend that decision makers and field practitioners aim to achieve as many of these principles as possible. We also identify research priorities for refining the principles further in future.

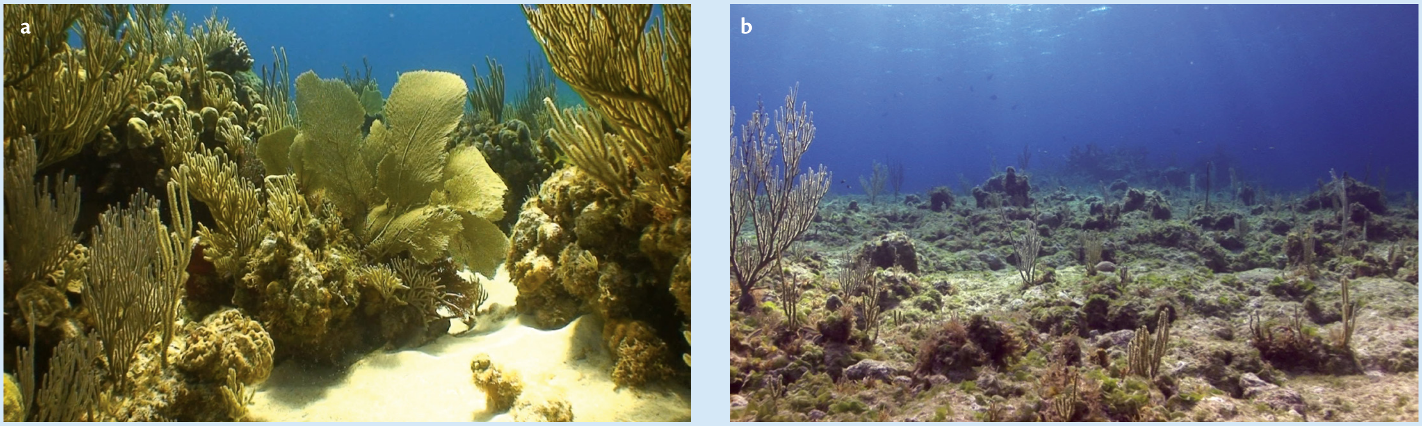


Figure 4. Contrasting habitats: complex *Orbicella* dominated coral reef (a) versus relatively flat hard bottom or Gorgonian plain (b).

Habitat Representation

Represent 20-30% of each major habitat type in RZs.

Different species use different habitats in the MAR (Mumby *et al*. 2008). Therefore, to protect all species (including focal species) and maintain the health, integrity, and resilience of the ecosystem, adequate examples of each major habitat should be protected within RZs (McLeod *et al*. 2009, Gaines *et al*. 2010, Green *et al*. 2014a). Where major habitats in the MAR include different types of:

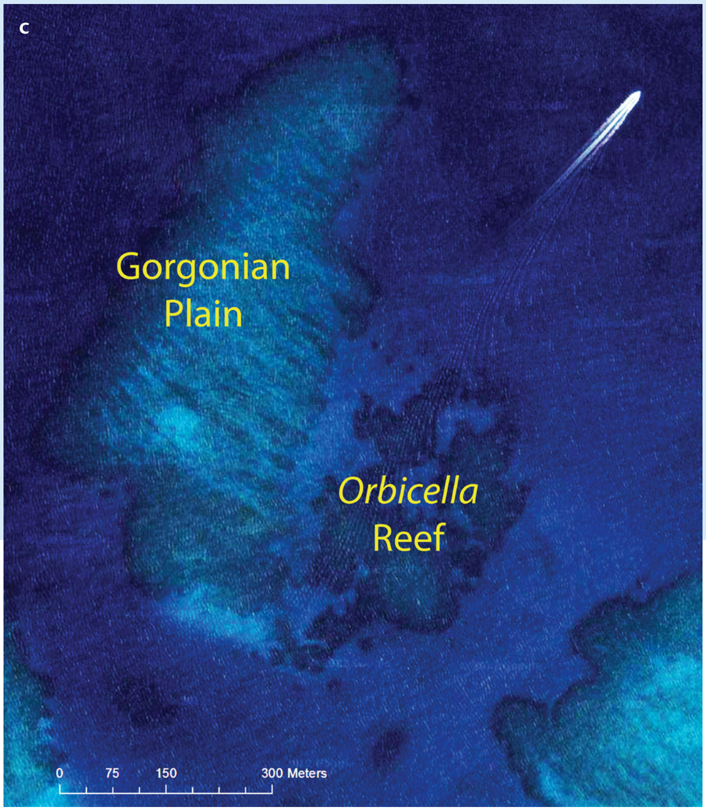
- Coral reef habitats, which vary by reef type, zone, exposure and distance to the coast and major rivers (Figure 4).
- Mangrove forests, which vary based on mangrove species composition and seascape features.
- Seagrass beds, which vary based on seagrass species, density and seascape features.
- Algal mats, which are dominated by different species of algae (Mumby and Harborne 1999).
- Other habitats with consolidated substrate, such as pavement areas and gorgonian plains (Figure 4), which characterize fore-reefs with high wave exposure (Williams *et al*. 2015) and could be more resilient to herbivore fishing (Mumby 2014).
- Unconsolidated substrate habitats, such as sand flats and areas dominated by rubble or mud (Mumby and Harborne 1999).

To determine how much of each habitat to protect, it is important to consider that populations can only be maintained if they produce enough eggs and larvae to sustain themselves (Botsford *et al* 2001, 2009a, 2014). This threshold is not known for most marine populations (Botsford *et al*. 2009a, 2014). Therefore, 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).

Early studies indicated that protecting a minimum of 20% of the stock could be enough to prevent the collapse of the populations (PDT 1990, Mace and Sissenwine 1993, NRC 2000). However, more recent meta-analyses suggest that keeping this threshold above 35-40% of unfished stock levels ensures adequate replacement over a range of species (Botsford *et al*. 2001, 2014, Fogarty and Botsford 2007, FAO 2011).

To approximate the level of protection of this threshold, 20-40% of the habitats used by focal species should be protected in RZs (Bohnsack *et al*. 2002, Fogarty and Botsford 2007, Moffitt *et al*. 2009), where habitat protection is used as a proxy for protecting fisheries stocks. The exact level of protection needed in each region will depend of

Both habitats can be discriminated on high-resolution satellite imagery (c).
From Mumby. (2014).



the focal species, the state of its stock, its biology, the local patterns of currents and spatial distribution of its habitats (Botsford *et al*. 2001, 2009b, Bohnsack *et al*. 2002, Gaines *et al*. 2003). While lesser levels of habitat protection (but not less than 10%) may be sufficient in areas with low fishing pressure (Botsford *et al*. 2001, 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).

Percent habitat representation should also consider the vulnerability, diversity or rarity of the habitat, and the ecosystem services it provides (Mumby *et al*. 2008, Harborne 2009). For example, it may be important to protect a larger proportion of medium-high relief coral dominated forereefs and *Acropora* dominated reef crests, based on the scarcity of the corals that build these reefs and their importance for supporting biodiversity and associated ecosystem services (e.g. shoreline protection).

To apply this approach on the MAR, RZs should encompass at least 20–30% of each major habitat (i.e. each type of coral reef, mangrove forest and seagrass bed; modified from Green *et al*. 2014a). Each country will determine the percent habitat representation that they will aim for, where the recommended percentage should be determined based on the focal species considered, fishing pressure, whether there is effective fisheries management in place outside RZs, as well as the condition of the resources. If fishing pressure is high, and populations of focal species and habitats are in poor condition and the only protection offered to fisheries species will be within RZs, then the proportion of each major habitat protected within RZs should be 30%. If fishing pressure is low or effective fisheries management is in place outside RZs, and populations of focal species and habitats are in good condition, then a lesser level of protection (20%) can be used. Depending on the country, this level of habitat protection may be similar to, or higher than, the 10-20% that they have already committed to protecting in their territorial waters (see *Appendix II*).

The first step towards ensuring habitat representation within RZs in the MAR would be to define a common list of major habitat types in the region, and quantify their representation in the current network of RZs.

Figure 5. Nassau grouper FSA, Sian Ka´an Biosphere Reserve, Mexico (left: © Alfredo Barroso) and Cubera Snapper FSA, Belize (right: © Douglas David Seifert).

Risk Spreading

Protect at least three replicates of each major habitat in RZs in each ecologically distinct region of the MAR.

Large-scale disturbances can cause serious impacts on the tropical marine ecosystems of the MAR (e.g. coral bleaching and major storms: Sheng *et al*. 2007, McField *et al*. 2008, see also *Adapting to Changes in Climate and Ocean Chemistry*).

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, dredging, ship-generated discharges, aquaculture expansion: Kramer and Kramer 2002), it is important to protect examples of each major habitat type (see *Habitat Representation*) in at least three widely separated RZs to reduce the chance that all examples of a habitat type will be adversely impacted by the same disturbance at the same time (Salm *et al*. 2006, McLeod *et al*. 2009, Green *et al*. 2014a). Thus, if one example of a major habitat type is severely damaged, others may remain to provide the larvae required to replenish the affected area.

Furthermore, since variations in communities and species within major habitats are often poorly understood, habitat replication through risk spreading also increases the likelihood that examples of each are represented within the RZ network (McLeod *et al*. 2009, Gaines *et al*. 2010, Green *et al*. 2014a).

However, since the MAR comprises at least five ecologically distinct regions with different biological communities in the same habitat type (Chollett *et al*. 2012b, see *Introduction*), this principle of protecting examples of each habitat in different RZs should be replicated within each of these distinct regions to maximize the possibility of protecting all species. Some progress has been made towards identifying distinct ecological regions throughout the entire Caribbean (Chollett *et al*. 2012b), and Chollett *et al*. (*in press*.) are in the process of refining this work to identify ecologically distinct regions that can be used to apply this principle to design a network of RZs for the MAR.

Table 2. **Different habitats used by three commercially important fisheries species during different life history phases.**

Species	Life History Phase			Source
	Settlement	Juvenile	Adult	
Queen Conch	Sand banks macroalgae	Seagrass	Sand/seagrass	Stoner and Ray 1993
Spiny Lobster	Nearshore hard bottom and seagrass beds, macroalgae, small shelters	Patch reefs and mangroves	Patch/fore reef	Marx y Herrnkind 1985 Acosta y Butler 1997 Briones-Fourzán y Lozano-Álvarez 2001 Eggleston y Dahlgren 2001
Nassau grouper	Nearshore hard bottom macroalgae, small shelters	Patch Reef	Patch/fore reef	Eggleston 1995 Dahlgren and Eggleston 2001.

Protecting Critical, Special and Unique Areas

Protect areas of importance during the entire life cycle of focal species, sites with high endemism, sites with high abundance of rare and/or threatened species, healthy areas and areas with high habitat complexity in RZs.

Protecting critical areas in the life history of focal species

Some focal fisheries species use areas that are critically important for maintaining their populations (e.g. nursery and spawning areas), and protecting these areas can yield significant benefits for fisheries and biodiversity conservation (Green *et al*. 2014a, b).

Fish spawning aggregations (FSAs: Figure 5) 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 (e.g. Nassau grouper) can travel long distances of tens to hundreds of kilometres to form FSAs for relatively short periods of time (days or weeks: Domeier 2012, Dahlgren *et al*. 2016). For these species, such gatherings are the only opportunities to reproduce, and they are crucial to population maintenance.

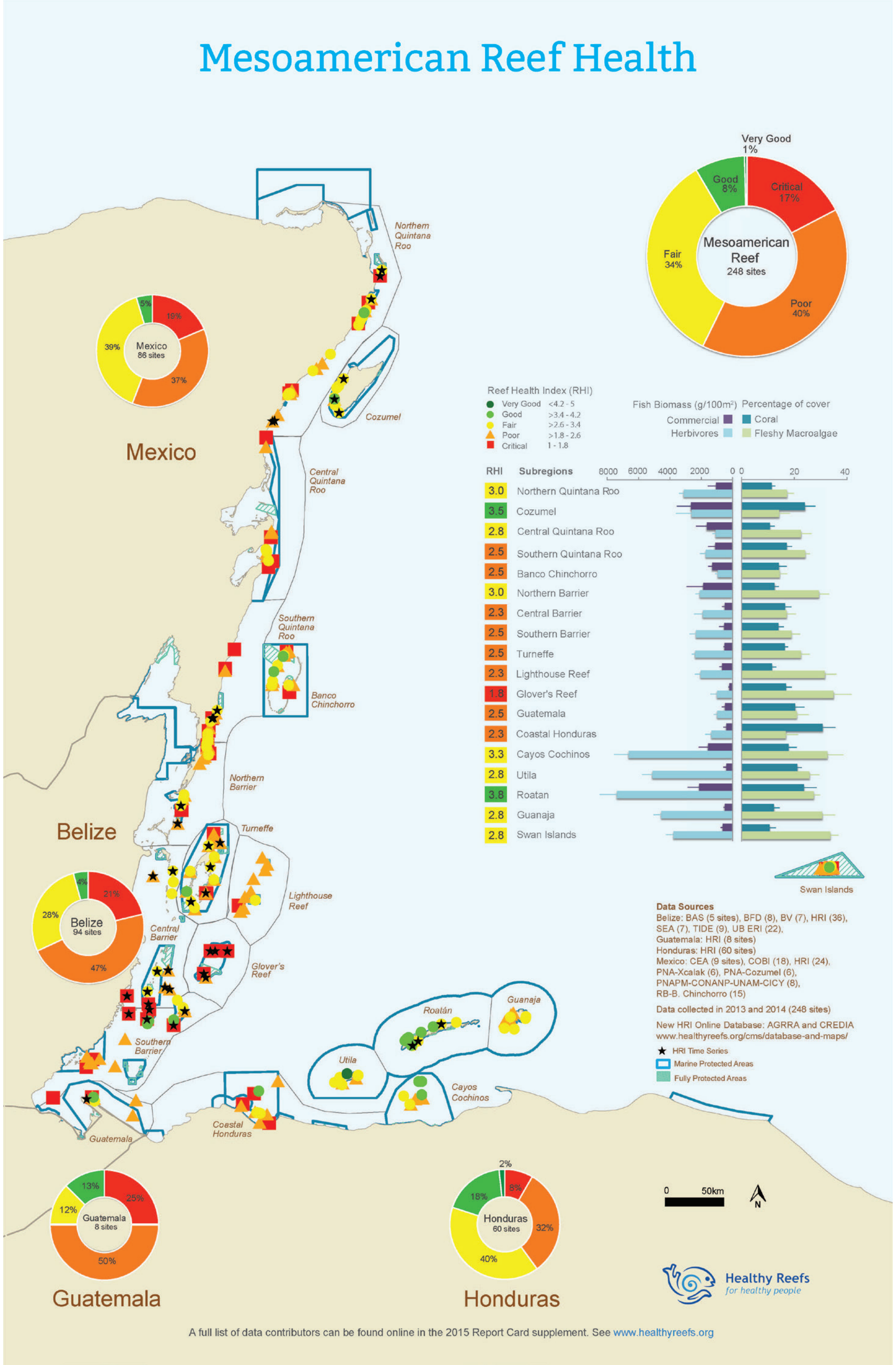
Some fisheries and herbivorous species (e.g. snappers and parrotfishes) also group together in feeding, resting or nursery areas (e.g. Nagelkerken *et al*. 2001). For example, some species use different habitat types (i.e. mangroves and seagrasses) as nursery areas before moving to their adult habitat on coral reefs (e.g. some parrotfishes, grunts, snappers, surgeonfishes, jacks, barracuda, groups, goatfishes and wrasses: reviewed in Green *et al*. 2014b). Other species use different depths or zones on coral reefs at different stages in their life history (e.g. some jacks, butterflyfishes, surgeonfish and sharks: reviewed in Green *et al*. 2014b).

Several studies have also demonstrated that three commercially important fisheries species on the MAR use different habitats as nursery areas (Table 2). For example, both Caribbean spiny lobsters and Nassau grouper settle onto nearshore hard bottom areas with small shelters, seagrass or macroalgae, often in mangrove areas, before moving to patch and fore reefs as they grow (Table 2). Queen Conch settle onto sand banks and in macroalgae, before moving to their juvenile and adult habitats in seagrass beds (Table 2). In some cases, the value of specific areas as a nursery may be influenced by seascape features such as the distribution of these habitats relative to each other, sources of larvae or other ecological processes affecting growth and survival (e.g. Acosta 1999, Stoner 2003, Adams *et al*. 2006).

These ontogenetic shifts in habitat use have important consequences for the structure of coral reef assemblages and populations of key species (Nagelkerken 2007). For example, Mumby *et al*. (2004) demonstrated that the presence of juvenile habitat (mangroves) in the vicinity of coral reefs exerted a profound impact on community structure by elevating the adult biomass of parrotfishes, grunts and snappers on reefs in the MAR (Belize and Mexico). Furthermore, they demonstrated that the largest herbivorous fish in the Caribbean, the rainbow parrotfish *Scarus guacamaia*, is functionally dependent on mangroves and has suffered local extinctions after mangrove removal (Mumby *et al*. 2004).

Therefore, it is important to protect the range of habitats that species use throughout their lives in RZs, particularly areas used during critical life history phases (particularly FSAs and nursery areas: Adams *et al*. 2011, Gaines *et al*. 2010, Rhodes *et al*. 2012, Green *et al*. 2014a, b). If the temporal and spatial location of these areas is known, they should be protected in RZs (Gaines *et al*. 2010, Rhodes *et al*. 2012, Dahlgren *et al*. 2016: see also Seasonal Closures in *Allowing Time for Recovery*). If the location of these areas is unknown, or the scale of movement is too large to include in individual RZs (e.g. spawning migrations of Nassau grouper), they should be protected within a network of RZs 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, Dahlgren *et al*. 2016).

Figure 6. Blue Hole, Belize (top); Whitelined Toadfish, an endemic species of Cozumel (Mexico) and Belize (middle: © Humann and Deloach 2014); and whale shark, Isla Mujeres, Mexico (bottom: © Elena Nalesso).



Data Sources
Belize: BAS (5 sites), BFD (8), BV (7), HRI (36), SEA (7), TIDE (9), UB ERI (22),
Guatemala: HRI (8 sites)
Honduras: HRI (60 sites)
Mexico: CEA (9 sites), COBI (18), HRI (24), PNA-Xcalak (6), PNA-Cozumel (6), PNAPM-CONANP-UNAM-CICY (8), RB-B. Chinchorro (15)

Data collected in 2013 and 2014 (248 sites)

New HRI Online Database: AGRRA and CREDIA
www.healthyreefs.org/cms/database-and-maps/

A full list of data contributors can be found online in the 2015 Report Card supplement. See www.healthyreefs.org

Figure 7. Mesoamerican Reef Health, showing areas that range from critical to very good condition (Kramer *et al.* 2015).

Protecting special and unique areas

Special and/or unique areas should also be included in RZs to ensure that all examples of biodiversity are protected (Jones *et al*. 2007, McLeod *et al*. 2009, Green *et al*. 2014a). These areas are important to protect because they include unique biodiversity, important habitats for species that are more vulnerable to extinction or habitats that have a higher likelihood of persisting in future. On the MAR these areas include:

- Areas with unique geological features (e.g. blue holes: Figure 6), assemblages and populations.
- Areas with high endemism (species with restricted distribution: Figure 6).
- Areas that have high abundance of rare or threatened species (e.g. see Miloslavich *et al*. 2010).
- Areas that appear to be particularly healthy and resilient (see Figure 7).
- Areas that have high habitat complexity, which are generally associated with higher fish diversity, greater abundance of key species, higher abundance of small-bodied fish and longer food chains (Rios–Lara *et al*. 2007, Wilson *et al*. 2010, Alvarez-Filip *et al*. 2011).

Some rare and threatened species also aggregate and use habitats that are crucial to their population maintenance (e.g. sea turtle and crocodile nesting areas, manatee habitat, cetacean migratory corridors and calving grounds, and whale shark feeding areas: Figure 6). These areas should be protected in RZs used in combination with other management approaches (e.g. hunting regulations and restrictions on the use of nets in cetacean migratory corridors).

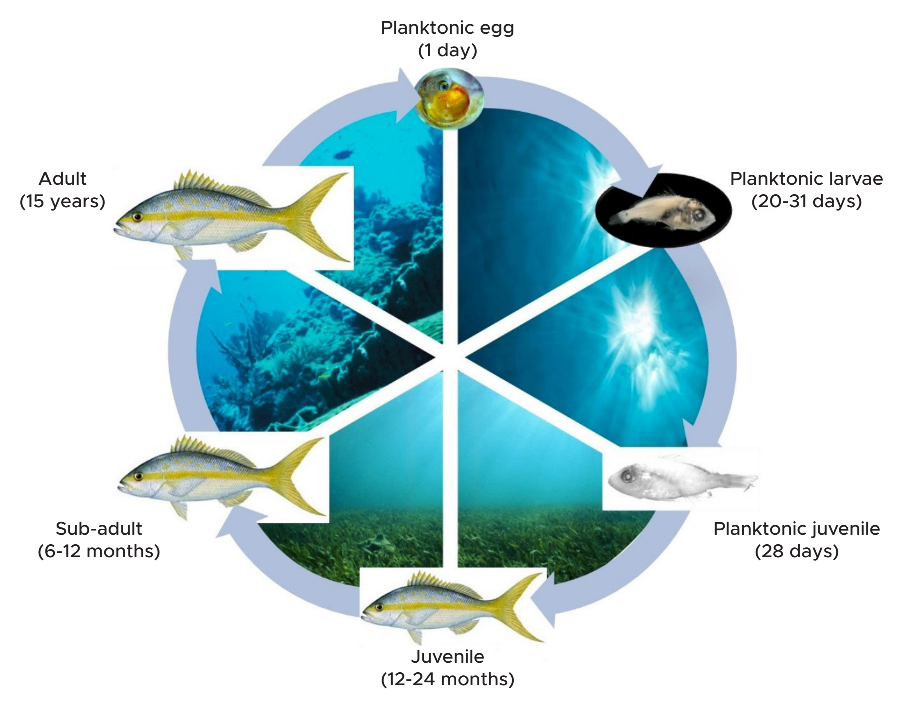


Figure 8. The yellowtail snapper's life cycle and shifts in habitat use with growth and size (Mumby *et al*. 2014a).

Incorporating Connectivity

Connectivity (the demographic linking of local populations through the dispersal of individuals as adults, juveniles or larvae: Jones *et al*. 2009) is an important factor to consider in designing networks of RZs, since it has important implications for the persistence of metapopulations and their recovery from disturbance (Botsford *et al*. 2003, McCook *et al*. 2009, Green *et al*. 2014a, b).

Most coral reef and coastal pelagic marine species have a bipartite life cycle where the larvae are pelagic before settling out of the plankton and spending the rest of their lives more closely associated with the benthos (Figure 8). Species vary greatly in how far they move during each life history stage (Palumbi 2004), although larvae of most species tend to move longer distances (10s-100s of km) than adults and juveniles that tend to be more sedentary (see review in Green *et al*. 2014b). Exceptions include species where adults and juveniles exhibit large-scale ontogenetic habitat shifts (where juveniles use different habitats than adults) or spawning migrations (10s-100s km), and pelagic species that move very long distances (100s to 1,000s of km: see review in Green 2014a, b).

When adults and juveniles leave a RZ, they become vulnerable to fishing pressure, while larvae leaving a RZ can generally disperse without elevated risk because of their small size and limited exposure to the fishery (Gaines *et al*. 2010). Therefore, for RZs to protect biodiversity and enhance populations of species in heavily fished areas, they must be able to sustain adults and juveniles of focal species (particularly fishery species) within their boundaries, and be located so they can function as mutually replenishing networks of larvae while providing recruitment subsides to fished areas (see reviews in Green *et al*. 2014a, b).

Therefore, movement patterns of focal species at each stage of their life history is an important factor to consider in designing networks of RZs (Bostford *et al*. 2003, Palumbi 2004, Green *et al*. 2014a, b). Where movement patterns of focal species are known, this information can be used to define the configuration (size, shape and location) of RZs to maximize benefits to both fisheries and conservation (Hastings and Bostford 2003, see review in Green *et al*. 2014a, b).

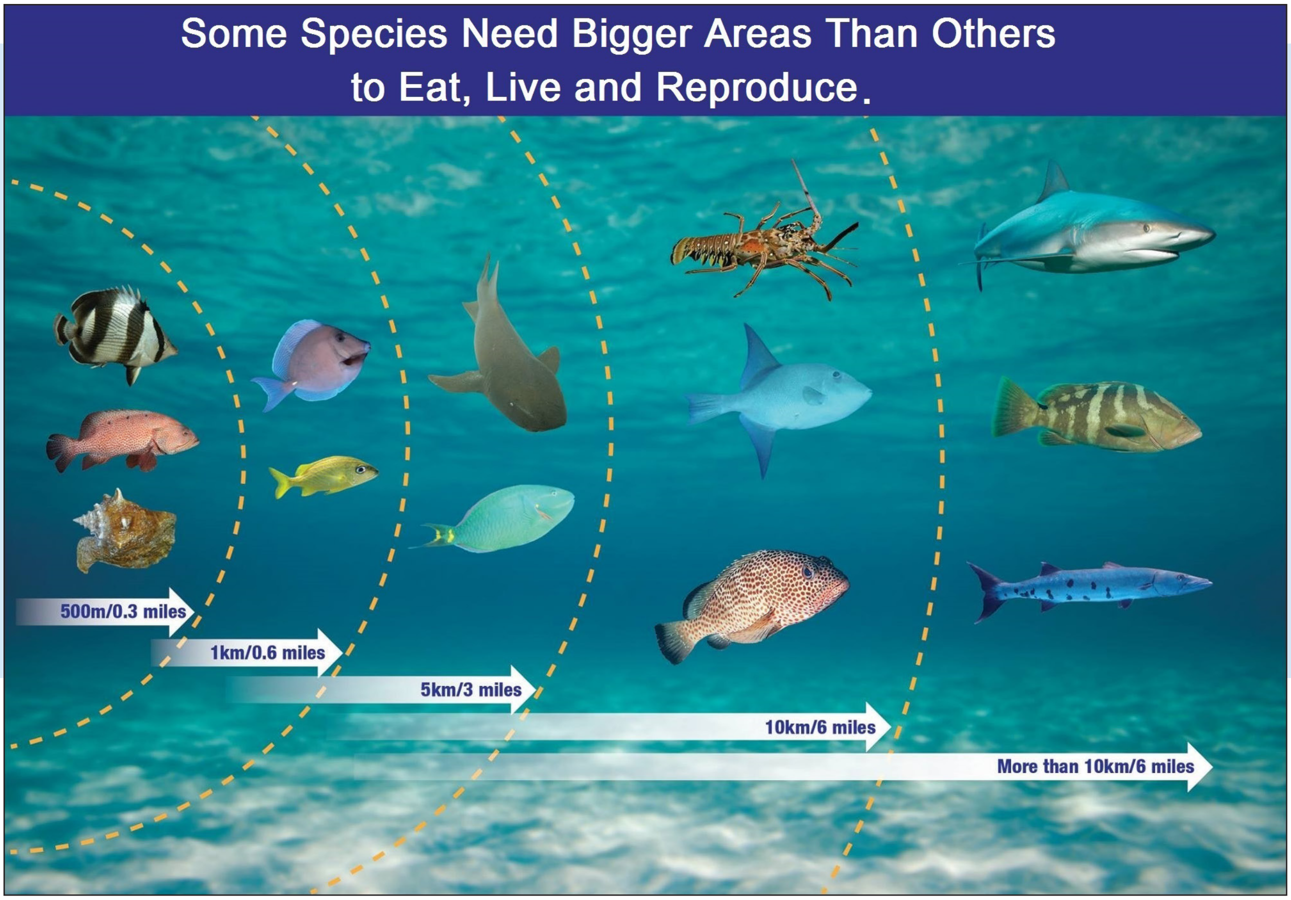


Figure 9. Replenishment zones should be more than twice the size of the home range of focal species for protection, and integrated with other fisheries management tools to manage wide ranging species that cannot be protected within their boundaries. [Poster modified from "The Bahamas Protected MPA Infographic Series 2017", where movement distances are from Green *et al.* (2014, this report)].

Consider movement patterns of adults and juveniles of focal species when determining the size of RZs

RZs should be more than twice the size of the home range of adults and juveniles of focal species for protection; and RZs must be integrated with other fisheries management tools to manage wide ranging species that cannot be protected within RZs.

For RZs to protect biodiversity and contribute to fisheries enhancement outside their boundaries, they must be large enough to sustain fisheries species within their boundaries during their adult and juvenile life history phases (Palumbi 2004, Gaines *et al*. 2010, Green *et al*. 2014a, b). This allows for the maintenance of spawning stock, by allowing individuals in RZs to grow to maturity, increase in biomass and reproductive potential, and contribute more to stock recruitment and regeneration (Russ 2002, Green *et al*. 2014a, b).

Where movement patterns of focal species are known, they can be used to identify the minimum recommended size of RZs (Green *et al*. 2014, b). For example, Green *et al*. (2014b) provided a global review of movement patterns (e.g. home ranges, ontogenetic shifts and spawning migrations) of 34 families and 210 species of coral reef and coastal pelagic fishes (including 29 families and 81 species of Caribbean species), and used this information to provide recommended minimum size of RZs for these species based on the movement patterns of adults and juveniles. Green *et al*. (2014b) recommended that RZs should be more than twice the size of the home range of focal species for protection (Green *et al*. 2014b). However, it is important to note that these minimum size recommendations must be applied to the specific habitats that the focal species use (in all directions), rather than the overall size of the RZ (Green *et al*. 2014a, b). Ideally this sort of analysis should be combined with knowledge of key factors that influence movement patterns (e.g. size, sex, behaviour, density, habitat characteristics, season, tide and time of day), and how individuals are distributed to determine how many in-

Table 3. **Movement patterns of three focal fisheries species on the MAR**

Species	Movement Type	Distance	Source
Queen Conch	Daily (home range)	0.012-0.25 km (0.005-0.06 km^2)	Delgado and Glazer 2007, Bissada-Gooding and Oxenford 2009, Glazer *et al*. 2013
	Ontogenetic shifts	~ 0.4-0.7 km	Peel and Aldana Aranda 2012
	Seasonal (spawning)	0.17-0.4 km	Hesse 1979, Stoner and Sandt 1992
Spiny Lobster	Daily (home range)	0.2-1 km; up to 3-7 km over longer times (0.09-1 km^2)	Davis 1977, Acosta 2002, Bertelsen and Hornbeck 2009
	Ontogenetic shifts	1-10 km; max 210 km	Davis 1977, Davis and Dodrill 1989, Dahlgren *unpubl*. data
	Seasonal (spawning)	0.5-10 km	Herrnkind *et al*. 1973, Davis 1977, Bertelsen and Hornbeck 2009, Bertelsen 2013, Dahlgren *unpubl*. data
Nassau grouper	Daily (home range)	0.1-0.2 km (~0.018 km^2)	Bolden 2001
	Ontogenetic shifts	1-10km; max 20 (estimated)	Dahlgren *unpubl*. data
	Seasonal (spawning)	20-250 km	Bolden 2000, Semmens 2006, Starr *et al*. 2007, Dahlgren *et al*. 2016

dividuals a RZ of a specific size will protect (Green *et al*. 2014b).

Species whose movement patterns are larger than the size of RZs will only be afforded partial protection, although RZs can provide benefits for these species if they protect specific locations where individuals aggregate and become especially vulnerable to fishing mortality (e.g. FSAs: see *Protecting Critical, Special and Unique Areas*). Thus, RZs will need to be integrated with other fisheries management tools to manage wide ranging species that cannot be protected within the boundaries of RZs (Green *et al*. 2014a, b).

To facilitate using this approach for the MAR, we've provided the best available information on movement patterns of Caribbean species, which field practitioners can use to determine the size of their RZs based on the movement patterns of focal species. To do this we used the movement information provided by Green *et al*. (2014b) for Caribbean fish species, and added new information for Nassau grouper and bonefish (see *Appendix III*, Figure 9 and Table 3). Some Caribbean fish species move <0.1–0.5 km (e.g. some angelfishes, surgeonfishes, parrotfishes, groupers, grunts, jacks and goatfishes) or 0.5–3 km (e.g. some surgeonfishes, groupers, grunts, drummers, snappers and parrotfishes), while others move tens to hundreds (e.g. some groupers, jacks, bonefishes, mackerel, barracudas, snappers, parrotfishes, sharks and rays) or thousands of kilometres (e.g. some sharks, tuna and billfishes). Therefore, RZs of different sizes are likely to benefit different species.

We also adapted this approach to include movement data for two commercially important invertebrates: queen conch and spiny lobsters (Table 3). Queen conch do not move very far, moving less than 0.3-0.7km on a daily basis (i.e. their home ranges) or during ontogenetic shifts and spawning movements (Table 3). Therefore, small to moderately sized RZs (<1-2 km across) are likely to benefit this species. In contrast, spiny lobsters have home ranges of <7km and move longer distances during their ontogenetic shifts and spawning migrations (<10 to 210 km: Table 3). Therefore, larger RZs will be required for spiny lobsters (i.e. 14 km across to protect their home ranges), which need to be combined with other

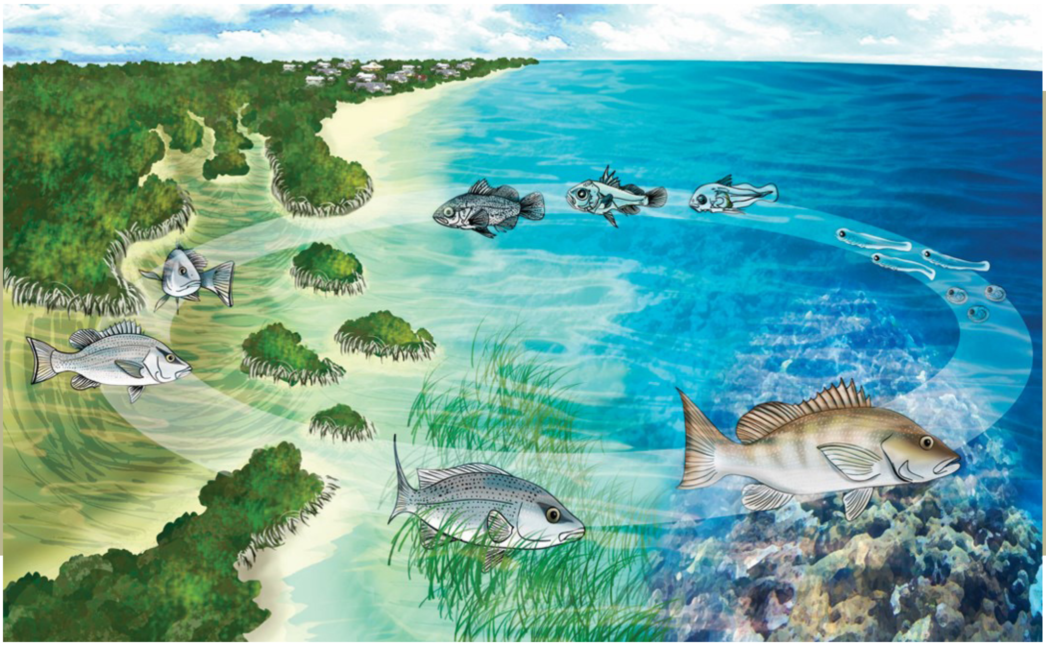


Figure 10. Gray snapper use different habitats throughout their lives (Brumbaugh 2014).

management tools (e.g. seasonal closures) to manage this species while they are undergoing ontogenetic shifts or spawning migrations outside of RZs.

Research priorities include developing a common list of focal species that are significant for the entire region, and conducting empirical studies of movement patterns of focal species required to refine this approach in the MAR.

Ensure RZs are close enough to allow for the movement of focal species between habitats used throughout their life cycle.

Some species use different habitats throughout their lives (e.g. for home ranges, nursery and spawning areas: reviewed in Green *et al*. 2014b). Thus, the location of RZs should be informed by the distribution of key habitats used by focal species, and the movement patterns of adults and juveniles among these habitats (e.g. via ontogenetic habitat shifts or spawning migrations: Figure 10, Green *et al*. 2014b) to include all of the habitats required by these species to complete their life cycles.

For example, some coral reef species undergo ontogenetic shifts where they use different habitat types (e.g. mangroves and seagrasses) as nursery grounds before moving to their adult habitat on corals reefs (Figure 10: reviewed in Green *et al*. 2014b, see *Protecting Critical, Special and Unique Areas*).

To provide adequate protection for species that undergo these ontogenetic habitat shifts, each habitat utilized by juveniles and adults should be protected within individual RZs. If this is not possible (e.g. for long distance ontogenetic movements that can't be accommodated within individual RZs), the different habitats that focal species use at different times can be protected within multiple smaller RZs, provided that the location of these RZs allows for ontogenetic movements of focal species among protected habitats (Green *et al*. 2014).

For species that undertake spawning migrations, like many economically important grouper and snapper species (see *Protecting Critical, Special and Unique Areas*), it is important to protect fish spawning aggregations (FSAs), migratory corridors and staging areas, in addition to protecting the home range of a sufficiently

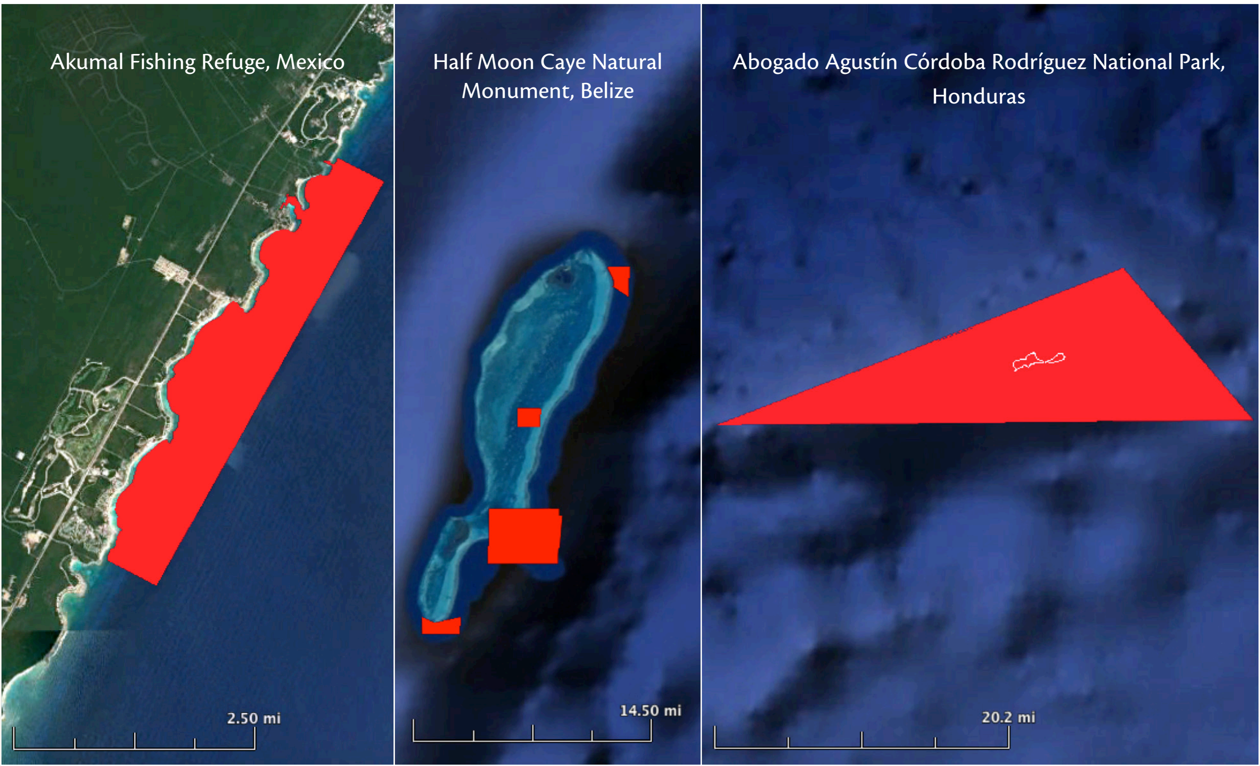


Figure 11. Examples of: an elongated RZ based on reef shape in Mexico (left); a RZ with a compact shape in Belize (middle); and a RZ covering the entire reef system in Honduras (right).

large proportion of their population (Rhodes and Tupper 2008, Rhodes *et al*. 2012). If the temporal and spatial location of these critical areas is known, they should be protected in RZs (Zeller 1998, Sadovy and Domeier 2005, Rhodes & Tupper 2008, Rhodes *et al*. 2012). If the location of these areas is not known, or if their scale of movement is too large to include in individual RZs (e.g. long distance spawning migrations), other management actions will be required (e.g. seasonal closures: Dahlgren *et al*. 2016, see *Allowing Time for Recovery*).

RZs should include, where possible, entire ecological units.

Including whole ecological units (e.g. offshore reefs or mangrove forests) in RZs (McLeod *et al*. 2009, Green *et al*. 2014a: Figure 11), helps maintain the integrity of RZs, since many species are likely to stay within their preferred habitat type (Chapman and Kramer 2000, Farmer and Ault 2011).

Design RZs using compact shapes rather than elongated ones.

In places where RZ boundaries are heavily fished, compact RZ shapes (e.g. squares: Figure 11) should be used because they minimize edge effects by limiting the spillover of adults and juveniles more than other shapes (e.g. elongated ones such as long thin rectangles). This helps maintain the integrity of RZs, and therefore the sustainability of their contribution to biodiversity protection, fisheries production and ecosystem resilience (IUCN-WCPA 2008, McLeod *et al*. 2009, Green *et al*. 2013, 2014a, b).

An exception may be where the habitats to be protected are naturally long and elongated themselves. For example, many sections of the Mexican MAR are characterized by a linear coast and reefs and steep bathymetry, in which case elongated shapes might be more desirable (Figure 11).

Design a network of RZs to maintain larval connectivity within and among RZs, and to maximize dispersal to fishing areas.

Most marine species release fertilized gametes to the water column (Figure. 8) where they are dispersed by wind drift, wave drift, ocean currents and mesoscale oceanic eddies. These passively transported eggs metamorphose into mobile larvae that are also transported by water movement, but have the ability to actively modify their vertical and horizontal positions to some extent. This large-scale movement of propagules makes connectivity between spawning and nursery areas a key element to consider in the design of networks of RZs, and is perhaps the most important scientific gap in marine protected area network design (Heyman *et al*. 2008).

For populations 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). Where lesser levels of dispersal may play an important role in helping populations recover after disturbance (seeding dispersal), they are not sufficient to sustain populations over time.

In heavily fished areas where there is little or no reproduction outside RZs, population persistence of focal species within RZs depends upon recruitment to local populations in one of two ways through:

1. Self-persistence where populations in individual RZs are self-sustaining through larval retention (where >10-20% of larvae return to their natal source: Gaines *et al*. 2010), which is more likely where RZs are large (Botsford *et al*. 2014, Green *et al*. 2014b). However, even small RZs can provide recruitment benefits within and close to their boundaries where self-recruitment is common (e.g. for coral reef fishes: Jones *et al*. 2007, Green *et al*. 2014a, b).
2. Network persistence where populations of focal species are sustained within a network of RZs that cover an adequate fraction of the habitat (see *Habitat Representation*), where each RZ contributes to the growth rate of the metapopulation (Gaines *et al*. 2010, *Botsford et al*. 2014). In this situation, larval connectivity among RZs allows the population distributed across the entire network to be sustained even when individual RZs are too small to be self-sustaining (see Botsford *et al*. 2014).

Where fishing pressure is low or the fishery is well managed (at or below Maximum Sustainable Yield), larval input from fished areas can be important in ensuring persistence of a species and must also be considered in the design process (Botsford *et al*. 2014).

A network of RZs that produces fisheries benefits should balance two different objectives: ensure enough larvae remains in the network so it is self-sustained or persistent, and maximize the movement of larvae to fishing grounds to benefit the fishery through larval spillover (Hastings and Botsford 2003). Both persistence and spillover depend on the connectivity patterns of the region of interest, but the configuration of a network of RZs that maximizes either one of these objectives will frequently not be the best design to maximize

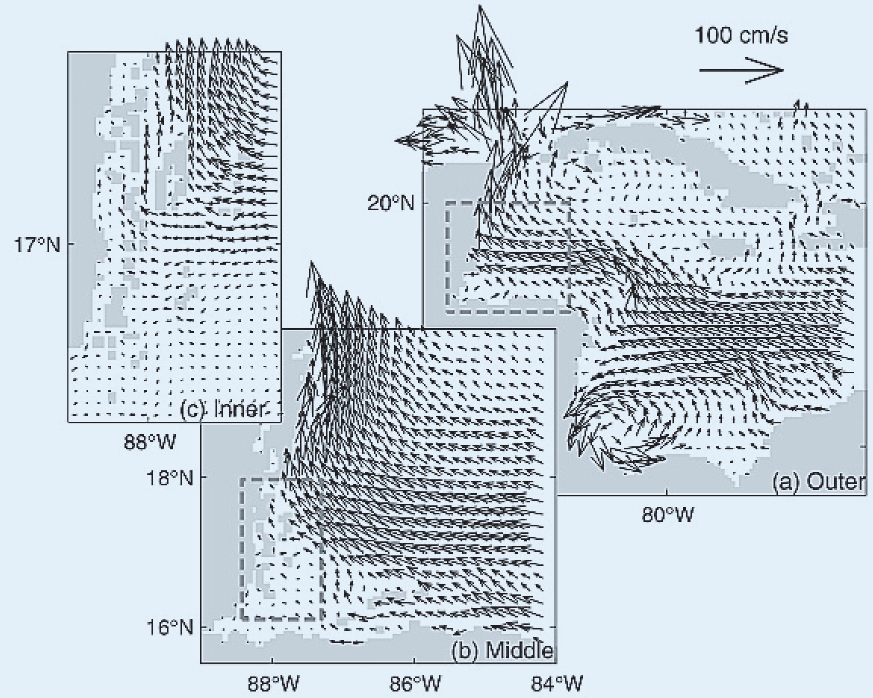


Figure 12. Mean near-surface currents in the MAR at three levels of spatial detail (Tang *et al.* 2006)

the other (Hastings and Botsford 2003, Lester *et al*. 2013, Chollett *et al*. *in press*) and both need to be considered explicitly in marine spatial planning. Therefore (where possible), comprehensive and detailed spatial models of population persistence of focal species should be used that take all relevant factors into account (including larval dispersal and fishing pressure) to determine the optimal configuration for networks of RZs that will produce both conservation and fisheries benefits (Botsford *et al*. 2014).

To date there has been a great deal of research in the Caribbean that has made advances towards understanding its oceanographic (e.g. Richardson 2005, Alvera-Azcárate *et al*. 2009) and larval connectivity patterns, either using larval dispersal models (e.g. Cowen *et al*. 2006, Schill *et al*. 2015) or genetic data (e.g. Foster *et al*. 2012, Jackson *et al*. 2014). Specific work on the MAR has elucidated its complicated oceanographic patterns either using drifters (e.g. Ezer *et al*. 2005, Tang *et al*. 2006, Carillo *et al*. 2015: Figure 12) or satellite ocean colour data (e.g. Sheng *et al*. 2007, Soto *et al*. 2009). There have been also some efforts in identifying connectivity pathways from genetic data but these lack the comprehensive coverage throughout the region that would be required for marine spatial planning (e.g. Sánchez *et al*. 2014, Truelove *et al*. 2015).

Recently, methods have been developed to balance the influence of larval dispersal patterns in both conservation and fisheries objectives when designing networks of RZs (Rassweiler *et al*. 2014, Chollett *et al*. *in press*). For example, Chollett *et al*. (*in press*) used modelled larval dispersal data for spiny lobster for planning for a network of RZs in Eastern Honduras that will ensure both fisheries benefits and the sustainability of the resource, using data sources and approaches that are transferable to the MAR. These approaches, however, only consider modelled connectivity data (which is a proxy for real connectivity patterns), and do not include any other elements into the design (e.g. trade-offs with other uses).

Although there are several sources of connectivity data in the MAR, and there are presently tools to design networks of RZs to maintain larval connectivity within and among the network and to maximize dispersal to fished areas, further studies are required before a particular approach can be used in the region. Research priorities include:

1. Reviewing all previous studies of oceanographic connectivity, larval dispersal modelling and genetic connectivity in the MAR;
2. Assessing the potential and value of combining these three types of data to inform marine spatial planning; and
3. Using region specific data (Steps 1 and 2) to identify the best approach for using larval dispersal to design a network of RZs for the MAR to ensure fisheries benefits and resource sustainability.

Allowing Time for Recovery

RZs should be in place permanently to allow for the population recovery of all focal species, and to enhance fisheries production in the long term.
Seasonal RZs can be used to protect focal species during critical life stages (e.g. in spawning and nursery areas).

Recovery in RZs can be achieved in several ways depending on management objectives. For example, recovery of marine populations for biodiversity protection may be achieved when populations have reached their full carrying capacity (Abesamis *et al*. 2014), or when they have recovered to 90% of their unfished biomass (MacNeil *et al*. 2015). Alternatively, recovery of marine populations for fisheries management could be achieved when they have recovered to a level where they can sustain fishing pressure (e.g. where 35-40% of unfished stock levels of reproductive biomass are protected to ensure adequate replacement of stocks for a range of species: Botsford *et al*. 2001, Fogarty and Botsford 2007, FAO 2011). Another approach is to assess recovery in terms of when populations have recovered enough to maintain their functional role in the ecosystem (e.g. see Mumby *et al*. 2013, MacNeil *et al*. 2015, McClanahan *et al*. 2015).

Species differ in their intrinsic vulnerability to fishing and their rates of population recovery after fishing ceases in RZs (reviewed in Abesamis *et al*. 2014; Figure 13). Many factors influence the recovery times of marine populations including their life history characteristics (e.g. maximum body size, individual growth rate, longevity, age or length at maturity and rate of natural mortality) and trophic level (Abesamis *et al*. 2014). Therefore, populations of larger-bodied carnivorous species (e.g. groupers, snappers and jacks) tend to take longer to recover than smaller-bodied species lower in the food web (e.g. planktivores and herbivores: Abesamis *et al*. 2014). The rate of population recovery also depends on the species composition of local ecosystems, the size of the RZ, habitat type and quality, local productivity, the size of the remaining population, the reduction of mortality due to fishing, predator-prey and competition dynamics, recruitment variation and metapopulation structure (Abesamis *et al*. 2014).

Empirical data from long term monitoring (> 40 years) has demonstrated how long term protection in RZs is necessary for all groups of coral reef fishes to recover to their full carrying capacity after overexploitation (reviewed in Abesamis *et al*. 2014). For example, in heavily fished areas in the Philippines, populations of planktivores (e.g. fusiliers) and some herbivores (e.g. parrotfishes) recovered in <5–10 years in RZs, however populations of large predators (e.g. groupers and snappers) took 20-40 years to recover (Stockwell *et al*. 2009, Russ and Alcala 2010). Faster recovery rates have been recorded in RZs where fishing pressure is lower (e.g. Great Barrier Reef and Papua New Guinea: Russ *et al*. 2008, Hamilton *et al*. 2011), while longer recovery rates have been

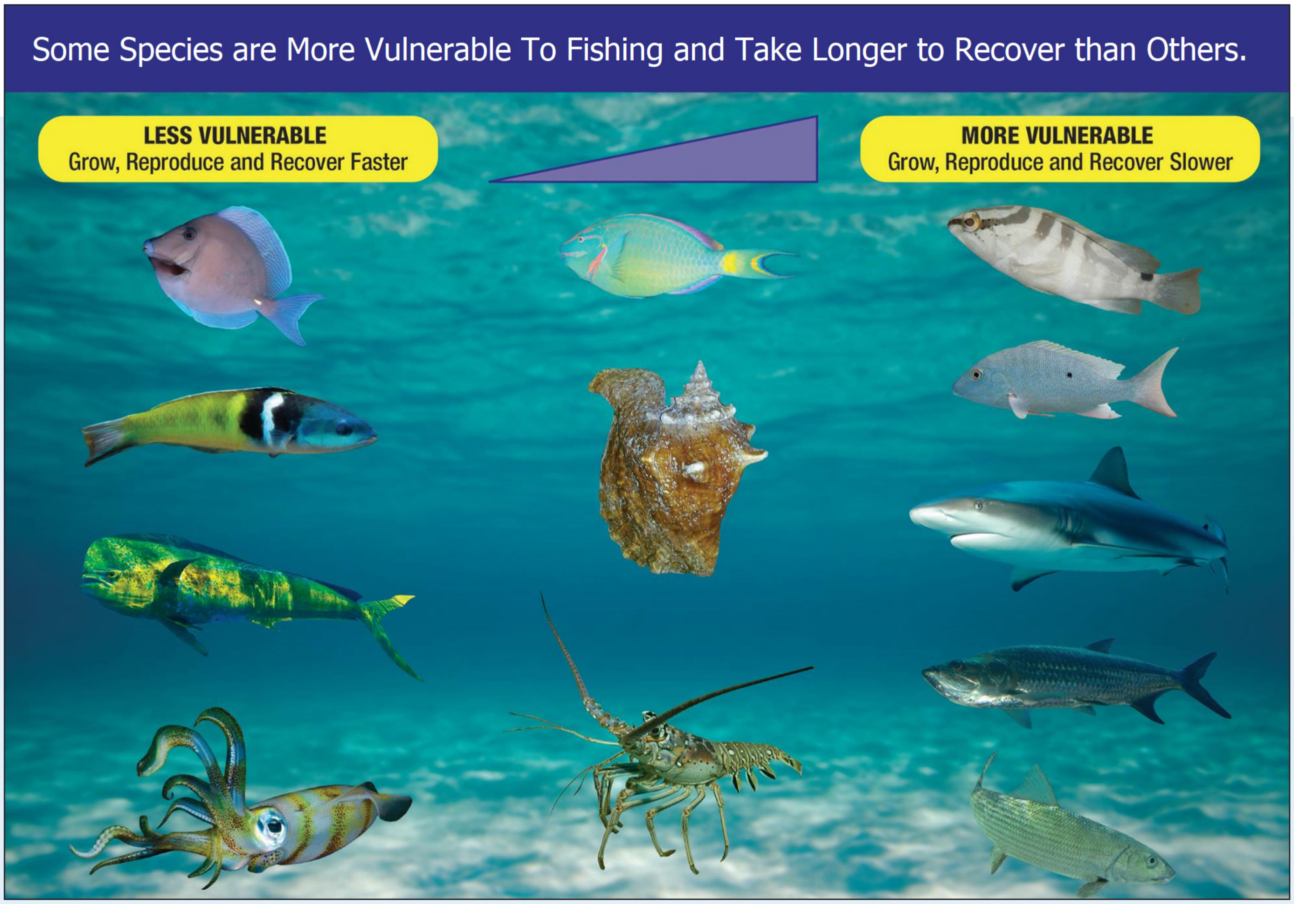


Figure 13. Replenishment zones should be in place permanently to allow for population recovery of all focal species, and to enhance fisheries production in the long term. [Poster developed by "The Bahamas Protected MPA Infographic Series 2017", based on population doubling times reported by www. fishbase.org].

recorded in other heavily fished areas (e.g. parrotfish populations took 20-25 years to recover in Kenya: McClanahan *et al*. 2007).

Empirical data on recovery times of focal species in RZs on the MAR are limited, although they do provide some useful insights. For example, Polunin & Roberts (1993) showed a greater abundance, size or biomass of 23% of fished species (e.g. some snapper, parrotfishes and surgeonfishes) in Hol Chan RZ in Belize after four years of protection.

Limited monitoring data is also available for elsewhere in the region. For example, the Exuma Cays Land and Sea Park is one of the largest RZs (456 km^2) in the Caribbean, and monitoring showed that within 8 years of protection (starting in 1986): Nassau grouper abundance was 1.7-2 times higher in the Park than in fished areas; conch density was ~10 times higher inside the Park, and spiny lobster density was ~4 times greater than in similar habitats elsewhere (Dahlgren 2004 and references therein). Similarly, conch populations in RZs within the Glover's Reef Marine Reserve in Belize increased 4-5x their density from 1997-2000, but populations in fished areas decreased on average (Acosta 2006).

Other studies in the region have also demonstrated that parrotfish populations were able to recover within six to seven years (in terms of biomass and sex ratios) after they were effectively protected by a trap fishing ban in Bermuda in 1990 (O'Farrell *et al*. 2015a, b).

Since long term monitoring data of focal species in RZs in the region is limited, it is unclear how long full recovery of all focal species is likely to take. Although based on experiences in other coral reefs ecosystems around the world (see above), recovery of all focal species within RZs in the MAR is likely to take decades (>20-40 years).

Therefore, long-term protection in RZs will be required for all species to grow to maturity, increase in biomass and contribute more, and more robust, eggs and larvae to replenish populations, enhance adjacent fisheries, and maintain ecosystem health and resilience (reviewed in Abesamis *et al*. 2014, Green *et al*. 2014a) in the MAR. Permanent protection will ensure that these benefits are maintained over the long-term (Russ and Alcala 2004, Hart 2006, Kaplan *et al*. 2010). Strict enforcement will also be necessary to guarantee full recovery to maximise the benefits within and adjacent to RZs (Abesamis *et al*. 2014).

Short-term (< 5 years) or periodically harvested RZs are sometimes used for fisheries management. In other regions of the world (e.g. in Papua New Guinea and Solomon Islands) periodically harvested RZs are used to address particular management needs, e.g. where communities wish to stockpile fisheries resources for feasts or to close areas to fishing for cultural reasons (Foale and Manele 2004). In Guatemala, short-term (5 years) RZs are currently being implemented inside Punta de Manabique Wildlife Refuge, under the assumption that these will promote the sustainability of fisheries resources. However, while these closures may provide short-term benefits for some species and communities, they have limited benefits for conserving biodiversity, providing long term fisheries benefits or building resilience, where the aim is to build and maintain healthy, natural communities and sustain ecosystem services (Jupiter *et al*. 2012, Abesamis *et al*. 2014, Green *et al*. 2014a). This is because the benefits of short-term or periodic RZs are quickly lost when the RZs revert to open access unless fisheries are managed very carefully to ensure that the amount harvested is less than the amount built-up during protection (Jupiter *et al*. 2012).

RZs should therefore be in place permanently. Short-term RZs are not recommended as they only provide limited benefits to some species in the short term, which are quickly lost once these areas are opened for fishing unless they are very carefully managed (which is seldom the case). Therefore, if short term RZs are used, they should be used in addition to, rather than instead of, permanent RZs. The exception is seasonal closures to protect critical areas at critical times (e.g. FSAs or nursery areas), which can be very important to protect or restore populations of focal fisheries species (see *Protecting Critical, Special and Unique Areas*).

Long term monitoring (>20-40 years) is now required to understand more about recovery rates of all focal species within RZs, which can be used to provide reasonable expectations regarding the time frames required to see the full benefits of RZs for biodiversity conservation and fisheries enhancement on the MAR.

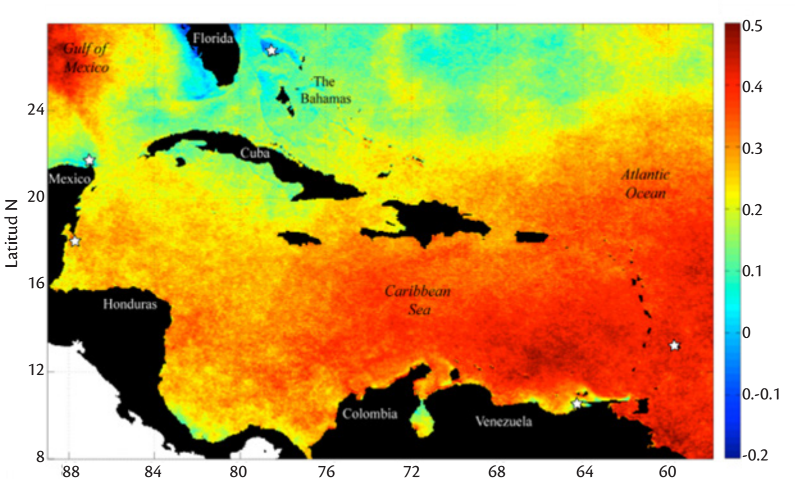


Figure 14. Trends in sea surface temperature in the Caribbean during the period 1985-2009 (satellite AVHRR pathfinder data: Chollett *et al.* 2012a)

Adapting to Changes in Climate and Ocean Chemistry

Address threats from rising sea temperatures and sea levels, and changes in ocean chemistry, by: increasing percent habitat representation; spreading the risk; and increasing protection of key species that increase ecosystem resilience.

Changes in climate (e.g. by rising sea temperatures and sea levels) and ocean chemistry represent a serious and increasing threat to tropical marine ecosystems worldwide (Burke *et al*. 2011). Of particular concern, is the increasing frequency and severity of mass coral bleaching 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 *et al*. 2007, Lovelock and Ellison 2007, Pandolfi *et al*. 2011). These threats may have serious consequences for marine habitats and species on the MAR, along with possible effects of climate change on rainfall patterns, ocean currents and storm intensity (CATIE and TNC 2012).

Increasing sea temperatures show large spatial heterogeneity in ocean warming at both the global (IPCC 2014) and Caribbean scale (Chollett *et al*. 2012a). In the Caribbean, warming has been fast within the period 1985-2009, averaging 0.29º/decade in the entire basin and about 0.20º/decade in the MAR, which is heating up in a relatively homogeneous way throughout the region (Chollett *et al*. 2012a: Figure 14).

Observed patterns of coral bleaching on the MAR have been highly spatially and temporally variable during the Caribbean-wide coral bleaching events in 1995, 1998, 2005, 2010 and 2015 (CARICOMP 1997, Goreau *et al*. 2000, Eakin *et al*. 2010, Kintisch 2010, Rivera-Sosa *et al*. 2016), with thermal stress and significant bleaching only being observed in MAR reefs after the 1998 event (Mumby 1999, Aronson *et al*. 2002). During each coral bleaching event, the driving forces influencing bleaching differ among locations, possibly due to differences in coral species and their vulnerability to bleaching or localized adaptations.

Ocean temperatures are predicted to increase in the future (IPCC 2014). Global, coarse (about 1 degree) climate models have been downscaled using statistical and dynamic approaches to produce projections as detailed as 11 km spatial resolution (e.g. Hooidonk *et al*. 2015). These projec-

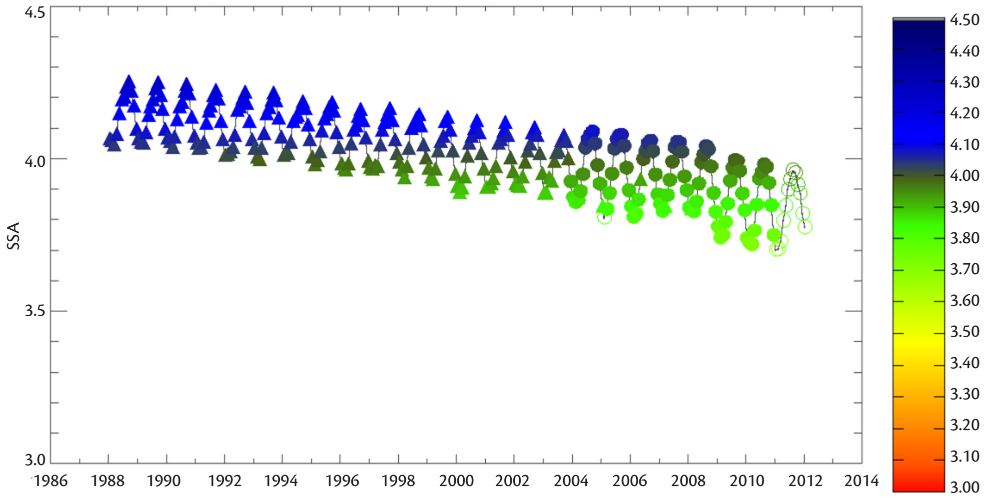


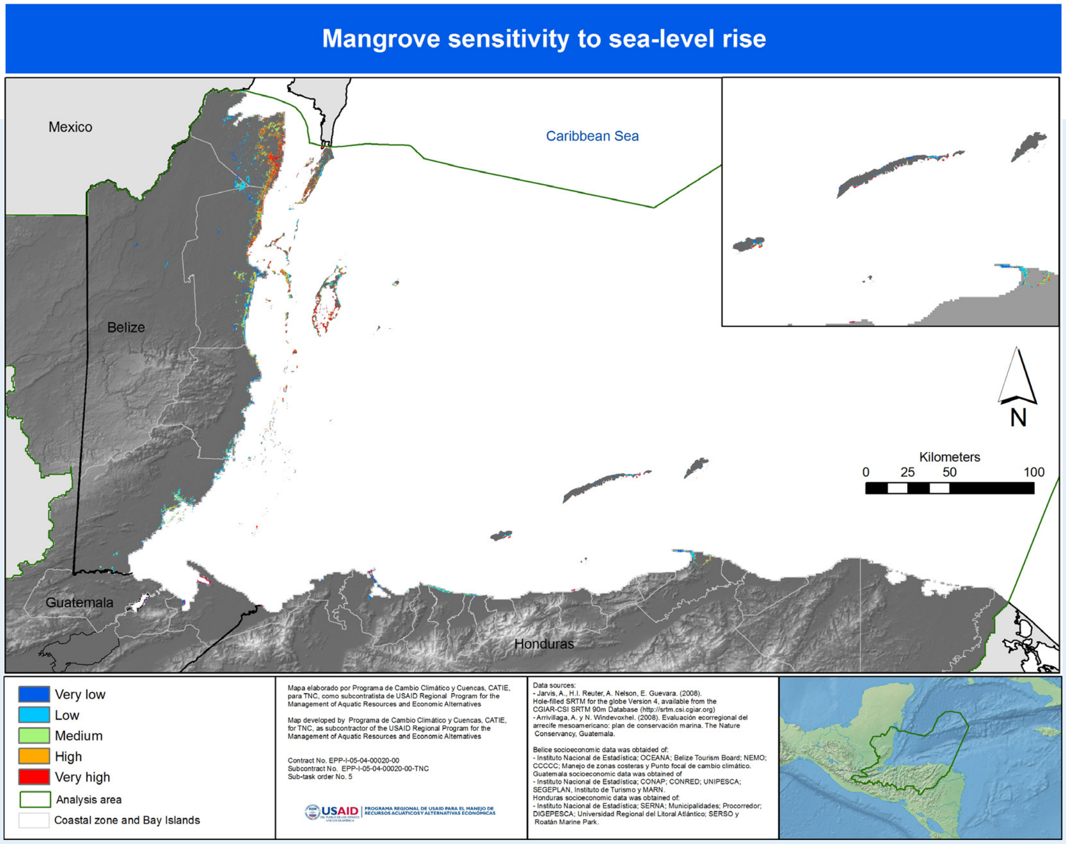
Figure 15. Time-series of average aragonite saturation state for the Greater Caribbean region (http://coralreefwatch.noaa.gov, accessed 24/08/2016)

tions could inform conservation planning in the region once the relevance and accuracy of the products is thoroughly assessed.

Patterns of change in ocean acidification have also been described at both the global (IPCC 2014) and Caribbean scale (Gledhill *et al*. 2008: Figure 15), which predict a strong decrease in aragonite saturation state (Ωarg) in the Caribbean at a rate of approximately -0.012 Ωarg/yr. pH and aragonite saturation state are predicted to further decrease in the future (IPCC 2014). However, to date, climate models only provide predictions at a coarse scale (1 degree), so it is unclear how this may affect habitats and species on the MAR at a spatial scale that is relevant for planning.

Predicting ecosystem responses to multiple climate change threats is a complex task, particularly because most studies of climate-related stress on marine ecosystems focus on experiments and specific stressors, organisms and/or physiological processes and then extrapolate to ecosystem scales (Mumby and van Woesik 2014). Some studies have included multiple aspects into models that predict ecosystem responses (e.g. Mumby *et al*. 2014b, Bozec *et al*. 2016). However, there is still a lot of uncertainty regarding how organisms modify their physical environment, the roles of indirect interactions among species, and how much scope there is for acclimation and adaptation which will modify the outcomes.

Research priorities for taking changes in climate and ocean chemistry into account in designing networks of RZs on the MAR in future include: assessing climate change models that are currently available, in terms of their relevance, accuracy, and usefulness for planning in the region; conducting additional field surveys during bleaching events, and producing an overall analysis of the bleaching data available not only to refine and validate the climate change models but to identify the sources of resistance and resilience to bleaching in the MAR; and using, expanding and validating models and approaches to identify habitats and species that are more or less threatened by changes in climate and ocean chemistry, so they can be used to prioritize areas for protection (e.g. Game *et al*. 2008, McLeod *et al*. 2009). For example, Mumby *et al*. (2014b) coupled a coral reef model with climate change predictions to map coral communities that are likely to be more vulnerable or resilient to climate change. The model was produced for Belize's reefs, and used the observed state of its reefs and current levels of environmental stress as inputs. These maps were then used to refine the design of a network of RZs in Belize to maximize the number



Mapa elaborado por Programa de Cambio Climático y Cuencas, CATIE, para TNC, como subcontratista de USAID Regional Program for the Management of Aquatic Resources and Economic Alternatives

Map developed by Programa de Cambio Climático y Cuencas, CATIE, for TNC, as subcontractor of the USAID Regional Program for the Management of Aquatic Resources and Economic Alternatives

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Subcontract No. EPP-I-05-04-00020-00-TNC
Sub-task order No. 5

USAID | PROGRAMA REGIONAL DE USAID PARA EL MANEJO DE RECURSOS ACUÁTICOS Y ALTERNATIVAS ECONÓMICAS

Data sources:
- Jarvis, A., H.I. Reuter, A. Nelson, E. Guevara. (2008). Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database (http://srtm.csi.cgiar.org)
- Arrivillaga, A. y N. Windevoxhel. (2008). Evaluación ecorregional del arrecife mesoamericano: plan de conservación marina. The Nature Conservancy, Guatemala.

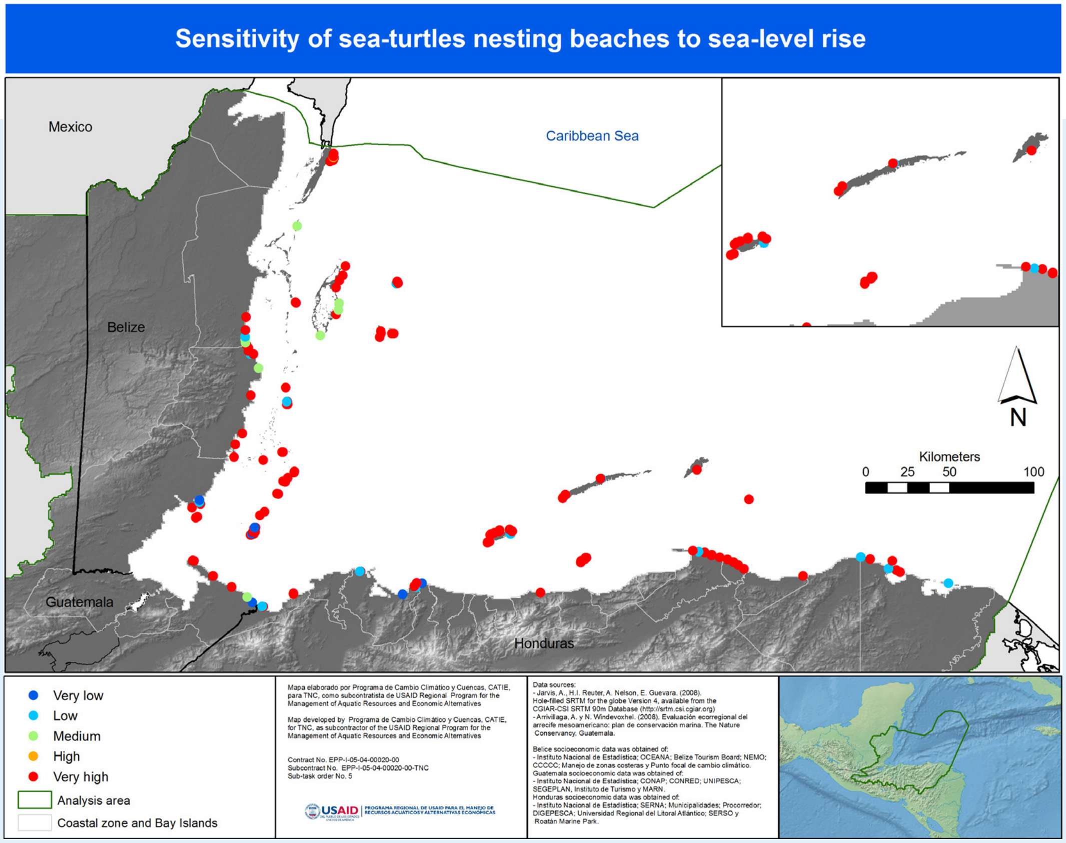
Belice socioeconomic data was obtaided of:
- Instituto Nacional de Estadística; OCEANA; Belize Tourism Board; NEMO; CCCCC; Manejo de zonas costeras y Punto focal de cambio climático.
Guatemala socioeconomic data was obtained of
- Instituto Nacional de Estadística; CONAP; CONRED; UNIPESCA; SEGEPLAN, Instituto de Turismo y MARN.
Honduras socioeconomic data was obtained of:
- Instituto Nacional de Estadística; SERNA; Municipalidades; Procorredor; DIGEPESCA; Universidad Regional del Litoral Atlántico; SERSO y Roatán Marine Park.

Figure 16a. Mangrove sensitivity to sea level rise in Belize, Guatemala and Honduras (CATIE and TNC 2012).

of protected reefs with at least 50% probability of remaining in good condition by the year 2030 under a business as usual scenario (Cruz *et al*. 2016).

Until more information on future impacts of changes in climate and ocean chemistry on major habitats and species is available, it will be necessary to spread the risk by protecting multiple examples of each major habitat type in RZs. This can be achieved by applying the design principles on *Habitat Representation* (Principle 1) and *Risk Spreading* (Principle 2) discussed above. Additionally, the uncertainty due to climate change effects can be addressed by adding a climate change buffer to the principle on *Habitat Representation* (Principle 1) by increasing percent habitat representation by a factor (Allison *et al*. 2003). The exact value of this 'insurance factor' needs to be calculated for the MAR taking into account the vulnerability of the region to changes in climate and the ability of the different ecosystems to withstand change and/or recover. For example, a value of 1.65% was adopted for rezoning the Great Barrier Reef Marine Park in Australia (Fernandes *et al*. 2005). This approach will need to be reviewed once more detailed information on the impacts of changing climate and ocean chemistry on major habitats and focal species becomes available.

Meanwhile, although climate change cannot be prevented at the local level, managers can improve the outlook for their region by increasing protection of species that play a key role in ecosystem resilience. For example, several studies have shown that protecting and restoring herbivorous parrotfish populations can delay or offset the impacts of climate change, by allowing reefs to keep their structural complexity (Bozec *et al*. 2015) and maintain a positive carbonate budget, thus avoiding functional collapse (Kennedy *et al*. 2013).



Mapa elaborado por Programa de Cambio Climático y Cuencas, CATIE, para TNC, como subcontratista de USAID Regional Program for the Management of Aquatic Resources and Economic Alternatives

Map developed by Programa de Cambio Climático y Cuencas, CATIE, for TNC, as subcontractor of the USAID Regional Program for the Management of Aquatic Resources and Economic Alternatives

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Sub-task order No. 5

Data sources:
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Honduras socioeconomic data was obtained of:
- Instituto Nacional de Estadística; SERNA; Municipalidades; Procorredor; DIGEPESCA; Universidad Regional del Litoral Atlántico; SERSO y Roatán Marine Park.

Figure 16b. Sensitivity of sea turtle nesting beaches to sea level rise in Belize, Guatemala and Honduras (CATIE and TNC 2012).

Prioritize the protection of coastal habitats (e.g. mangrove forests and turtle nesting beaches) that have greater probability of surviving sea level rise.

Existing models predicting sea level rise are also available at the global scale and coarse resolution (IPCC 2014), but there are no models at present that can be used to inform the design of RZs at the appropriate spatial scale throughout the MAR.

There are, however, differences in land use, coastal elevation and slope that could be used to identify coastal habitats that are more or less threatened by sea level rise. This information can be used to prioritize areas for protection in RZs. For example, one study examined climate change vulnerability of natural and social systems in the coastal zone of three countries in the MAR (Belize, Guatemala and Honduras) to identify priority areas for adaptation actions (CATIE and TNC 2012). This study found that high vulnerability to sea level rise is a function of multiple challenges such as topography, infrastructure development and low adaptive capacity expressed by social indicators. Several of the maps they produced show sensitivity of coastal habitats (mangroves and sea turtle nesting beaches: Figure 16) to sea-level rise, which could be used to prioritise areas for protection where coastal habitats have the lowest vulnerability to sea level rise.

Minimizing and Avoiding Local Threats

Prioritize placing RZs where there are, or are more likely to be, low levels of threats now and in future.

Marine ecosystems have been degraded by local threats in the MAR (Figure 17), including from habitat destruction (e.g. dredging and filling of coastal wetlands), unsustainable fishing practices (e.g. overfishing of key species, fishing on spawning areas, capturing undersized individuals and using destructive fishing methods), unregulated coastal development (e.g. rapid tourism growth and un-

Figure 17. Local threats that degrade ecosystems and their ecosystem services on the MAR: A. Pollution (inadequate sewage and waste control), B. Unregulated coastal development (growing tourism industry along the coast), C. Unsustainable fishing practices (overfishing). Source information Kramer *et al.* (2015).

sustainable practices), the introduction of invasive species (e.g. invasion of the lion fish *Pterois volitans*) and pollution (e.g. inadequate sewage and sold waste management, and runoff of sediment and nutrients from poor watershed and coastal zone management: Iniciativa Arrecifes Saludables 2010, Aguilar-Perera 2013, Kramer *et al*. 2015).

These threats decrease ecosystem health and productivity, adversely affecting many species (including focal species), and severely undermining the long-term sustainability of marine resources and the ecosystem services they provide (Burke *et al*. 2011). Such threats can also decrease ecosystem resilience to other stressors, including climate change (Salm *et al*. 2006). Therefore, it is important to minimize or avoid these threats in RZs, and prioritize areas for protection that are more likely to contribute to ecosystem health, fisheries productivity, and resilience to climate change (Green *et al*. 2014a).

Local threats that originate within their boundaries (e.g. overfishing and destructive activities) can be managed within RZs, although effective management remains one of the greatest challenges facing marine conservation and management (Velez *et al*. 2014, White *et al*. 2014). Other threats that originate beyond their boundaries (e.g. runoff of sediments and nutrients from land) must be addressed by integrating RZs within broader management frameworks (Salm *et al*. 2006, see *Integrating Replenishment Zones within Broader Management Frameworks*).

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 (modified from IUCN-WCPA 2008, Green *et al*. 2014a):

- Avoid placing RZs where ecosystems have been, or are likely to be, degraded by local threats that cannot be managed effectively (e.g. river runoff with unnaturally high levels of sediments and nutrients, and pollutants such as pesticides); and
- Prioritize placing RZs in areas where there are, or are more likely to be, healthy ecosystems and low levels of threats (e.g. areas influenced by healthy river systems with natural levels of sediment and nutrients and no pollutants).

DISCUSSION

Biophysical Principles for Designing Networks of Replenishment Zones for the MAR

Well designed and effectively managed RZs can reduce local threats and maximize their contribution to enhancing fisheries, conserving biodiversity and adapting to climate and ocean change, particularly in heavily fished areas such as the MAR (Green *et al*. 2014a, b).

Here we provide 13 biophysical design principles that can be used to design a network of RZs for the MAR, which aim to maximize biological objectives by taking into account key biological and physical processes in the region. Since each of these principles are important for designing networks of RZs, full application of the principles will maximize the ecological benefits for enhancing fisheries, conserving biodiversity and climate change adaption. These principles 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. large reef fishes and sea turtles: Green *et al*. 2014a).

In practice, it is often difficult to apply these biophysical design principles due to information gaps and socioeconomic, cultural and political considerations (e.g. McCay and Jones 2011, Green *et al*. 2014a). Therefore, these principles must contribute to a larger planning process that includes addressing research priorities for refining these principles (see *Research Priorities*), and designing networks of RZs 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, Green *et al*. 2014a). Well-defined principles, such as those provided here, can establish a foundation for the design of RZs against which tradeoffs between ecological and other factors can be evaluated (Green *et al*. 2014a, b).

It is also important that these principles are applied using the precautionary approach and best available information. Adaptive management systems should also be used that will allow practitioners to adapt or refine these principles as more information becomes available (e.g. see Botsford *et al*. 2014) or as the ecological and social context changes (e.g. due to climate change: West and Salm 2003, IUCN-WCPA 2008, Green *et al*. 2014a).

Integrating Replenishment Zones within Broader Management Frameworks

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

Where possible, all of the ecosystem (or as large an area as possible) should be included within a large multiple-use marine managed area that includes, but is not limited to, RZs (Green *et al*. 2014b). This will ensure that different types of protection in different zones can offer synergistic benefits to achieve multiple objectives simultaneously by addressing threats that arise within the marine environment (Salm *et al*. 2006, FAO 2011, Green *et al*. 2014b).

RZs should also be embedded within broader management frameworks (Salm *et al*. 2006, Jones *et al*. 2007). For example, fisheries objectives can be addressed more effectively if RZs are integrated within an Ecosystem Approach to Fisheries (EAF: FAO 2011) or with other fisheries management approaches (e.g. to address transboundary fisheries issues: Perez 2009).

RZs should also be integrated within broader spatial planning (e.g. Álvarez-Romero *et al*. 2011) and management regimes (e.g. Ecosystem Based Management or EBM, and Integrated Coastal Management or ICM) that address multiple threats and opportunities including those arising from land (e.g. coastal development and runoff from poor land use practices: White *et al*. 2005, Salm *et al*. 2006, Christie *et al*. 2009b).

Research Priorities

During this process, we identified several key ecological considerations that need to be taken into account when designing networks of RZs in the MAR. However, the scientific information required is currently not available to apply some of the principles. Therefore, we identified several research priorities for adapting and refining these design principles in future, particularly regarding:

- Larval Dispersal: Review all previous studies of oceanographic connectivity, larval dispersal modelling and genetic connectivity in the region; assess the potential and value of combining these three types of data to inform marine spatial planning; and use this region´s specific data to identify the best approach for using larval dispersal to design networks of RZs for the MAR to ensure fisheries benefits and resource sustainability.

- Changes in Climate and Ocean Chemistry: Use, expand and validate models to identify habitats and species that are more or less threatened by changes in climate (e.g. by rising sea temperatures and sea levels) and ocean chemistry, so they can be used to prioritize areas for protection.
- Ecology of Focal Species: Identify focal species and conduct studies of their ecology (regarding the movement of adults and juveniles, larval dispersal and recovery rates) that can be used to refine the configuration of individual RZs within a network.
- Habitat Representation: Identify a common list of major habitat types on the MAR, and quantify their representation in the current network of RZs.

Next Steps for Designing a Network of Replenishment Zones for the Mesoamerican Reef System

Over the last year, 37 scientists and managers from 21 research, government and non-government organisations from all four countries in the MAR, the U.S.A. and Australia contributed to developing biophysical principles for designing a network of RZs for the MAR (Table 1). This represent a critical first step towards developing a regional network of RZs for the region.

At the workshop to adopt biophysical principles for designing a network of RZs in the MAR System in July 2016, representatives from all four countries developed a common vision for the future of: A network of replenishment zones in the MAR that promotes healthy fisheries and resilient marine ecosystems, based on a harmonized legal and political framework with societies more informed and conscious of the value of marine ecosystems (Zepeda *et al*. 2016). They also:

- Developed an action plan for adopting these principles in each of the four countries.
- Identified available data and data gaps for applying these principles to design a network of RZs for the MAR.
- Established working groups to: address research priorities and compile GIS data layers required to apply these design principles; review and compile legal instruments for establishing RZs in each country; develop communication materials to disseminate information to stakeholders; develop regional socioeconomic and governance principles for the MAR; and fundraise to support the design and implementation of a network of RZs for the MAR.

Thus, progress is well underway towards a collaboration among the four countries to design and implement a network of RZs for the MAR to benefit people and nature by enhancing productivity of coastal fisheries, while protecting biodiversity in the face of climate change. Next steps may include:

- Identifying socio-economic and governance principles to design and manage a network of replenishment zones in the MAR.
- Using biophysical, socio-economic and governance principles to design a network of replenishment zones throughout the MAR.
- Developing and identifying indicators of biophysical, socio-economic and governance principles to evaluate the successful design of a network of replenishment zones in the MAR.

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Appendix I. Contributors

Participants in the inception meeting in Mexico City (21-22nd January, 2016) and the workshop to "*Adopt Biophysical Principles for Designing a Network of Replenishment Zones in the Mesoamerican Reef System*" in Cancun (11-15th July, 2016: Zepeda *et al*. 2016).

Name	Institution (Country)	Mexico City	Cancun
Ernesto Arias	Cinvestav (Mexico)		X
Héctor Reyes Bonilla	UABCS (Mexico)		X
Lorenzo Álvarez Filip	UNAM (Mexico)		X
Melanie McField	HRI/SI (U.S.A.)		X
Craig Dahlgren	Perry Institute of Marine Sciences (U.S.A.)		X
Iliana Chollett	Smithsonian Institution (U.S.A.)	X	X
Alison Green	TNC (Australia)	X	X
Antonio Fuentes	Cobi/Inapesca (Mexico)	X	X
Claudia Padilla Souza	Inapesca (Mexico)		X
Judith Morales	WWF (Mexico)		X
Manuel Cárdenas Magaña	Conapesca (Mexico)		X
Alvin Suárez	Cobi (Mexico)	X	X
Elena Nalesso	Cobi (Mexico)		X
María José Espinosa	Cobi/Inapesca (Mexico)	X	X
Stuart Fulton	Cobi (Mexico)		X
Marisol Rueda	HRI (Mexico)		X
Alba González-Posada	Conabio (Mexico)		X
Ralna Lewis	WCS (Belize)	X	X
Seleni Cruz	TNC (Belize)	X	X
Julie Robinson	TNC (Belize)		X
Claudio González	MAR Fund (Guatemala)		X
Blanca Rosa García	Dipesca/MACA (Guatemala)		X
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Jeanette Noack	ADA2 (Guatemala)		X
Alejandra Reyes	ICF (Honduras)		X
Diana Vázquez	CEM (Honduras)		X
Jimmy Andino	CEM (Honduras)	X	X
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Rosa María Loreto	Amigos de Sian Ka'an (Mexico)		X
Inés López	Alianza Kanan Kay (Mexico)		X
Noemí Espinosa	UABCS/UNAM (Mexico)		X
Gonzalo Merediz	Amigos de Sian Ka'an (Mexico)		X
Kim Ley Cooper	Razonatura (Mexico)		X
Eloy Sosa	Ecosur (Mexico)	X	
Juan Bezaury	TNC (Mexico)	X	
Juan Francisco Torres Origel	TNC (Mexico)	X	

Appendix II. National Commitments to Habitat Protection and Progress to Date

Total area of MAR territorial waters, current levels of marine protection in all MPAs and RZs only, and national commitments to establishing RZs in each of the four countries with jurisdictions in the Mesoamerican Reef (MAR).

Country	Total area of MAR territorial waters (km^2)	Current Levels Of Marine Protection In Mar Territorial Waters				Source[1]
		MPA area (km^2)	RZ area (km^2)	% of area in RZs	RZ national commitments	
Belize	19,027.06	4,021.77	588.00	3.09	10%	Territorial waters – Shapefile produced by the Lands and Survey Department (2015), provided by Seleni Cruz Marine protection – Shapefile produced by TNC (2015), provided by Seleni Cruz. All data EPSG 26716
Guatemala	1,559.7	1,063.78	2.23	0.14%	10%[2]	Territorial waters – Shapefile produced by HRI (2016), provided by Lorenzo Alvarez-Philip Marine protection: Convenio de cooperación para la protección y aprovechamiento sostenible de los recursos hidrobiológicos en Bahía la Graciosa y Laguna Santa Isabel, refugio de Vida Silvestre Punta de Manabique (RVSPM), Izabal (2012); FUNDARY, CONAP and TNC (2006); Consorcio para la Coadministración, la conservación de los recursos naturales y el desarrollo integral de los pueblos indígenas del Área Protegida "Área de Uso Múltiple Río Sarstún" (2009)
Honduras	19,564.15	9,572.76	482.06	2.46%	20%[3]	Territorial waters - calculated using the Global Self-consistent, Hierarchical, High-resolution Shoreline (GSHHS v2.2: Wessel and Smith 1996) for the coastline and the VLIZ Maritime Boundary Geodatabase (VLIZ 2012) for the Exclusive Economic Zones Marine protection – Shapefile produced by the Smithsonian Institution (2015), provided by Iliana Chollett. All data EPSG 32616

→

[ends]

Country	Total area of MAR territorial waters (km^2)	Current Levels Of Marine Protection In Mar Territorial Waters				Source[1]
		MPA area (km^2)	RZ area (km^2)	% of area in RZs	RZ national commitments	
México	20,172.79	19,804.06	801.49	3.97%	(20%[4])	Territorial waters - Bezaury-Creel and Torres (2010) Marine protection - Shapefiles produced by the Alianza Kanan Kay (2016), provided by Stuart Fulton, complemented with shapefiles for the new Reserva de la Biosfera del Caribe Mexicano (CONANP 2016, provided by Juan Bezaury). All data EPSG 32616. Territorial Quintana Roo Waters - Bezaury-Creel, Fulton Stuart, Torres-Origel. (2017)
MAR	**60,323.70**	**34,462.37**	**1,873.78**	**9.66%**		

Notes:

[1] Limits of the MAR ecoregion were provided by the Healthy Reefs Initiative. Source shapefiles were only edited to (1) conform the indicated EPSG; (2) dissolve polygons in order to calculate non-overlapping areas.

[2] The Guatemalan government has not set specific targets for protection.

[3] For simplicity and comparability the regional baseline was defined for territorial waters within the MAR boundaries. In Honduras, however, 20% of protection is aimed to fishable waters.

[4] The commitment of 20% of territorial waters is not governmental, but agreed by the Kanan Kay Alliance.

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Appendix III. Movement Patterns of Adult and Juvenile Coral Reef and Coastal Pelagic Fishes in the Caribbean

Modified from Green et al. (2014b) by C. Dahlgren with additional data on home ranges, ontogenetic shifts and spawning movements of Nassau grouper (*Epinephelus striatus*, from Bolden 2001, Dahlgren et al. 2016 and Dahlgren *unpubl.* data) and bonefish (*Albula vulpes*, from Colton and Alevison 1983, Murchie et al 2013, Haley 2009).

Family	Species	Movement (linear distance in km)			
		Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long term movements (core areas of use)
Osteichthyes (bony fishes)					
Acanthuridae (surgeonfishes)	*Acanthurus chirugus* and *A. coeruleus*	<0.3	-	-	-
	Acanthurus bahianus	<3	-	-	-
Albulidae (bonefishes)	*Albula vulpes*	-	>100	-	<15
Balistidae (triggerfishes)	*Balistes capriscus*	-	-	-	<20
Carangidae (jacks)	*Caranx ruber*	<5	-	-	-
	Seriola dumerili and *S. riviolana*	-	-	-	<3000 (<5)
Chaetodontidae (butterflyfishes)	*Chaetodon striatus*	<0.3	-	-	-
Coryphaenidae (dolphinfishes)	*Coryphaena hippurus*	-	-	-	<70
Epinephelidae (groupers)	*Cephalopholis cruentata*, *Epinephelus adscensionis* and *E. fulvus*	<0.1	-	-	-
	Epinephelus guttatus	0.3	<30	-	-
	Mycteroperca phenax	-	-	<20	-
	Mycteroperca microlepis	<1	-	300 (<20)	-
	Epinephelus morio	-	-	<250 to 800 (<70)	-
	Epinephelus striatus	<0.2	<300	<1 to 20	-
Haemulidae (grunts)	*Haemulon carbonarium* and *Haemulon chysargyreum*	<0.1	-	-	-
	Haemulon flavolineatum	<0.5		<3	-
	Haemulon plumieri	<1	-	-	<10
	Haemulon sciurus	<1	-	-	-
Holocentridae (soldierfishes and squirrelfishes)	*Holocentrus adscensionis*, *H. rufus* and *Myripristis jacobus*	<0.1	-	-	-

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[continues]

Family	Species	Movement (linear distance in km)			
		Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long term movements (core areas of use)
Istiophoridae (billfishes)	*Istiophorus platypterus*	-	-	-	<4000
	Makaira indica and *M. nigricanus*	-	-	-	<15000
Kyphosidae (drummers)	*Kyphosus sectatrix*	<3	-	-	-
Labridae (wrasses)	*Bodianus rufus, Halichoeres garnoti* and *Thalassoma bifasciatum*	<0.1	-	-	-
Lutjanidae (snappers)	*Ocyurus chrysurus*	<0.1	-	-	-
	Lutjanus apodus	<1	-	<0.3	-
	Lutjanus griseus	<1	-	-	<20
	Lutjanus campechanus	<1	-	-	<400 (<5)
Monacanthidae (filefishes)	*Cantherhines pullus*	<0.1	-	-	-
Mullidae (goatfishes)	*Mulloidichthys martinicus*	<0.5	-	-	-
Muraenidae (moray eels)	*Gymnothorax moring*	<0.1	-	-	-
Pomacanthidae (angelfishes)	*Holocanthus tricolor, Pomacanthus arcuatus* and *P. paru*	<0.3	-	-	-
Pomacentridae (damselfishes)	*Stegastes adustus*	<0.02	-	-	-
	Microspathodon chrysurus	<0.07	-	-	-
	Abudefduf saxatilis	<0.2	-	-	-
Scaridae (parrotfishes)	*Scarus iserti, Scarus vetula* and *Sparisoma chrysopterum*	<0.1	-	-	<30
	Sparisoma aurofrenatum, S. rupripinne and *S. viride*	<0.5	-	-	<20 (3)
	Scarus coeruleus and *S. taeniopterus*	<1	-	-	-
Scombridae (mackerel and tuna)	*Scomberomorus cavalla*	<50	-	-	-
	Thunnus obesus	-	-	-	<100 (<75)
	Thunnus albacares	-	-	-	<3000 (<600)
	Thunnus thynnus	-	<7000	-	-
Sphyraenidae (barracudas)	*Sphyraena barracuda*	-	-	-	<200 (<20)
Sygnathidae (seahorses)	*Hippocampus reidi*	<0.2	-	-	-
Xiphiidae (swordfishes)	*Xiphias gladius*	-	-	-	1000s

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[ends]

Family	Species	Movement (linear distance in km)			
		Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long term movements (core areas of use)
Chondrichthyes (sharks and rays)					
Carcharhinidae (requiem sharks)	*Carcharhinus brevipinna* and *C. leucas*	-	-	-	<20
	Carcharhinus perezi	-	-	-	<40 (<10)
	Carcharhinus falciformis	-	-	-	<200
	Carcharhinus plumbeus	-	<200	-	-
	Carcharhinus galapagensis	-	-	-	<3000 (<100)
	Carcharhinus limbatus and *C. longimanus*	-	-	-	<3000
	Galeocerdo cuvier	<35	-	-	<8000 (<500)
	Negaprion brevirostris	<5	-	-	<1000 (<2)
Ginglymostomatidae (nurse sharks)	*Ginglymostoma cirratum*	-	-	-	<600 (<10)
Myliobatidae (manta and eagle rays)	*Manta birostris*	<40	-	-	<200
	Rhinoptera bonasus	-	-	-	<20 (<2)
Pristidae (sawfishes)	*Pristis pectinata*	-	-	-	<20
Rhincodontidae (whale sharks)	*Rhincodon typus*	-	-	-	<2000 to <13000
Sphyrnidae (hammerhead sharks)	*Sphyrna lewini* and *S. tiburo*	<10	-	-	<200
	Sphyrna mokarran	-	-	-	<400

Appendix IV. Acronyms

ADA2	Environmental Law Alliance (Alianza de Derecho Ambiental - Guatemala)
AKK	Kanan Kay Alliance
BCH	Honduras Central Bank (Banco Central de Honduras)
CARICOMP	Caribbean Coastal Marine Productivity Program
CATIE	The Tropical Agricultural Research and Higher Education Center
CEM	Center for Marine Studies (Centro de Estudios Marinos) - Honduras
CINVESTAV	Center for Research and Advanced Studies - Mexico
COBI	Community and Biodiversity
CONABIO	National Commission for the Knowledge and Use of Biodiversity (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) - Mexico
CONAP	National Council of Protected Areas (Consejo Nacional de Áreas Protegidas) - Guatemala
CONAPESCA	National Commission of Aquaculture and Fisheries (Comisión Nacional de Acuacultura y Pesca) - Mexico
DIPESCA	Directorate of Fishery and Aquaculture Standards (Dirección de Normatividad de la Pesca y Acuicultura) - Guatemala
EBM	Ecosystem Based Management
ECOSUR	The College of the South Border (El Colegio de la Frontera del SUR) - Mexico
FAO	Food and Agriculture Organization
FSA	Fish Spawning Aggregation
GDP	Gross Domestic Product
GEBCO	General Bathymetric Charts of the Ocean
GIS	Geographic Information System
GSHHG	High-resolution Shoreline
HRI	Healthy Reefs Initiative
ICF	Institute for Forest Conservation (Instituto de Conservación Forestal) - Honduras
ICM	Integrated Coastal Management
IHT	Honduran Institute of Tourism (Instituto Hondureño de Turismo)
INAPESCA	National Fisheries Institute (Instituto Nacional de Pesca) - Mexico
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
MAR	Mesoamerican Reef System
MPA	Marine Protected Area
NRC	National Research Council
PDT	Plan Development Team
RZ	Replenishment Zones
SI	Smithsonian Institute
SST	Sea Surface Temperature
TNC	The Nature Conservancy
UABCS	Autonomous University of Baja California Sur (Universidad Autónoma de Baja California Sur) - Mexico
UNAH	National Autonomous University of Honduras (Universidad Nacional Autónoma de Honduras)
UNAM	National Autonomous University of Mexico (Universidad Nacional Autónoma de México)
WCPA	World Commission on Protected Areas
WCS	Wildlife Conservation Society
WWF	World Wildlife Fund

The Nature Conservancy
Conservando la naturaleza.
Protegiendo la vida.

Smithsonian Institution

COBI
Comunidad y Biodiversidad

Alianza KANAN KAY

CEM
Centro de Estudios Marinos

Healthy Reefs
for healthy people

Perry Institute
FOR MARINE SCIENCE