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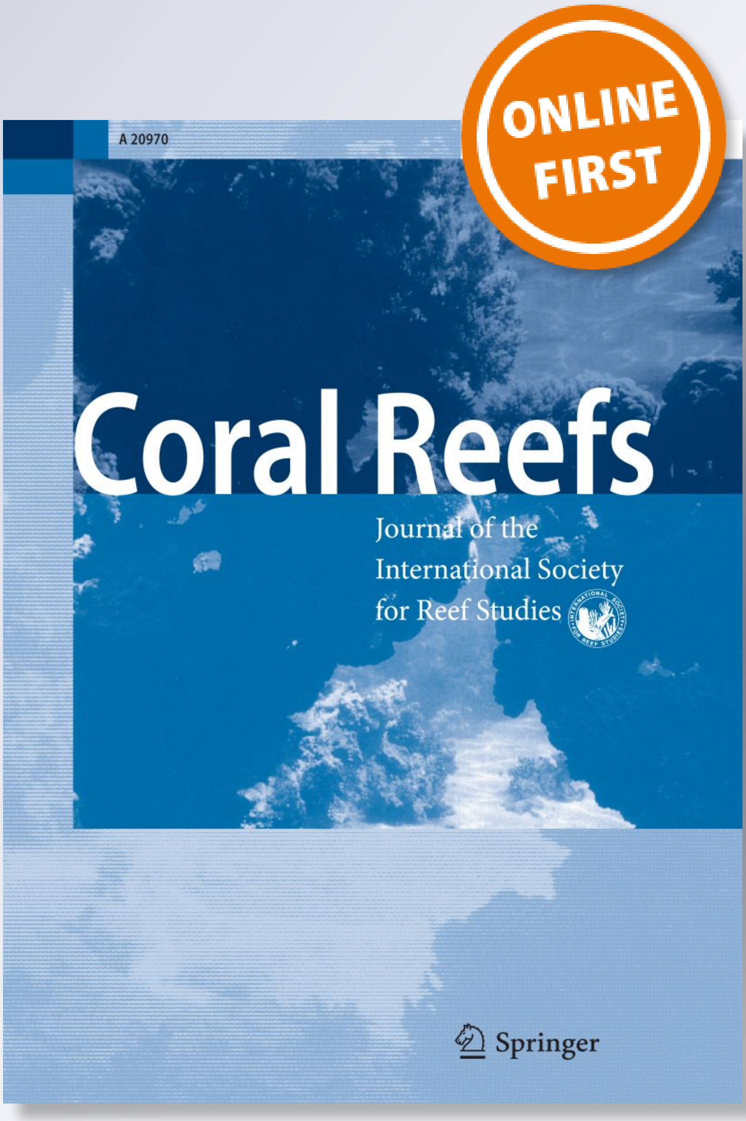

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REPORT

A case for redefining the boundaries of the Mesoamerican Reef Ecoregion

Iliana Chollett[1,2] · **Lysel Garavelli**[3] · **Daniel Holstein**[4] · **Laurent Cherubin**[3] · **Stuart Fulton**[5] · **Stephen J. Box**[1,6]

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Abstract The Mesoamerican Reef (MAR) is an interconnected system that supports the local economies of four countries through the provision of seafood and tourism. Considerable financial, research and management effort has been invested in this priority ecoregion, whose boundaries were defined more than 18 yr ago based on best available data on oceanographic patterns, reef and watershed distribution. The long-term persistence of the MAR depends, however, on ensuring that all of its constituent parts are appropriately managed, and the current boundaries may not respond to this need. Here we assess the suitability of the current boundaries of the MAR using information on physical environments and larval connectivity of three key species. Our research indicates the boundaries of the ecoregion require an adjustment, as the exclusion of key areas in eastern Honduras might jeopardize the persistence of the entire network of connected reefs, and areas in northern Yucatan belong to a different environmental regime and may require different management strategies.

Keywords Caribbean · Connectivity · Oceanography · Biogeography · Tropical coastal ecosystems

Introduction

The Mesoamerican Reef (MAR) is an interconnected system of coastal habitats which constitutes a priority region for conservation in the world (Olson and Dinerstein 2002; Fig. 1). The MAR is the longest barrier reef system in the western hemisphere and the second longest in the world, extending over one thousand kilometres along the coastlines of Mexico, Belize, Guatemala and Honduras. The region is a biodiversity and cultural hotspot (Roberts et al. 2002) and has great ecological, aesthetic, cultural and economic value, sustaining nearly two million people from the four countries (FAO 2000).

Identifying the boundaries of the ecoregion was one of the first steps to start coordinated conservation efforts in the MAR. Collective work in the region started with the Tulum Declaration during the first International Year of the Reef in 1997. At this time, the governments of Mexico, Belize, Guatemala and Honduras committed to work together to promote the conservation and sustainable use of their shared resource. The declaration catalysed the work of several non-governmental and governmental organizations that produced a conservation blueprint for the region and delineated the limits of the ecoregion (Kramer and Kramer 2002). Since then, the MAR has become an international conservation priority ecoregion (Olson and Dinerstein 2002), stimulating targeted research, monitoring and management.

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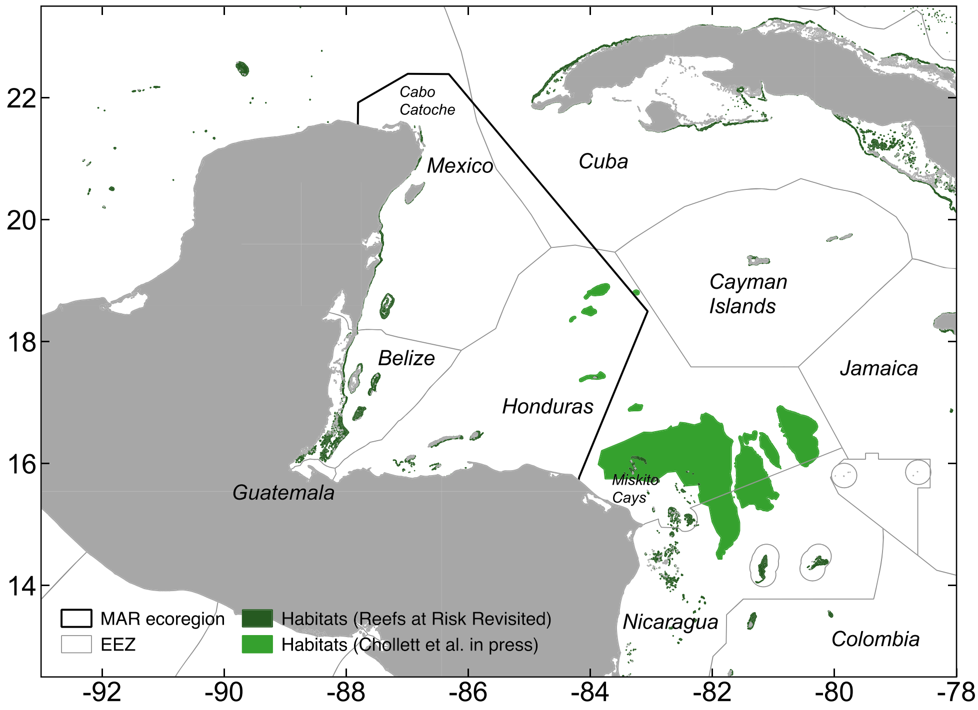


Fig. 1 Map of the MAR indicating the current ecoregional boundary, exclusive economic zones (EEZ) and consolidated marine habitats. Habitat data for eastern Honduras from Chollett et al. (2016b) and other data from the Reefs at Risk Revisited project (Burke et al. 2011)

Ensuring the persistence of this large network of interconnected reefs, the main objective of the ecoregion (Kramer and Kramer 2002), requires careful management of all its components. However, the MAR's boundaries may not respond to this need, and requires reassessment. The boundaries of the ecoregion were defined more than 18 yr ago using the best available information at the time. The process started in 1999 with an initial meeting in Belize City of experts who detailed all the biological and oceanographic data needed to carry out the ecoregional planning (Jorge 1999). The datasets were later collected to identify the ecoregional boundaries that were presented to and approved by stakeholders in Cancun in 2000 (Kramer and Kramer 2002). The MAR ecoregional boundaries were initially identified based on oceanographic patterns, reef and watershed distribution; however, the northern and southern ecoregional boundaries were finally established to coincide with the limits of major watersheds on land (Ria Lagartos in Mexico and Patuca River in Honduras; Kramer and Kramer 2002). Since then, research on habitat distribution, connectivity and physical environments has advanced (Cowen et al. 2006; Chollett et al. 2012, 2016b; Holstein et al. 2014). A full assessment of the ecoregional boundary needs to be considered taking into account the information now available for the area.

Here, we assess the suitability of the current boundaries of the MAR to ensure the long-term persistence of the ecoregion, its primary objective (Kramer and Kramer 2002). This work focuses on larval connectivity and physical environments, which provide insight into ecological continuities and breaks in the region. This research contributes to the management of the MAR as a connected system and to ensuring the persistence of an ecoregion that can support the local communities that depend on it.

Materials and methods

Identifying areas connected to the MAR

We identified which sites in the Caribbean are tightly connected to the MAR ecoregion by first identifying connectivity units (areas strongly connected) within the basin, and then which sites outside the boundaries of the current ecoregion belong to the same connectivity unit as the MAR.

We considered three key species relevant for Caribbean reef ecosystem provision and fisheries in our connectivity analyses. The species were boulder star coral (*Orbicella annularis*), yellowtail snapper (*Ocyurus chrysurus*) and spiny lobster (*Panulirus argus*), which have contrasting larval characteristics. Boulder star coral constitutes the foundation species of coral reefs in the region and has a pelagic larval duration of about 30 d (Vermeij et al. 2006). Yellowtail snapper is an increasingly desirable target in the Caribbean because of its fast growth and prolific reproduction (Saillang et al. 2012) and as an alternative to groupers and other slow-growing snappers that have been depleted throughout the region (Sadovy and Domeier

2005). Yellowtail larvae spend about 47 d in the plankton (Lindeman et al. 2000). Finally, spiny lobsters constitute the most desired marine resource in the MAR (Cochrane and Chakalall 2001) and their larvae can spend up to 196 d in the plankton (Goldstein et al. 2008). All connectivity data were produced for previous published studies and have been described before (Holstein et al. 2014; Chollett et al. 2016b). An overview of the larval connectivity matrices can be found in the Electronic Supplementary Material (ESM Table S1). The most relevant difference among datasets is the use of different habitat coverage; while Holstein et al. (2014) used a global coral reef map produced for the Millennium Coral Reef Mapping Project (Andréfouët et al. 2006) for boulder star coral and yellowtail snapper, Chollett et al. (2016b) complemented data from the Reefs at Risk Revisited project (Burke et al. 2011) with fishing grounds mapped in eastern Honduras (Fig. 1).

Connectivity units were defined using the method described by Jacobi et al. (2012). The method identifies subpopulations separated by dispersal barriers. Briefly, the algorithm applies a minimization procedure that recursively splits the population so that the connectivity between subpopulations is minimal. The method produces several partitions (ESM Fig. S1). Using all partitions as input, we quantified the proportion of times each site in the Caribbean was identified as belonging to the same connectivity unit as the MAR for each species. The method was applied using the latest version of the R package *ConnMatTools* (Andrello 2016) considering 20 cycles, 20 values of the parameter β and a maximum of 400 partitions.

Identifying different environments in the wider MAR

We classified the wider MAR (12–24N, 80–89W) in different environments following a clustering approach previously used in the Caribbean and other regions (Chollett et al. 2012; Wang et al. 2015). The environment of the MAR was originally described in terms of sea surface temperature (mean, summer and winter values), mean chlorophyll concentration, salinity and current speed. After initial data exploration, mean temperatures and salinity were excluded from the clustering analyses. Mean temperature was highly correlated with winter temperatures ($R^2 = 0.87$, $p < 0.001$), and variability in salinity was minimal throughout the region (less than 1 psu). Different environments in the wider MAR were identified using self-organized maps, a type of neural network (Kohonen 2001). The optimal number of classes (aka environments) was defined using the Calinski and Harabasz index (Calinski and Harabasz 1974). The R packages *raster* (Hijmans 2015), *kohonen* (Wehrens and Buydens 2007) and *fpc* (Hennig 2015) were used for image analysis, neural network analyses and cluster validation, respectively.

The data sources used are briefly described below. Night-time sea surface temperature (SST) and chlorophyll concentration (chl-a) data at 1-km spatial resolution were extracted from the sensor MODIS aboard the Aqua satellite. We used monthly climatologies covering the period 2003–2010 as input. From the 12-monthly climatological values, we calculated the mean (for SST and chl-a), and the minimum and maximum values (for SST). Mean surface salinity and current speed were extracted from the ocean model HYCOM which produces data for the Caribbean at 1/12° spatial resolution (Chassignet et al. 2007). We used global data-assimilative runs for the period 2008–2011. These analyses differ from Chollett et al. (2012) in two aspects, the spatial scale and the data sources. This work focuses in obtaining patterns only in the Mesoamerican Reef area. The inputs include a salinity dataset with better spatial resolution and incorporate current speed as an additional driver, which is important in this region of the Caribbean.

Results

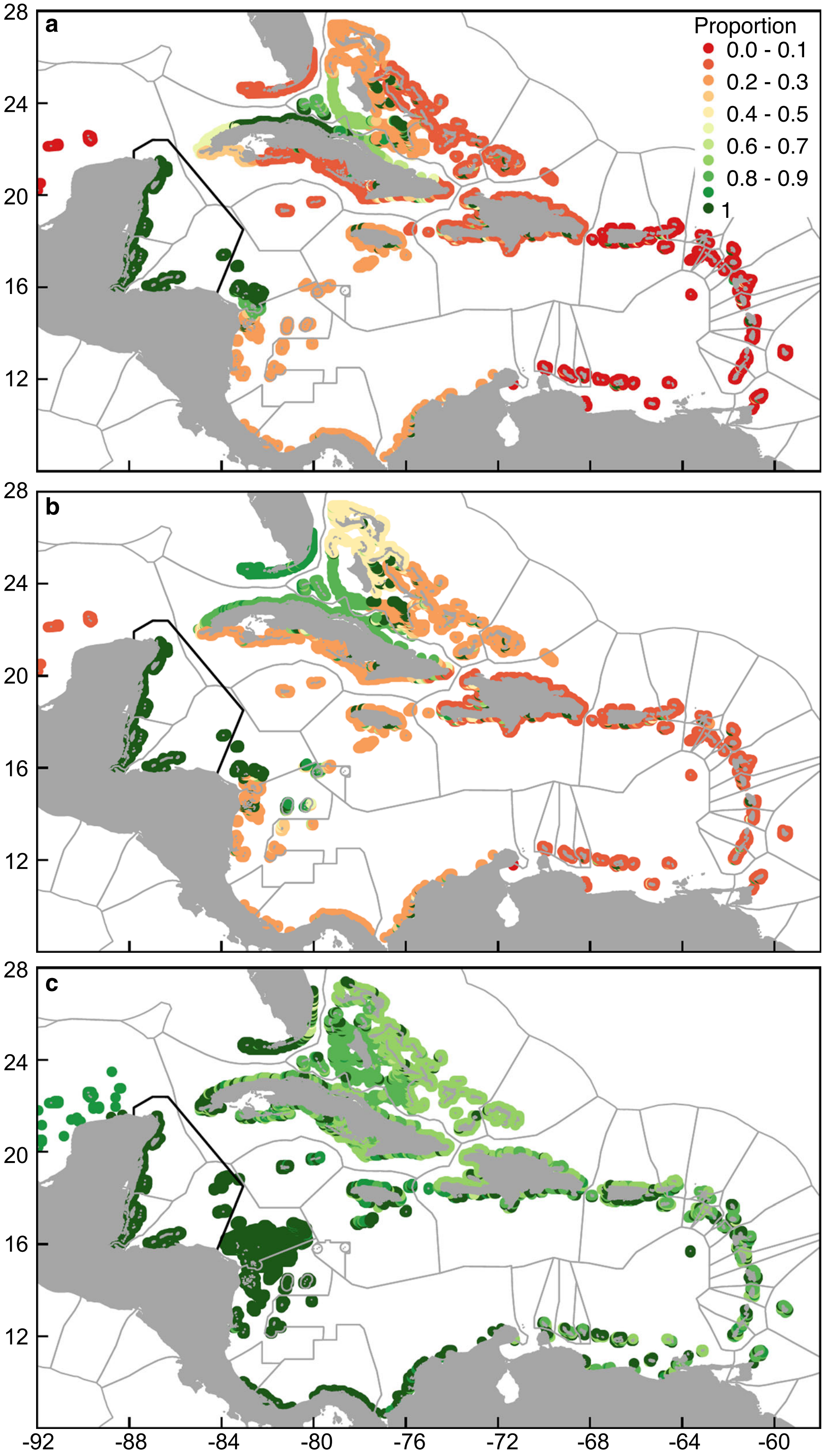
Identifying areas connected to the MAR

Eastern Honduras is the only region that is consistently connected to the MAR no matter the species considered. This region was always identified as belonging to the same connectivity unit as the MAR (proportion = 1, areas in dark green in Fig. 2).

Other regions had tight connections to the MAR ecoregion, but they were dependent on the species considered. Downstream from the MAR and therefore receiving larvae produced by the region, Northern Cuba (for star boulder coral; Fig. 2a), Florida (for spiny lobster; Fig. 2c) and some areas of the Bahamas are highly connected. These regions are connected to the MAR through the fast Yucatan and Loop currents that flow through the Yucatan passage towards eastern Florida (Richardson 2005).

Upstream, and therefore seeding the region, some of the Nicaraguan Miskito Cays and offshore banks in Colombia (Quitasueño, Serrana and Serranilla) are highly connected for yellowtail snapper (Fig. 2b). Additionally, the entire Central American region appears to contribute spiny lobster larvae to the MAR (Fig. 2c), possibly related to the long time the larvae of this species spend in the plankton (Goldstein et al. 2008).

Fig. 2 Proportion of times each site outside the current MAR ecoregion boundary has been identified as belonging to the same connectivity unit as the MAR for **a** boulder star coral, **b** yellowtail snapper, **c** spiny lobster. Limits of the MAR Ecoregion in *black*, and Exclusive Economic Zones in *grey*. *Dark green* sites are always (proportion = 1) connected to the MAR, independently of the strength of the partition



Identifying different environments in the wider MAR

The optimal partition for the MAR was found when considering six clusters (Fig. 3a). This partition classified the wider MAR ecoregion into six different physical environments (Fig. 3b). The clustering procedure produced homogeneous clusters with well-defined boundaries, even though no spatial information was given as an input. Not all environment classes are the same, and some are more similar than others (Fig. 3c); clusters 1 and 2 are characterized by high current speed, while cluster 6 has the minimum winter temperatures. Clusters 3–5 represent offshore waters with similar characteristics, which translates into weak gradients along the map (Fig. 3b).

Most of the MAR presents relatively homogeneous waters characterized by clusters 3–5, the exception being interior waters along bays and the region around Cozumel in Mexico characterized by very fast currents (clusters 1, 2). The most defined boundary within the ecoregion is located in its northern tip, where a colder front (cluster 6) seems to separate the waters of the Gulf of Mexico and the Caribbean.

Discussion

Research on connectivity and physical environments confirms that the boundaries of the MAR ecoregion require some adjustment, particularly the inclusion of key areas in eastern Honduras that are tightly connected to the MAR, whose addition might boost the persistence of the entire network of connected reefs. Furthermore, areas in northern Yucatan are under the influence of a very different environment and therefore could benefit from different management strategies.

The suggested redefinition of the boundaries coincides with other classifications available for the basin: the expert-derived ecoregions of the world (Spalding et al. 2007) and the data-driven Caribbean physicochemical provinces (Chollett et al. 2012). The northern break due to upwelling has been recognized by both classifications (Spalding et al. 2007; Chollett et al. 2012), while the fuzzy southern break has been represented in our previous work (Chollett et al. 2012). The absence of a biogeographical break in this region in Spalding's work is not surprising giving the lack of information on eastern Honduran and Nicaraguan reefs (Chollett et al. 2014), which to this date, remain largely unexplored by researchers.

Refining the boundaries of the MAR: northwest

Several lines of evidence suggest the existence of a natural break inside the MAR along its northwest corner. This region is characterized by a cold front (Fig. 3b) due to the influence of upwelling offshore from Cabo Catoche, altering the oceanographic characteristics of the waters (Merino 1997; Melo-González et al. 2000), which translates into pronounced differences in marine benthic (Espinoza-Avalos 1996) and pelagic (de la Parra-Venegas et al. 2011) communities, as well as target fisheries resources. Benthic communities are so different that there

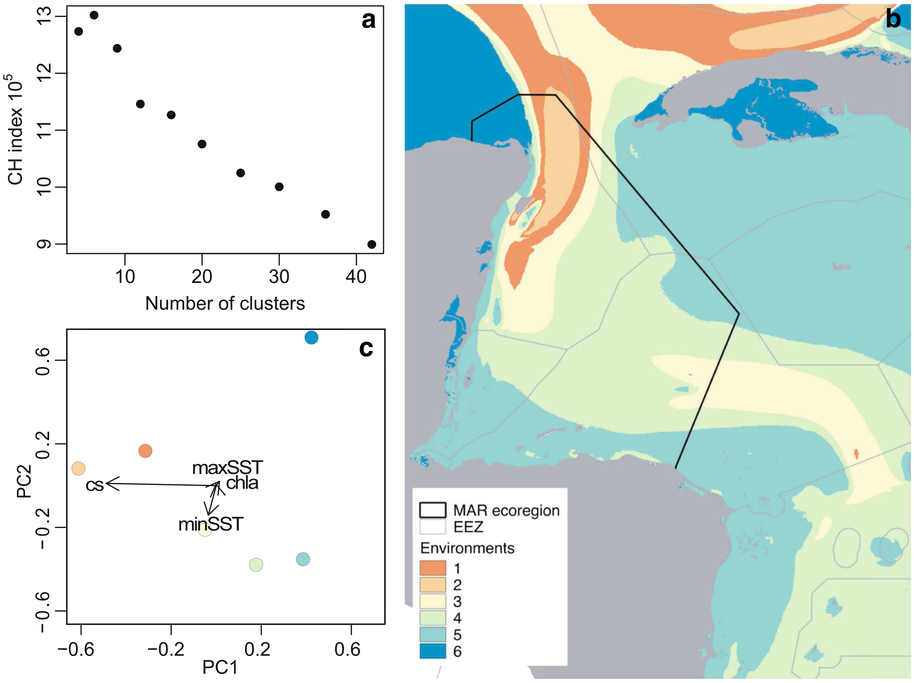


Fig. 3 Different environments in the MAR using minimum monthly sea surface temperature (minSST), maximum monthly sea surface temperature (maxSST), chlorophyll concentration (chla) and current speed (cs). **a** Calinski and Harabasz index for classifications with different cluster sizes; a higher value indicates a better partition. **b** Physical environments along the wider MAR (12–24N, 80–89W). **c** Principal component ordination showing differences among environments (*dots*) and the role of each input variable (*arrows*). The first two principal components explain 99% of the variance

is a discontinuity in consolidated habitat distribution around this area (Fig. 1). Furthermore, the fast flow of the Caribbean Current through the Yucatan Channel produces a strong connectivity break between the Mexican Caribbean and the Gulf (Fig. 2).

Originally, Cabo Catoche was identified as the northern limit of the MAR by experts in the region, but the boundary was moved towards the west to accommodate the limit of the watershed of Ria Lagartos (Kramer and Kramer 2002). Setting aside (important) issues of practicality associated with maintaining the status quo, the need to move the boundaries of the ecoregion in the north ought to be discussed. Excluding this region from the MAR, however, would not jeopardize the persistence of the MAR as a connected ecoregion.

Changes in the environment produce profound changes in the fisheries resources that live in the northern tip of the MAR. For example, while Nassau grouper thrives in the Caribbean, red grouper dominates the Gulf of Mexico. The species have different life histories and spawn at different times of the year, therefore requiring different minimum landing sizes and closed seasons (Aguilar-Perera et al. 2008). Even if the boundaries remain the same in this section of the MAR, this region may require a different fisheries management approach. Mexico would benefit from acknowledging the differences in environment and species distribution in this region, and translating this information into more targeted management measures for its fisheries species.

Refining the boundaries of the MAR: southeast

Eastern Honduras is the only region that is consistently connected to the MAR. The exact location of the MAR's south-eastern connectivity break, however, changes slightly according to the species and lies between the southern Honduran Miskito Cays and the Nicaraguan Miskito Cays (Fig. 4). The Miskito Cays are located at the northern limit of the Panama–Colombia gyre (Andrade and Barton 2000) which flows counter-clockwise with a seasonally variable northernmost range, explaining the fuzzy nature of this boundary. Although our analyses do not include every species in the Caribbean, they encompass a diverse range of species that allows quantifying the repeated occurrence of boundaries, allowing certain generalizations to be drawn. The presence of the south-eastern connectivity break has been qualitatively suggested by earlier connectivity work, which has highlighted strong

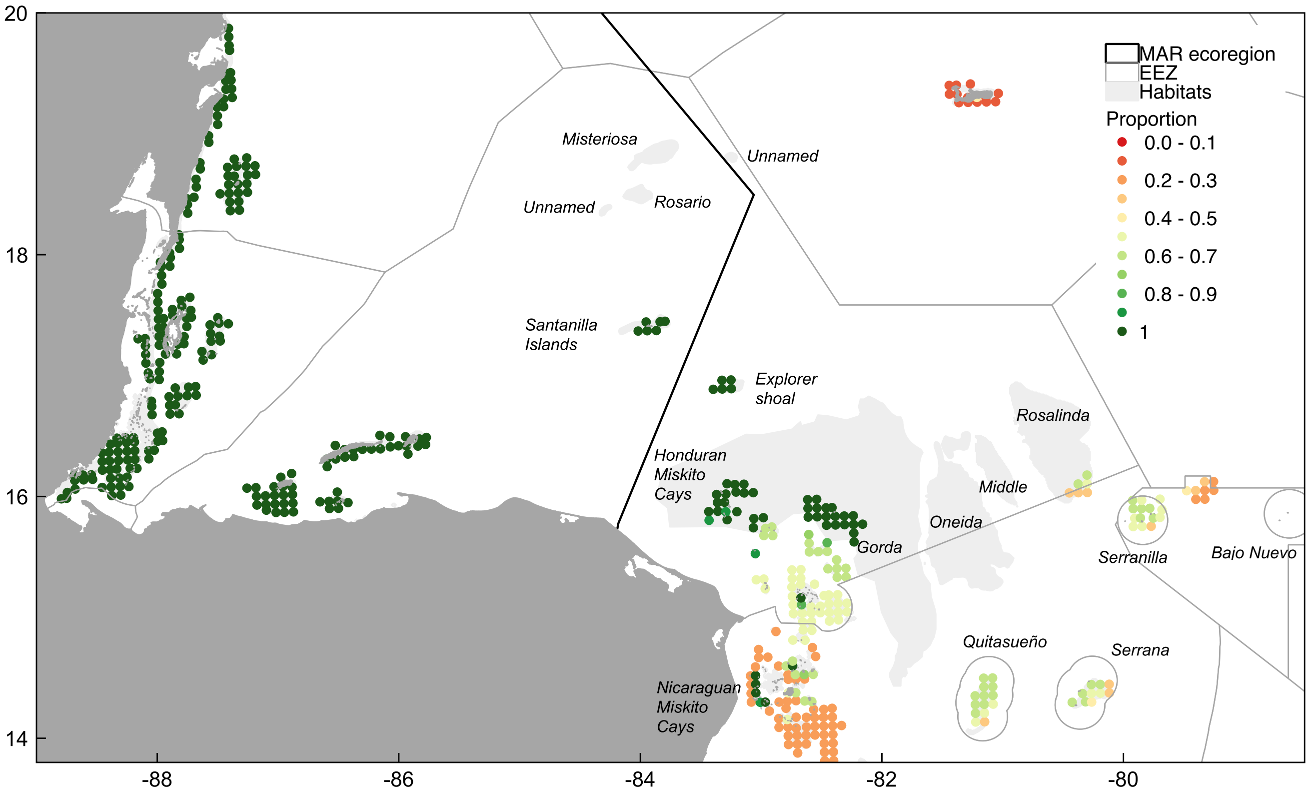


Fig. 4 Detail of Fig. 2 showing the proportion of times each site around the south-eastern boundary of the current MAR ecoregion was identified as belonging to the same connectivity unit as the MAR for boulder star coral and yellowtail snapper (average proportion shown). Spiny lobster was not included given that proportion = 1 for the entire area. *Dark green* sites are always (proportion = 1) connected to the MAR

connections between western and eastern Honduras and limited larval exchange between Honduras and Nicaragua (Cowen et al. 2006; Bustamante and Paris 2008).

Most connectivity work in the Caribbean (Cowen et al. 2006; Holstein et al. 2014; Schill et al. 2015) has used global maps of reef distribution as templates (Bryant et al. 1998; Burke et al. 2011), therefore missing some key regions in the area, such as the banks in eastern (Gorda, Oneida, Middle and Rosalinda; Fig. 4) and northern Honduras (Misteriosa, Rosario, and two unnamed banks). To draw a definitive boundary for the ecoregion, further connectivity work with a comprehensive coverage of the area is needed. Additionally, in situ surveys in standard habitats would be desirable. These could provide information on biodiversity and demographic connectivity that could help validate the presumed biogeographical breaks. In the meantime, we recommend the inclusion of the rest of the Honduran consolidated habitats within the boundaries of the ecoregion. These areas are likely integral to regional population replenishment and beneficial mostly to species with intermediate larval dispersal duration.

Adding this new region to the MAR brings some challenges. Although there is little conflict of use in this undeveloped area, which is currently only used for industrial fishing (Chollett et al. 2016a), and land-based threats are unlikely to affect the distant (>50 km) consolidated habitats, their remoteness could represent a challenge for management and enforcement. In this sense, two elements are key: the involvement of local stakeholders (indigenous Miskitu, currently mostly employed by the industrial fishing fleet) in the use and management of the area through the development of safer, more profitable artisanal fisheries; and the use of vessel monitoring system technology, available from the Honduran Fisheries Department, for enforcement of the region.

In summary, collective work in the MAR to ensure a better management of the ecoregion would benefit from: (1) including all eastern Honduras as part of the ecoregion; (2) acknowledging the differences in environment throughout the MAR to ensure both that different regions are managed with appropriate fisheries management tools and that examples of each environment are well represented in networks of marine protected areas (Margules et al. 2002). Here we provide the science evidencing the need to redraw the boundaries of the MAR ecoregion. We hope that once this information is in the hands of donors, managers and researchers, comprehensive work in the MAR will follow, directed to expand management efforts in eastern Honduras and tailor the work in northern Yucatan. To formalize the new boundaries, however, this evidence should be discussed by stakeholders in the region, as it was in 2000 when the MAR was first defined.

The adjustment of the MAR boundaries would allow funding, research and implementation to reach the entire region of connected reefs. This issue is of particular urgency now that an international initiative has begun to develop a network of marine reserves in the MAR led by The Nature Conservancy, Comunidad y Biodiversidad, Centro de Estudios Marinos, Healthy Reefs and the Smithsonian Institution. By ensuring monitoring and management efforts are directed to the entire ecoregion, we will work towards sustaining the long-term persistence of this iconic reef system and the human communities that depend on it.

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References

Aguilar-Perera A, Gonzalez-Salas C, Villegas-Hernandez H (2008) Fishing, management, and conservation of the Nassau Grouper, Epinephelus striatus, in the Mexican Caribbean. Proc Gulf Caribb Fish Inst 61:313–319

Andrade CA, Barton ED (2000) Eddy development and motion in the Caribbean Sea. J Geophys Res Oceans 105:26191–26201

Andréfouët S, Muller-Karger FE, Robinson JA, Kranenburg CJ, Torres-Pulliza D, Spraggins SA, Murch B (2006) Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. In: Proceedings 10th International Coral Reef Symposium 2:1732–1745

Andrello M (2016) ConnMatTools: Tools for working with connectivity matrices. R package version 0.3–2, https://github.com/dmkaplan2000/ConnMatTools.git

Bryant D, Burke L, McManus K, Spalding M (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington, p 56

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, p 114

Bustamante G, Paris CB (2008) Marine population connectivity and its potential use for the nomination of new World Heritage Sites in the wider Caribbean. In: Grober-Dunsmore R, Keller BD (eds) Caribbean connectivity: implications for marine protected area management. Proceedings of a special symposium, 9–11 November 2006, 59th annual meeting of the Gulf and Caribbean Fisheries Institute, Belize City, Belize. Marine Sanctuaries Conservation Series NMSP-08-07, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD, pp 97–112

Caliński T, Harabasz J (1974) A dendrite method for cluster analysis. Commun Stat Theory Methods 3:1–27

Chassignet EP, Hurlburt HE, Smedstad OM, Halliwell GR, Hogan PJ, Wallcraft AJ, Baraille R, Bleck R (2007) The hybrid coordinate ocean model (HYCOM) data assimilative system. J Mar Syst 65:60–83

Chollett I, Stoyle G, Box SJ (2014) Honduran Miskito Cays: among the last unexplored reef systems in the Caribbean. Coral Reefs 33:155

Chollett I, Box SJ, Mumby PJ (2016a) Quantifying the squeezing or stretching of fisheries as they adapt to displacement by marine reserves. Cons Biol 30:166–175

Chollett I, Mumby PJ, Muller-Karger FE, Hu C (2012) Physical environments of the Caribbean Sea. Limnol Oceanogr 57:1233–1244

Chollett I, Garavelli L, O'Farrell S, Cherubin L, Matthews TR, Mumby PJ, Box SJ (2016b) A genuine win-win: resolving the "conserve or catch" conflict in marine reserve network design. Conserv Lett. doi:10.1111/conl.12318

Cochrane KL, Chakalall B (2001) The spiny lobster fishery in the WECAFC region—an approach to responsible fisheries management. Mar Freshw Res 52:1623–1631

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

de la Parra-Venegas R, Hueter R, Cano JG, Tyminski J, Remolina JG, Maslanka M, Ormos A, Weigt L, Carlson B, Dove A (2011) An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean sea. PLoS One 6:e18994

Espinoza-Avalos J (1996) Distribution of seagrasses in the Yucatan Peninsula, Mexico. Bull Mar Sci 59:449–454

FAO (2000) Conservation and sustainable use of MBRS. Threat and root cause analysis. Report#000/008 CP-CAM. FAO/World Bank Cooperative Program, Centroamerica. p 46

Goldstein JS, Matsuda H, Takenouchi T, Butler MJ (2008) The complete development of larval Caribbean spiny lobster *Panulirus argus* in culture. J Crustacean Biol 28:306–327

Hennig C (2015) fpc: Flexible procedures for clustering. R package version 2.1-10. https://CRAN.R-project.org/package=fpc

Hijmans RJ (2015) Raster: geographic data analysis and modeling. R package version 2.5-2. https://CRAN.R-project.org/package=raster

Holstein DM, Paris CB, Mumby PJ (2014) Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. Mar Ecol Prog Ser 499:1–18

Jacobi MN, André C, Döös K, Jonsson PR (2012) Identification of subpopulations from connectivity matrices. Ecography 35:1004–1016

Jorge M (1999) Results of the preliminary meeting of experts on the Mesoamerican Caribbean Reef. World Wildlife Fund, Belize City

Kohonen T (2001) Self-organizing maps. Springer-Verlag, Berlin

Kramer PA, Kramer PR (2002) Ecoregional conservation planning for the Mesoamerican Caribbean Reef. World Wildlife Fund, Washington, p 140

Lindeman KC, Pugliese R, Waugh GT, Ault JS (2000) Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bull Mar Sci 66:929–956

Margules CR, Pressey RL, Williams PH (2002) Representing biodiversity: data and procedures for identifying priority areas for conservation. J Biosci 27:309–326

Melo-González N, Müller-Karger FE, Cerdeira-Estrada S, Pérez de los Reyes R, Victoria del Río I, Cárdenas-Pérez P, Mitrani-Arenal I (2000) Near-surface phytoplankton distribution in the western Intra-Americas Sea: the influence of El Niño and weather events. J Geophys Res Oceans 105:14029–14043

Merino M (1997) Upwelling on the Yucatan Shelf: hydrographic evidence. J Mar Syst 13:101–121

Olson DM, Dinerstein E (2002) The Global 200: priority ecoregions for global conservation. Ann Mo Bot Gard 89:199–224

Richardson PL (2005) Caribbean current and eddies as observed by surface drifters. Deep Sea Res Part 2 Top Stud Oceanogr 52:429–463

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Sadovy Y, Domeier M (2005) Are aggregation fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262

Saillang EA, Renshaw MA, Cummings NJ, Gold JR (2012) Conservation genetics and management of yellowtail snapper, *Ocyurus chrysurus*, in the US Caribbean and South Florida. Fish Manag Ecoogy 19:301–312

Schill SR, Raber GT, Roberts JJ, Treml EA, Brenner J, Halpin PN (2015) No reef is an island: integrating coral reef connectivity data into the design of regional-scale marine protected area networks. PLoS One 10:e0144199

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57:573–583

Vermeij MJA, Fogarty ND, Miller MW (2006) Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*. Mar Ecol Prog Ser 310:119–128

Wang M, Ahmadia GN, Chollett I, Huang C, Fox H, Wijonarno A, Madden M (2015) Delineating biophysical environments of the Sunda Banda Seascape, Indonesia. Int J Environ Res Public Health 12:1069–1082

Wehrens R, Buydens LMC (2007) Self- and super-organising maps in R: the kohonen package. J Stat Softw 21:1–19