Management of Marine Resources in the Mesoamerican Reef Ecoregion

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Contents

Abstract

This thesis investigates the application of a range of tools to marine resource management problems, and understanding their capabilities and limitations, with a particular focus on the Mesoamerican reef (MAR) ecoregion. In chapter two, I reconstruct landed catches within the Honduran fisheries to assess trends within different fishing sectors and identify the importance of small-scale fisheries to the Honduran economy. In chapter three, I test three different tools with the capability of assigning fish to specific fish stocks. Here I assess their ability to assign individual fish to their fishing ground at small spatial scales on the model species *Ocyurus chrysurus* (yellowtail snapper) and identify that morphometric analysis was not only the most accurate but also the most time-efficient, and cost-effective tool. In chapter four, I use a panel of microsatellite markers to assess the genetic structure of colonies of *Acropora cervicornis* (staghorn coral) on three banks within a protected area, and identify genetic structure despite low genetic diversity. These findings reinforce the importance of including genetic diversity within restoration initiatives, through ensuring the potential for evolutionary processes in adapting to changing environmental conditions. In chapter five, I conduct a fine-scale genetic analysis on a small parcel of *Rhizophora mangle* (red mangrove) forest, using single-nucleotide polymorphisms. I identify higher levels of genetic structure than previously considered at this scale within these ecosystems and demonstrate the importance of these findings to spatial planning and restoration initiatives. In chapter six, I conduct a review of the current management of mangroves throughout the MAR ecoregion. Geopolitical differences exist between the four countries, and differences in the perception of threats between Ramsar site managers and researchers, which elicit specific needs to promote management of mangroves at the national and regional scale. Finally, I conclude the thesis with a general discussion of how the methods and findings of the previous chapters can be applied to marine resource management, and the caveats that should be considered when implementing them as part of a management strategy.

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Declaration

I hereby declare that I have personally undertaken all the work described in this thesis.

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Dedication

To William and Emmeline, my nephew and niece, I hope that you get to see and experience all of the amazing biodiversity of the Mesoamerican reef ecoregion.

Abbreviations

BCZMAI	Belize Coastal Zone Management Authority and Institute
BFD	Belize Fisheries Department
BFoD	Belize Forestry Department
CONANP	Comisión Nacional de Áreas Naturales Protegidas (México)
CONAP	Consejo Nacional de Áreas Protegidas (Guatemala)
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DNA	Deoxyribonucleic Acid
EEZ	Exclusive Economic Zone
FAO	Food and Agriculture Organization of the United Nations
HRI	Healthy Reefs Initiative
ICF	Instituto Nacional de Conservación y Desarrollo Forestal
ICP-MS	Inductively Coupled Plasma Mass Spectrometry
IHT	Instituto Hondureno de Turismo
IUCN	International Union for Conservation of Nature
IUU	Illegal, Unreported and Unregulated fishing
MAR	Mesoamerican Reef
MPA	Marine Protected Area
NGO	Non-Governmental Organization
NTZ	No-Take Zone
PACT	Protected Areas Conservation Trust
PERMANOVA	Permutational Analyses of Variance
RAD	Restriction site Associated DNA
RADseq	Restriction site Associated DNA sequencing
TURF	Territorial User Rights Fisheries
UNEP	United Nations Environment Programme
SERMARNAP	Secretaría de Medio Ambiente, Recursos Naturales, y Pesca
SERMARNAT	Secretaría de Medio Ambiente y Recursos Naturales

Chapter 1

Thesis Introduction

1.1 Introduction

The Mesoamerican reef (MAR) ecoregion is the largest barrier reef system in the western hemisphere, shared by Mexico, Belize, Guatemala and Honduras (Kramer and Kramer 2002) (Figure 1.1). The ecoregion extends over 1000km of Caribbean coastline and was defined based on natural physical borders; to the north, persistent ocean currents of the Yucatán peninsula, Mexico, and to the south, the Patuca river, Honduras. There are three principal marine ecosystems: coral reefs; mangroves; and seagrass meadows, which support a diverse range of marine organisms and the marine resources of the ecoregion support over two million people (Kramer and Kramer 2002). The MAR ecoregion was officially decreed by the governments of the four countries as part of the Tulum declaration in 1997. The governments agreed to promote the sustainable use of the reef system, establish coordinated conservation efforts and cooperative programs and projects (Kramer and Kramer 2002), and renewed their support of these goals in 2006. The declaration of the MAR ecoregion, and subsequent renewals to the initial commitments, highlight the interest of the four countries in managing and protecting their shared marine resources. However, in 2017 the MAR was defined as a critically endangered ecosystem, using the IUCN Red List criteria, primarily based on the declining trends observed in coral cover and piscivorous fish biomass (Bland et al. 2017).

There is urgent need to promote sustainability within fisheries, and reduce the declining trends in coral, seagrass and mangrove cover within the MAR (Bland et al. 2017; Canty, Preziosi, and Rowntree 2018). The marine ecosystems of the MAR support a wide range of biodiversity, additionally they provide critical ecosystem services to the millions of people living in the coastal zone, for example, coral reefs provide coastal protection and underwater recreation (Woodhead et al. 2019), mangroves control erosion and sedimentation rates (Friess 2016), and seagrasses stabilize sediments and purify water (Nordlund, Koch, Barbier, & Creed, 2016). It is imperative that management actions are forward thinking, and build resilience within ecosystems and fisheries to unknown future environmental conditions (Hughes et al. 2017; Steneck and Pauly 2019), such as increasing sea-level (Kopp et al. 2014) and increased frequency of high intensity hurricanes (Murakami et al. 2018). Marine protected areas (MPAs) are seen as important tools in providing protection to habitats and fisheries (O'Leary et al. 2016), and marine spatial planning is a critical component in the design of MPAs (Harvey et al. 2018). Understanding how populations are connected across seascapes ensures that the benefits of protected areas have wider impacts, such as facilitating gene flow among populations (Palstra and Ruzzante 2008). Maintaining high genetic diversity within ecosystems is critical especially in an era of changing environmental conditions (Reynolds, McGlathery, and Waycott 2012), and therefore should be built into marine resource management and restoration frameworks (see Mijangos et al. 2015). However, the management of marine resources requires not only an understanding of the ecology and evolutionary history of species and ecosystems, but also knowledge of how and where they are used by coastal communities (Harvey et al. 2018), and there is a need to balance ecological and socio-economic demands (Chollett et al. 2016).

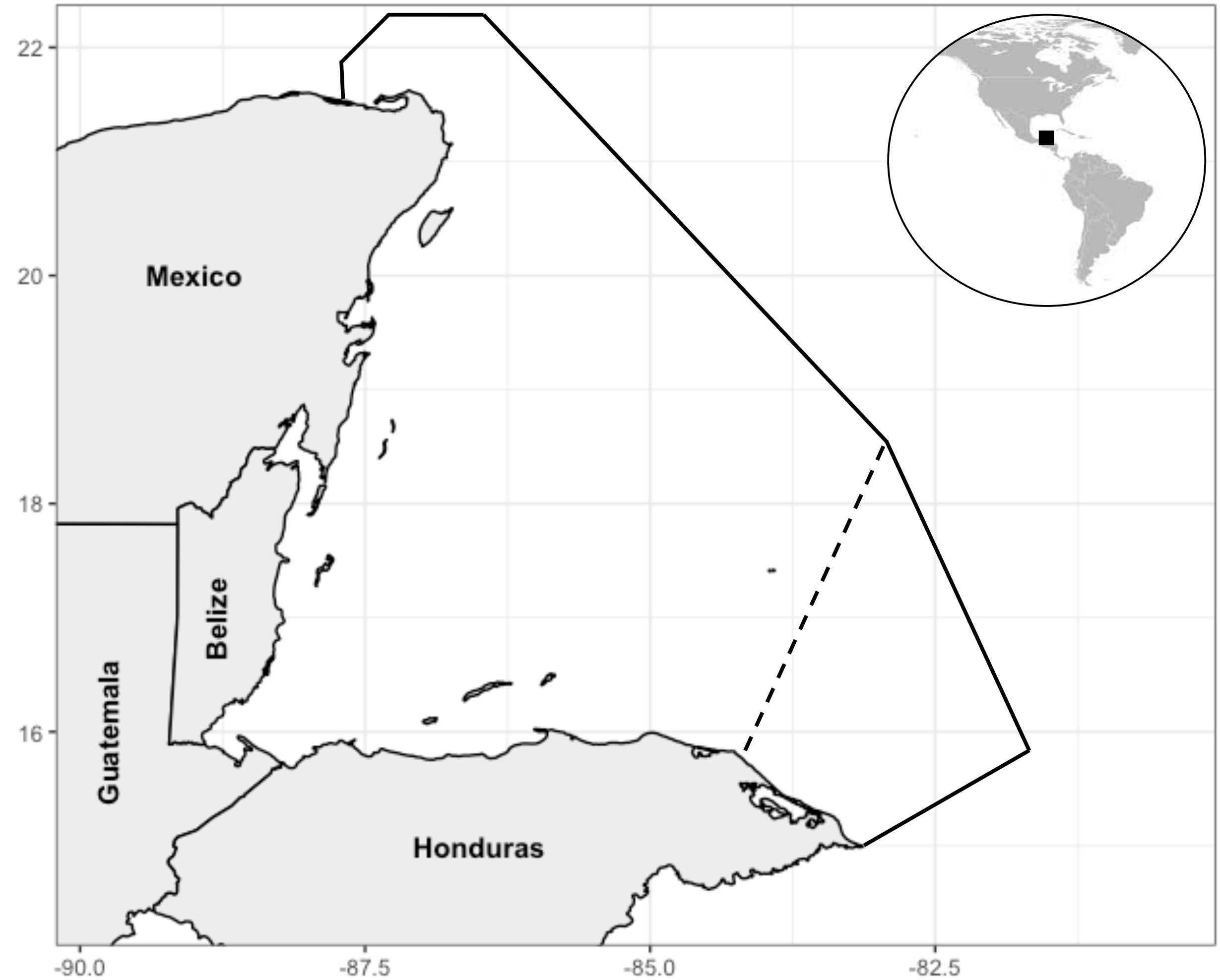

Figure 1.1. Map of the Mesoamerican Reef Eco-region. Solid line highlights the ecological boundary defined from connectivity studies (Chollett et al. 2017), the original and official boundary of the MAR is marked by the dotted line. Inset map highlights the MAR ecoregion (black square) within the Wider-Caribbean.

1.2 Marine resource management

Positive feedback loops exist between diverse and healthy fish populations and reef health and resilience, suggesting that management of species or ecosystem have wider benefits when considered together (Guannel et al. 2016). Within the MAR commercial fisheries are estimated to be worth an estimated US$ 81.5 – 103.2 million per year (Canty et al., 2019). Important species include *Panulirus argus* (Caribbean spiny lobster), *Lobatus gigas* (queen conch), and a fisheries complex of species belonging to the grouper (Serranidae) and snapper (Lutjanidae) genera. These fisheries are a shared resource within the region, with previous studies indicating high levels of connectivity in key fisheries species, e.g. *P. argus* (Truelove et al. 2015), *L. gigas* (Truelove et al. 2017) and *Ocyurus chrysurus* (yellowtail snapper) (Chollett et al. 2017). Connectivity of these shared fisheries resources highlights the need for management cooperation at the ecoregion level (Truelove et al. 2015). Important relationships exist between fisheries and the habitats that support them, coral reefs, seagrasses and mangroves, with healthy, connected ecosystems supporting greater fish biomass (Brown et al. 2019; Mumby 2006; Rogers and Mumby 2019). Additionally, ontogenetic shifts in habitat use by fish species with both economic and ecological importance underlines the value of ecosystem-based management which incorporates habitats and fisheries, for the effective management of fisheries (Harvey et al. 2018). With the additional benefits of building resilience in coral reef, seagrass and mangrove ecosystems (Guannel et al. 2016) and promoting well-being in coastal communities (Newton et al. 2007).

1.2.1 Fisheries

Small-scale fisheries are ubiquitous throughout the Caribbean and MAR, and underpin economies of coastal communities, in addition to providing food security (Zeller, Booth, and Pauly 2006). Despite the importance to the livelihoods of coastal communities' small-scale fisheries are often unassessed and not included in management plans (Costello et al. 2012). There are significant challenges in assessing, and therefore managing, small-scale fisheries, including: the cost of collection of fishery independent data; the difficulty in implementing monitoring on a permanent basis; the scattered distribution of coastal communities; and the reliability of catch and fishing effort statistics (De Graaf et al. 2011; Salas et al. 2007). To overcome the paucity of data in small-scale fisheries and to account for illegal, unreported and unregulated fishing, catch reconstructions have been used to provide conservative baseline estimates of fishing pressure at the country, regional and global scales (Pauly and Zeller 2014, 2016). Catch reconstructions have identified significant underestimation in not only catch volumes (Teh and Pauly 2018), but also the economic value (Zeller et al. 2006) of small-scale fisheries. Metanalyses of temporal data can provide a baseline understanding in current fishing trends, identify key fisheries species, shifts in target species, and economic status of entire fisheries. Whilst these data have inherent errors and biases, they can provide a useful overview in fisheries trends and can provide a baseline from which fisheries management actions can be monitored and evaluated. In this thesis (Chapter 2), I use catch reconstructions to assess total landed catches of the different Honduran fisheries sectors, to understand the importance of artisanal fisheries in Honduras. Additionally, I conduct an economic analysis of the MAR artisanal fisheries for the four countries to assess the value of this sector in comparison to industrial fisheries in the region. Catch reconstructions provide conservative estimates of landed catches for fisheries where there is a paucity of data. Which can provide critical insights into the relative importance and trends in landed catches of different fisheries sectors, and used to inform fisheries management strategies.

There are numerous efforts in the region to improve spatial planning of MPAs. These focus on the connectivity of key fisheries species for the improved designation of MPAs, territorial use rights for fisheries areas, and no-take zones, e.g., the spiny lobster fishery (Chollett et al. 2016). The goal of these different management strategies is to regulate fishing activity, and promote sustainability within the different fisheries. Specifically, they aim to prohibit all fishing activity in no-take zones, while enhancing surrounding open-access fisheries through the spill-over effect (Halpern, Lester, and Kellner 2009). Such efforts have and will continue to greatly improve fisheries management, and if combined with data collection initiatives, will allow for monitoring and evaluation of management actions. Whilst there are advances in obtaining data on individual fisher landed catches (Canty et al. 2019), gaps in knowledge regarding fishing pressure across the seascape remain. The ability to detect where seafood products were caught has a number of fisheries management implications, which include estimating fishing pressure at different fishing grounds, and compliance with protected area regulations. Traditional vessel patrols are associated with diminishing returns on investment (Dhanjal-Adams et al. 2016), and therefore other methodologies are required. Genetic markers, otolith chemistry and morphometric analyses have been used to identify fish stocks at a range of spatial scales (Cadrin 2000; Davies et al. 2011; Ferguson, Ward, and Gillanders 2011), and have the potential to be powerful tools in assessing compliance and fishing pressure across the seascape. However, financial and capacity limitations of practitioners must be accounted for, as these are two of the main limiting factors in MPA effectiveness (Gill et al. 2017).

1.2.1.1 Focal species: *Ocyurus chrysurus*

The yellowtail snapper, *Ocyurus chrysurus*, is found throughout the Western Atlantic, from its most northly limit of Massachusetts, United States, to Sao Paulo, Brazil in the south (Thompson and Munro 1973). Throughout its range it makes significant contributions to industrial and small-scale fisheries, in addition to comprising an important recreational fishery. Despite the value of this species, little to no management exists to promote the sustainability of this fishery. A key component of managing a fishery is knowing the provenance of fish to understand fishing pressures at different fishing grounds. Tracking fishing boats may appear to be the obvious solution and has been widely implemented in industrial fisheries. However, the cost of satellite or cell transmission and cell range coverage makes this problematic to bring to scale in small-scale or artisanal fisheries. In this thesis (Chapter 3) I use microsatellite genetic markers, rare earth element ratios of otoliths (fish ear stones), and morphometric (fish body shape) analyses to test the accuracy of different tools in assigning individual fish to their fishing ground of origin. The ability to assign fish to fishing grounds allows for the assessment of fishing ground productivity across seasons and years, and can provide insights into the health of a fishery and fishing patterns of fishers and fishing communities. These data are the foundation for the creation of fisheries management strategies, and can provide the required monitoring and evaluation feedbacks to assess the success of implemented management actions.

Figure 1.2. Yellowtail snapper (*Ocyurus chrysurus*) caught on a handline within the Utila Cays fishery, Honduras. Image rights: International League of Conservation Photographers / Claudio Contreras-Koob.

1.2.2 Coral Reefs

Declines in coral cover of around 80% of their original values have been observed in the Caribbean and the MAR (Gardner 2003), where reefs are undergoing a phase shift, changing from coral to algal dominance (Hughes et al. 2007; Mumby et al. 2006). Losses in coral cover are associated with reduced habitat complexity (Magel et al. 2019) and the ability of reefs to support diverse fish communities (Wilson et al. 2010), in addition to declines of numerous ecosystem services to coastal communities (Weijerman et al. 2017). The key driver in coral reef decline is over fishing, which has altered fish community composition and therefore altered the ecological roles provided by these communities (Edwards et al. 2013; Robinson et al. 2017; Spalding and Brown 2015; Wilson et al. 2010). Declines in coral cover are being exacerbated by both local (e.g. eutrophication and sedimentation), and global (e.g. ocean acidification and increasing sea surface temperatures) scale stressors (Spalding and Brown 2015). As environmental conditions change there is growing realization that coral reefs may not be capable of natural recovery, and restoration is increasingly required (Hughes et al. 2017).

Within the Caribbean, coral reef restoration projects are primarily focused on two important reef building and critically endangered species of coral, *Acropora cervicornis* and *A.*

palmata (Aronson et al. 2008a; 2008b). These corals almost became extinct during the 1980s due to an outbreak of white-band disease, in addition to hurricane damage, eutrophication and other factors, which reduced the population by 80 – 90% of its original size (Gardner 2003; Precht et al. 2002). To date there has been limited to no recovery of these populations (Aronson et al. 2008a; 2008b), and therefore, restoration projects are using colonies from remnant *Acropora* populations that have been identified in various locations throughout the Caribbean, including Mexico (Porto-Hannes et al. 2015), and Guadeloupe (Japaud, Fauvelot, and Bouchon 2014), and Honduras (Keck et al. 2005). Asexual reproduction through fragmentation, is the dominant form of reproduction in these species (Lirman 2000), and may be advantageous as it allows for comparatively easier propagation of colonies (Johnson et al. 2011). However, this can result in high levels of clonality within populations (Baums, Miller, and Hellberg 2006; Hemond and Vollmer 2010; Japaud et al. 2015). A lack of genetic diversity can reduce the fitness of restored populations (Mcleod et al. 2019), and therefore a knowledge of genetic structure within remnant populations is essential to inform restoration practices (Johnson et al. 2011), and for the management of remnant populations (Pacioni et al. 2020). Microsatellite markers are useful tools in estimating genetic structure (Nybom 2004; Powell et al. 1996) and have specific advantages which include; the selective neutrality of loci (Meloni et al. 1998), and very high levels of allelic polymorphism (Bhargava and Fuentes 2010). High levels of allelic polymorphism are useful when assessing species which exhibit very low levels of variation (Bhargava and Fuentes 2010), and thus may be more indicative when sampling at fine spatial scales, such as across remnant populations. Other advantages include, the targeting of markers that are designed for specific species, although markers can often be used for closely related species, e.g., *A. cervicornis* and *A. palmata* (Baums et al. 2009; Baums, Hughes, and Hellberg 2005). Additionally, microsatellites have been shown to work well with low quality or degraded DNA (De Barba et al. 2017). Importantly, a number of studies have successfully used microsatellite markers to assess the genetic structure of Acroporid populations throughout the Caribbean, e.g. (Baums et al. 2006; Drury et al. 2017; Japaud et al. 2015; Porto-Hannes et al. 2015). Understanding genetic structure at fine-scales can improve restoration practices (Johnson et al. 2011) and has implications for the large-scale analyses and management of species (Thomas et al. 2015). Combining such data with on-going spatial management plans within the region will promote greater management of a critical fisheries habitat.

1.2.2.1 Focal species: *Acropora cervicornis*

The staghorn coral, *Acropora cervicornis*, is a critically endangered species with a range limited to the wider-Caribbean (Aronson et al. 2008a). In the 1980s an outbreak of white band disease in combination with some climatic events decimated populations of *A. cervicornis* and *A. palmata* (elkhorn coral), between 80-95% of corals were lost (Gardner 2003). Within the MAR, a site of significance is the Cordelia Bank Site of Special Importance to Wildlife, in Honduras, a protected area with high densities of *A. cervicornis* thickets (Riegl et al. 2009). Little is known about the genetic structure of these colonies, but, due to high fragmentation rates within this species there is the potential that the banks are dominated by a few clonal genets. In this thesis (Chapter 4), I use microsatellite markers to assess the genetic structure of *A. cervicornis* colonies across three banks within the protected area, to inform management and restoration projects.

Figure 1.3. Staghorn coral (*Acropora cervicornis*) colonies on Cordelia Shoal within the Cordelia Bank Site of Special Importance to Wildlife, Roatan, Honduras. Image rights: International League of Conservation Photographers / Claudio Contreras-Koob.

1.2.3 Mangroves

Mangroves are a diverse group of flowering plants that form highly productive systems along the intertidal zone throughout tropical and subtropical coastlines (Tomlinson 1994), and provide a number of critical ecosystem services to coastal communities (Lee et al. 2014; UNEP

2014). Among these services are the provision of critical nursery grounds to economically and ecologically important species (Dorenbosch et al. 2006; Igulu et al. 2014; Nagelkerken et al. 2002), which can promote resilience in nearby coral reefs and the fisheries they support (Mumby 2006; Rogers and Mumby 2019). Additionally, mangroves are important in climate change adaptation, by reducing flood damage (Menendez et al. 2020), protecting communities from hurricanes (del Valle et al. 2020), and keeping pace with sea-level rise through sediment accretion (Saintilan et al. 2020), and also in climate change mitigation via the sequestration of carbon (Rogers et al. 2019). Despite the importance of these ecosystems globally mangrove cover has significantly declined, with populations estimated to be between 35-85% of their original extent and becoming increasingly fragmented (Duke et al. 2007). However, over the last decade global mangrove deforestation rates have significantly slowed, due to increased awareness and protection, and in some areas mangrove cover has increased, through restoration initiatives (Friess et al. 2019).

Ecosystem-based fisheries management does not only focus on fish species, but also the habitats that support them, such as coral reefs which support adult populations (Harvey et al. 2018), and also mangroves which are an important fish nursery grounds (Rogers and Mumby 2019). Genetic structure and connectivity of mangrove populations is required to inform the spatial-scales of management (Bradburd and Ralph 2019), and create effective networks of protected areas. Genetic structure has been observed at various spatial scales across mangrove populations, from estuaries to bioregions (Cisneros-de la Cruz et al. 2018; Kennedy et al. 2016; Ngeve et al. 2017; Wee et al. 2017). Yet limited studies have been conducted at the forest scale, potentially because mangroves are considered to have low genetic diversity at fine-scales, due to high rates of self-fertilization and self-recruitment (Kennedy, Sammy, et al. 2020; Lowenfeld and Klekowski 1992). To asses genetic structure at fine-scales, a large number of genetic markers is required to identify sufficient genetic diversity. Whilst more recently a number of microsatellite markers have been developed for *R. mangle* (Kennedy, Craig, et al. 2020), prior to the development of these markers only a limited number existed (Rosero-Galindo et al. 2002; Takayama, Tamura, and Tateishi 2008). Significant advances have been made in next generation sequencing techniques such as, restriction site-associated DNA sequencing (RADseq). This technique allows for the relative low-cost discovery and genotyping of hundreds to thousands of genetic markers for any species (including non- model species), with no prior requirement for genomic information for the taxa being studied (Andrews et al. 2016; Karl et al. 2012). However, the need for high concentrations of high-quality DNA can be problematic, and there can be issues associated with the short length of the markers produced when conducting de novo assembly (Etter et al. 2011). Whilst no genome exists for *R. mangle*, the genome for a close relative *R. apiculata* has been sequenced (Xu et al. 2017), and this can be used as a reference genome. Understanding genetic structure at fine-scales can inform seascape level population genetic analyses (Bradburd and Ralph 2019), and mangrove restoration initiatives to reduce losses of genetic diversity during such initiatives (Granado et al. 2018).

1.2.3.1 Focal species, *Rhizophora mangle*

The red mangrove, *Rhizophora mangle,* is found along tropical and sub-tropical coastlines of the Atlantic and East Pacific, throughout the Americas and Caribbean, and West Africa (Duke, Yuk Ling Lo, & Sun, 2002). This species inhabits the most exposed part of the intertidal zone, the cusp between land and sea, and is easily identified by its complex aerial and prop root system (Tomlinson, 1994). The Americas is one of the regions of concern regarding the decline in mangrove cover, in particular Mexico (Friess et al., 2019; Polidoro et al., 2010), and where concerted effort for their conservation and management is urgently required. The management of mangrove forests is receiving increasing attention; however, little is known about the connectivity of mangrove forests within the Mesoamerican reef ecoregion. Connectivity within this species is complicated due to high rates of self-fertilization (Lowenfeld & Klekowski, 1992), high rates of local recruitment (Yamashiro 1961 in Tomlinson, 1994). and the potential of long-range dispersal (Rabinowitz, 1978). Here (Chapter 5) I use a restriction site-associated DNA genotyping method based on sequencing uniform fragments produced from type IIB restriction endonucleases to assess genetic connectivity within a small isolated red mangrove forest, little is known about the relatedness of mangrove within a forest, previous studies infer low genetic structure due to high rates of self-pollination and self-recruitment (Kennedy, Sammy, et al. 2020; Lowenfeld and Klekowski 1992).

Evidence-based management is critical for effective management of marine resources (Christensen et al. 1996; Ruckelshaus et al. 2008). To facilitate the integration of research from genetic and other studies into mangrove management strategies in the MAR an understanding of the current status of mangrove management is required. In this thesis (Chapter 6), I review the current status of mangroves and research foci within each country to identify the threats to mangroves and the research being conducted to promote their management. Additionally, an overview of mangrove legislation will enable specific recommendations to be provided which account for the geo-political landscape across the MAR, where a regional approach to management is required due to the high levels of connectivity in this shared ecosystem (Chollett et al. 2017).

Figure 1.4. Red mangrove (*Rhizophora mangle*) trees along the Punta Gorda coastline, Belize. Image rights: Steven Canty.

1.3 Thesis aims and chapters

The aim of this thesis is to highlight how basic research can be applied to specific marine resource management problems, and be part of the solution in promoting sustainability. I show how different data types including, genetic sequencing, rare earth element analyses, morphometric analyses, and meta-data analyses can be used to inform marine resource management strategies. In addition, these tools can be used in the monitoring and evaluation of management actions, to provide important feedback mechanisms to management, and be part of adaptive management of marine resources.

A detailed outline of the specific goals of the thesis follows:

> (A). *Provide data and tools to promote the management of small-scale fisheries within the Mesoamerican reef ecoregion*:

(A.1). A study to assess the role of catch reconstructions in providing baseline data and trends in small-scale fisheries in Honduras;

(A.2). A study to assess the potential of microsatellites markers, otolith chemistry and morphometric analyses as fish traceability tools.

(B). *Assess the power of microsatellite genotyping for population genetics at small-spatial scales:*

(B.1). A study of the population genetics of the endangered coral species, *Acropora cervicornis,* in Cordelia bank site of special importance to wildlife, Honduras.

(C). *Support the effective management of mangroves within the Mesoamerican reef ecoregion*:

(C.1). A study of the population genetics of the red mangrove, *Rhizophora mangle*, at the forest scale, in Fort Cay, Honduras;

(C.2). A review of legislation and research of mangrove ecosystems within the Mesoamerican reef ecoregion.

The thesis is composed of five data chapters:

In *Chapter 2*, I use catch reconstructions to examine the total landed catches of Honduran fisheries from 1950 – 2015, and to assess the importance of small-scale fisheries relative to industrial fisheries. The aim of this chapter is to highlight the critical role of small-scale fisheries in Honduras and the MAR, and the need for greater management of these fisheries.

In *Chapter 3*, I test a range of tools to assign individual fish to their fishing ground of origin. Specifically, I compare microsatellite genetic markers, otolith rare element ratio analyses, and morphometric analyses, the aim of which is to provide a practicable tool for fisheries managers within the Mesoamerican reef ecoregion.

In *Chapter 4*, I assess the genetic structure of *Acropora cervicornis* colonies located on three banks within the Cordelia Bank Site of Special Importance to Wildlife using microsatellite markers. The goal is to provide a baseline of genetic structure of *A. cervicornis* colonies which can be used to inform management strategies, with a focus on restoration.

In *Chapter 5*, I undertake a fine-scale population genetics analysis of *Rhizophora mangle* trees within a small area of forest using next generation sequencing methods. The aim of this chapter is to test the hypothesis of limited genetic structure of mangrove systems at the forest scale, and inform management strategies, including restoration.

In *Chapter* 6, I review mangrove management within the Mesoamerican reef ecoregion to assess how mangroves are managed in each of the four countries, and how threats are perceived by Ramsar site managers and researchers. The aim is to provide recommendations to improve the management of mangroves at the national and regional level.

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Chapter 2

Honduran catch reconstructions

2.1 The hidden value of artisanal fisheries in Honduras

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Contribution: Within this chapter I worked with Manuela Funes to update the landed catch reconstructions of 1950 – 2010 to 1950 – 2015. I conducted the statistical analyses for both the reconstructed landed catch data and economic value data. I led the writing of the initial draft and subsequent revised drafts, with input from Manuela Funes on the methodology, all other authors provided edits to drafts.

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The hidden value of artisanal fisheries in Honduras

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2.3 Abstract

Declining fisheries catches are a global trend, with management failing to keep pace with growth in fishing effort and technological advances. We reconstructed Honduras's catches, estimating the economic value within the industrial and artisanal sectors. We found catches were 2.9 times greater than shown in official statistics between 1950 and 2015. A confounding factor was the merging of industrial and artisanal catch data, which masked the significant decline in industrial catches and hid the strong growth of artisanal fisheries. In 1996, annual artisanal fisheries landed catches that surpassed the industrial fishery sector and in 2000, the annual net value of artisanal fisheries eclipsed the industrial fisheries' value. These data highlight the importance of artisanal fisheries in Honduras and challenge the long-held belief that the industrial sector contributes more to the national economy. Global paucity of fisheries data highlights the need for comprehensive strategies to collect more detailed and accurate fisheries data.

2.4 Introduction

The Republic of Honduras is located on the Central America isthmus, with coastlines on both the Atlantic and Pacific Oceans (Figure 2.1). In accordance with the United Nations Convention on the Law of the Sea, Honduras claimed its Exclusive Economic Zones (EEZs) in both the Atlantic (within FAO statistical area 31) and the Pacific (within FAO statistical area 77). The north shore of Honduras, located within the Caribbean basin of the Atlantic Ocean, is the longer of the two coastlines and is bordered by the EEZs of Guatemala, Belize, Mexico, Cuba, the Cayman Islands, Jamaica, and Nicaragua. The Pacific coastline is much smaller and is exclusively within the Gulf of Fonseca, fully enclosed by the EEZs of El Salvador and Nicaragua (Figure 2.1). The sharing of EEZ borders with numerous countries, particularly within the Honduran Caribbean, has implications for transboundary fish stock management and the potential for cross-border fishing activities (Perez, 2009).

Fishing has been an important economic sector in Honduras for more than 100 years (MacKenzie & Stehlik, 1996), contributing 5% of the country's gross domestic product with an average value of US $385 million per year (Beltrán Turriago, 2011). Fishers employ a diverse range of gears to exploit lagoon and riverine systems, coral reefs, other near-shore habitats (e.g., seagrass beds), extensive offshore banks, and pelagic waters (Box & Canty, 2011; Soto, 2012). The main fisheries on the Caribbean coast are the Caribbean spiny lobster (*Panulirus argus*) and queen conch (*Lobatus gigas*), while the main fishery on the Pacific coast targets western white shrimp (*Litopenaeus occidentalis*) (FAO 2002).

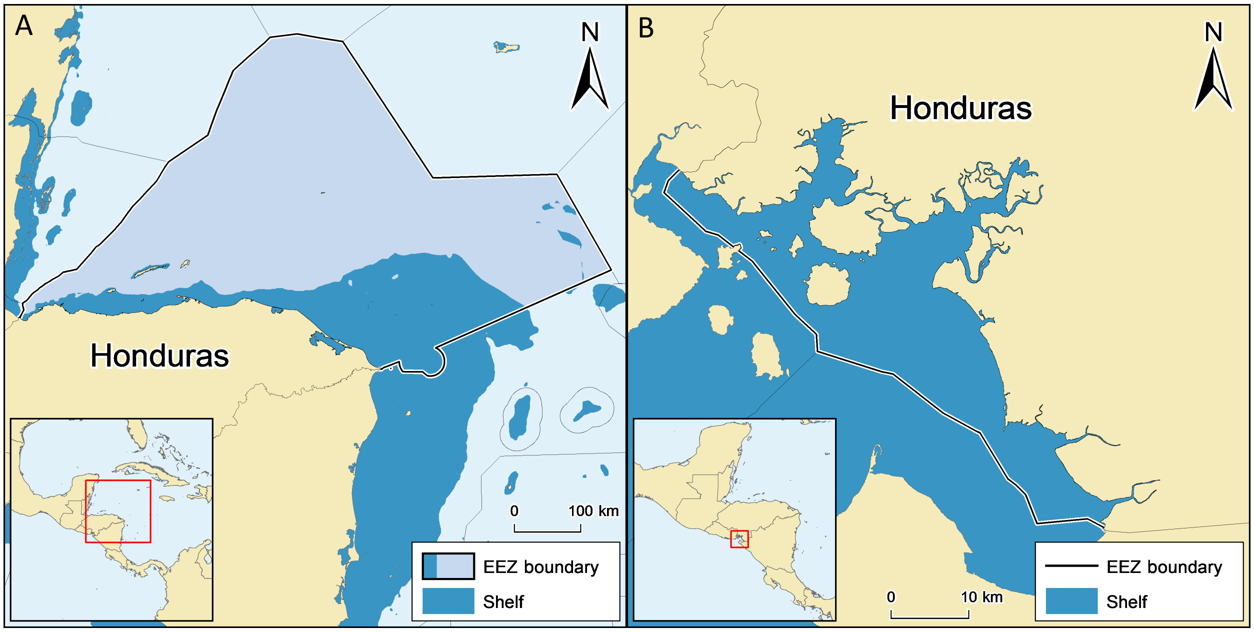

Figure 2.1. Maps of the two parts of the Honduran Exclusive Economic Zone (EEZ). A: Honduras' EEZ in the Caribbean covers 218,000 km2, of which 60,300 km2is shelf, i.e., less than 200 m deep. B: Honduras' EEZ in the Pacific is small (747 km2) and shallow, and consist only of the inner Gulf of Fonseca, shared between El Salvador in the North, Honduras, and Nicaragua in the South.

Artisanal and subsistence fisheries have been present in Honduras at least since the Mayan era; however, the large expansion of artisanal fisheries across the Caribbean and Pacific coasts is a relatively recent phenomenon, commencing in the 1970s (MacKenzie & Stehlik, 1996). Artisanal fisheries provide an essential source of nutrition and employment to coastal communities, especially in remote coastal areas where there are few other economic alternatives. Due to a lack of processing infrastructure, catches from the Honduran Pacific coast supply only national markets (Box and Bonilla Salgado, 2009), while artisanal fisheries on the Caribbean coast supply both national and international markets. In addition, the shallow hydrology precludes the deployment of larger boats within the Gulf of Fonseca, which restricts the Honduran industrial fishery to the Atlantic coast (Soto, 2012).

The Honduran national industrial fishery began in the late 1950s (FAO, 2002). Previously, only foreign industrial fleets, mainly from the United States, were fishing and landing in Honduras. As international fleets began to leave Honduran waters, the national industrial fishing fleet started to develop. An additional trigger was the collapse of the United States industrial conch fishery in 1975, which enabled the Honduran industrial fishery to start supplying the United States market. Currently, 90-95% of industrial marine catches are exported, primarily to the United States (Espinoza, 2007). Recreational fisheries are present across the Honduran shore in the Caribbean, but sport fishing operations are primarily located in the Bay Islands, where the majority of international tourism is concentrated, receiving over 700,000 tourists per year (INE, 2018).

Signs of overexploitation have been documented in Honduran fisheries. The conch fishery closed in 2003 due to a trade embargo placed on conch exports by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2003). The Nassau grouper (*Epinephelus striatus*) population collapsed in 2004 (Box & Bonilla Salgado, 2009). According to Honduran fishers, the decline and collapse of these fisheries was a consequence of irresponsible fishing practices, and habitat degradation via destructive fishing gears (Korda, Hills, & Gray, 2008), which mirrors trends in Jamaica (Hughes, 1994) and the Caribbean as a whole (Gobert et al., 2005).

Overfishing is a great challenge facing governments and the scientific community (FAO, 2016). As a minimum requirement, effective management requires reliable data, with catch data representing the most fundamental of all fisheries data. Comprehensive and accurate records of fisheries catches are important to allow monitoring of fisheries trends over time, with the effect of fisheries regulations to be observed, and subsequently adjusted if required (Belhabib, Koutob, Sall, Lam, & Pauly, 2014). However, while technological advances in fishing vessels and gears are evident, systems to record catch data and monitor fisheries have not kept pace. There is a chronic need for improvements in data collection and the incorporation of these data into fisheries management (Pauly et al., 2002). The status of the world’s fisheries maybe worse than we currently perceive, given that a large fraction of catches has been missing from national fisheries catch estimates in virtually every country of the world (Pauly & Zeller, 2016a, 2016b). Crucially, the pattern of missing data changed over time as an inadvertent by-product of well-intentioned efforts to improve data collection systems, resulting in a time series bias now known as ‘presentist bias’ (Zeller & Pauly, 2018). Thus, there is a concerted global effort led by the *Sea Around Us* initiative to reconstruct national, and by extension, regional and global fishing statistics that add comprehensive estimates for all unreported catches to officially reported landings data in order to derive a better and more comprehensive understanding of fisheries catches over time (Zeller, Booth, Davis, & Pauly, 2007; Zylich et al., 2014; Zeller, Harper, Zylich, & Pauly, 2015; Funes et al., 2015; Pauly & Zeller, 2016b, 2016a).

The starting point for reconstructions is the official reported landings data provided by national agencies to the Food and Agriculture Organization of the United Nations (FAO); these data are subsequently compared with the formal and grey literature, and inferences on additional, previously unreported catches are validated with local experts (Zeller et al., 2016). Funes et al., (2015) reconstructed marine fisheries catch data for the Republic of Honduras, by deriving the best time series estimates of unreported catches for 1950-2010, from both the Atlantic and Pacific coastlines to complement reported data. The present study revised, improved and extended the analysis performed in Funes et al. (2015), by updating the time series to 2015, rectifying all estimates of fishing categories, completing the lacking fishing categories and enhancing the sources of data. Once the corrected reconstructed catch was available aim was to statistically describe and compare the catch trends over the years, and to evaluate the economies of the fisheries sectors in Honduras and in the context of the Mesoamerican reef countries (Mexico, Guatemala, and Belize).

2.5 Methodology

2.5.1 Catch reconstructions

Honduran catch reconstructions were conducted using the method of (Zeller et al., 2007, 2016), following the principles described in (Pauly, 1998). We only addressed marine wild capture fisheries, therefore aquaculture production and freshwater catches are not included in our estimates, nor are catch records of marine mammal, turtles, worms, seaweed or algae. For a full list of the categories used in this reconstructed see supplementary materials (S1).

Industrial, artisanal, subsistence and recreational fisheries for fishing areas 31 and 77 (Figure 2.1) were estimated separately. Artisanal fishing was defined by the Honduran Fisheries Law of

1959, as “fishing within three nautical miles from the shore using boats with a capacity of three tonnes or less and employing basic fishing equipment”. All commercial fishing activities encompassed by this definition were considered artisanal. Commercial fisheries with vessels of greater capacity and fishing at greater distances were considered industrial. Subsistence fisheries were defined when landed catch was for personal consumption and no commercial transaction is associated with the landed catch. Recreational fisheries were defined as sport fishing, whereby individuals may pay for a fishing excursion, but retained landed catch was not sold.

2.5.1.1 The Caribbean Sea (FAO Area 31)

2.5.1.1.1 Reported industrial catch

Industrial fishing in Honduras is limited to Area 31 (Caribbean) with four fleets, licensed to exploit four resource types: Caribbean spiny lobster, queen conch, shrimp, and finfish (primarily grouper and snapper). The industrial sector is diverse, fishing vessel lengths vary from 4 to 78 m (13 to 258 feet), crews range from 6 to 85 people, and the duration of fishing excursions vary from 10 to 90 days, depending on the fishery (CITES, 2012). National industrial fisheries first appeared in Honduras during the late 1950s (FAO, 2002), at which time only limited catch data were reported. Given that industrial catches were always landed at major ports, all catches from 1950 to 1989 reported to FAO were considered industrial catch. In 1990, the governmental body DIGEPESCA was created and began to collate fisheries data; therefore for the period of 1990-2015 industrial landed catch data was obtained directly from DIGEPESCA records.

2.5.1.1.2 Illegal industrial catch

Illegal catch is any catch that is acquired or removed from the EEZ of a country without the consent of that country. In instances where these landed catches are processed through Honduran packaging plants they become included in official data, and contribute to the national economy. Here we estimated illegal catches taken by the Honduran fishing fleet from neighboring EEZ’s of Nicaragua and Jamaica. The Honduran Grand Banks are situated in the far eastern part of the EEZ, close to the Nicaraguan border, extending northeast to the Jamaican border, the Honduran fleet do enter into Nicaraguan and Jamaican EEZ waters illegally. In order to consider this and remain conservative, we estimated illegal catch as 15% of the total estimated industrial lobster catch, as a constant percentage over time. Estimations on foreign fishing vessels illegally entering to Honduran EEZ were not included in the analysis, however we assume that the illegal fishing within the Honduran EEZ to be equivalent to that of the Honduran fleet in other EEZ's and therefore include the illegal capture of the Honduran industrial fleet in our estimations.

2.5.1.1.3 Unreported industrial catch

Undeclared discards are part of the industrial unreported catch in Honduras. Discards are absent or minimal in the conch and lobster fisheries, as conch are hand-collected and lobster are either hand-collected or caught in traps. The capture of finfish is mainly from vertical long lines, where low valued bycatch is usually consumed and accounted for in the 'subsistence fishery' category (see below). Thus, the major non-selective industrial fishery component is the bottom-trawl shrimp fishery. To estimate unregulated shrimp discards we followed Davies et al., (2009) who suggested a bycatch rate of 78%, where no bycatch was landed. This percentage was applied to FAO reported shrimp landings for 1950-2015 to estimate what was taken from the sea to be discarded later. Any bycatch in the industrial finfish fishery was assumed to be either recorded in the official records or used for personal consumption and therefore estimated under 'subsistence'.

2.5.1.1.4 Reported artisanal catch

The large extension of the Caribbean coastline provides suitable fishing grounds across the Honduran mainland and island archipelagos, with more than 135 different fishing communities (Stephen Box, personal observation) with over 7,000 registered artisanal fishers included in the DIGEPESCA fisher registration system. The geographical expanse and remoteness of many of these communities has made it difficult to collect catch data from these fisheries, resulting in limited available data.

From 2001, FAO records included some artisanal fishing activity (Diana Vasquez, Centro de Estudios Marinos, personal communication). We assumed that the remainder of FAO catch unaccounted in DIGEPESCA data was artisanal catch for the period of 2001-2015, where FAO landings exceeded DIGEPESCA reports. Since artisanal fishing in this region was not reported until recently, the FAO landings data for the early time periods were assumed to be industrial fisheries. As a conservative estimate, the reporting of artisanal fisheries to the FAO was considered to improve linearly from 0% of catch reported to the FAO in 1989 to the calculated percentage of FAO catch estimated to be artisanal in 2001 (i.e., 74% of reported data).

2.5.1.1.5 Illegal artisanal catch

Transboundary fishing by artisanal fishers is a problem with Honduran boats making excursions into Belizean territorial waters and Guatemalans fishers making excursions into Honduran (and Belizean) waters (Perez, 2009). To incorporate this and remain conservative, we estimated illegal artisanal catch as 15% of the total estimated artisanal catch, as a constant percentage over time. These illegal catches were identified and labeled as Honduras fishing in Belizean waters. We did not estimate the catches of foreign artisanal fleets fishing illegally in Honduran waters. As per the industrial fishery, we assume that illegal fishing of others in Honduran waters is equivalent to the illegal transboundary fishing activity of the Honduran artisanal fleet and therefore include illegal landed catch within our estimates.

2.5.1.1.6 Unreported artisanal catch

Despite artisanal fisheries existing in Honduras since the pre-Columbian period, no data were available for the artisanal fishery for the period 1950-2000. Reporting of artisanal fisheries has occurred since 2001 primarily from the cities of La Ceiba, Puerto Cortez and Tela along the Caribbean coastline. However, no catch data have been collected from many of the smaller fishing communities in more remote location along the Honduran north shore, despite their considerable fishing effort (Stephen Box, unpublished data). In addition, large inconsistencies were found between the FAO dataset of 2011 and other sources of information. For example, differences in reported vary in magnitudes of 4.8 to 10 times, principally for lobster and finfish catch (e.g., FAO, 2002; Heyman and Granados-Dieseldorff, 2012). To remain conservative, our estimates of unreported artisanal catch assumed that reported artisanal catch reflected 50% of total catch from artisanal fisheries from 2001-2015. Total reconstructed artisanal catch from 2001 to 2015 was used to calculate an average catch rate per artisanal fisher: annual tonnage of the reported artisanal data (2001–2015) divided by the number of fishers for that time period, which led to an overall catch rate (i.e., tonnes of fish per fisher per year). In the period of 1950 to 2000, reconstructed artisanal annual catch was estimated by multiplying the catch rate by the number of artisanal fishers estimated for each year (FAO, 2002); see methodology of artisanal fisher's estimation in subsistence section.

2.5.1.1.7 Subsistence fisheries

Fishers from the artisanal sector may set aside a portion of their catch for personal consumption (MacKenzie and Stehlik, 1996); The artisanal fisheries-derived subsistence catch was estimated by multiplying the number of artisanal fishers by an amount of fish per capita for home consumption. FAO (2002) documented at total of 9,132 fishers on the Atlantic coast, which also matched well with grey literature estimates (Box and Canty, 2011). The artisanal fisher population was assumed to change over time as a fixed proportion (0.00177%) of the national population of Honduras from 1950–2015 (World Bank, 2017). The per-fisher level of subsistence catch was taken from a study conducted in the neighboring country of Guatemala (Trujillo et al., 2012), which estimated a take-home subsistence portion of 70 $kg \cdot fisher^{-1} \cdot year^{-1}$. This estimate is conservative considering that fishers share the catch with their family.

In addition, the common Caribbean donax (*Donax denticulatus*) is gathered by hand, usually by local women and children (MacKenzie and Stehlik, 1996). The donax catch is intended only for subsistence and not sold at markets (MacKenzie and Stehlik, 1996). As a minimum, we estimated an average of 5 kg of donax per year per artisanal fisher's household. Therefore, we estimated a total subsistence catch of 75 $kg \cdot fisher^{-1} \cdot year^{-1}$ for the Honduran Caribbean region. This is likely a very conservative estimate.

2.5.1.1.8 Recreational fisheries

We categorized recreational fisheries as the capture and non-release of sport fish species (e.g., mahi mahi, *Coryphaena hippurus*). To estimate catch from this sector, we firstly identified Honduran sport fishing companies using online searches via Google and Trip Advisor with combinations of the following search terms, "sport", "fish*", "recreation*", "trip*", "excursion*", "tourism", "activities", "Honduras", "Bay Islands", "Roatan", "Utila", "Guanaja", "Cayos Cochinos" (*represents derivatives of a search term, e.g., fish, fishing). Secondly, following Belhabib et al., (2016), YouTube videos were identified using names of sport fishing companies collated in the previous search. From each video, we identified and recorded the number of fish caught and their species. The weight of landed catch was sometimes reported by the fisher; where this did not occur, we estimated fish length and subsequently calculated their weight using species-specific parameters to transform length to weight from www.fishbase.org (Froese and Pauly, 2017). The number of annual trips of each company was estimated through tallying the number of reviews and Instagram posts each company received per year, these were cross-referenced to prevent duplication of fishing excursions. The number of reviews ranged from 16-18 for the most popular companies over the last three years, and the number of Instagram posts were around 150. We assumed that recreational tourism fishing to have officially started in 1985, based on information gained from the sport fishing company websites. The number of companies that offered fishing excursions were estimated to have grown linearly from 1 to 32 between 1985 and 2012, by which time all companies had been established. The number of fishing excursions per company was set to vary between 20 and 33 following trends in the number of annual visitors to Honduras (INE, 2018), as validated by local consultants (Mayra Nuñez, Centro de Estudios Marinos, personal communication).

In addition, since 1999 an international annual fishing tournament is held on Roatán, targeting mainly billfishes (Istiophoridae). The amount of fish taken during fishing tournaments was estimated. Lists of the capture, discriminated by participant, in each category, were available for past editions on the tournament's official Facebook page. Total catch was estimated by approximating each species´ weight (available on www.fishbase.org), and considering all the participants and days of tournament. Retained catches decreased after 2009 when the main target species started to be released (i.e., catch and release), but fishers still kept some bycatch species for example mahi mahi (*Coryphaena hippurus*) or wahoo (*Acanthocybium solandri*). In 2011, captures from tournaments increased as the island of Guanaja started to host an annual sports fishing event.

2.5.1.2 Gulf of Fonseca (FAO Area 77)

2.5.1.2.1 Reported artisanal catch

In the Gulf of Fonseca, an industrial fishery sector as defined by the Honduran Fisheries Law of 1959 is not present; all data reported by FAO are considered to be from the artisanal fisheries. Any Honduran-flagged offshore vessels were not considered in this study, as fishing activity occurs outside of Honduran waters (Schiller, 2014; Le Manach et al., 2016).

2.5.1.2.2 Illegal artisanal catch

Transboundary fishing activities are known to occur in Pacific waters; fishers from Honduras make fishing excursions into the waters of El Salvador and Nicaragua. We performed a conservative estimation of illegal catches to be a 5% of the total estimated artisanal finfish catch, a constant percentage over time. We assume that illegal transboundary fishing activity of El Salvadorian and Nicaraguan fishers within Honduran territorial waters is equal to the illegal fishing activity of the Honduran artisanal fishers, and therefore included all landed catch by the Honduran artisanal fleet within our estimates.

2.5.1.2.3 Unreported artisanal catch

Several reports on fishing activities within the Gulf of Fonseca (Box and Bonilla Salgado, 2009; Soto, 2012) presented significantly larger catches than reported in the FAO 2011 dataset. These reports consist of annual assessments in 2004 and 2008. For each major target group, crabs, clams, finfish and shrimp, there were differences between the catches in the assessments and the FAO dataset for the same years. We calculated an unreported catch ratio of the difference between the assessments and the FAO dataset for each of the major target groups and applied this as a fixed ratio of the reported catches through 2015. Although reporting within the artisanal fishery has improved, it remains low and fluctuates year by year. To minimize any bias, we assumed a constant percentage differential between reported and unreported catch throughout the period of 1950-2003.

Soto (2012) suggested that there are no significant discards in the shrimp fishery, because the majority of the fish caught as bycatch is retained and consumed. Therefore, any bycatch was assumed to be part of the catch of subsistence fisheries. Furthermore, as artisanal fisheries within this area employ trammel and cast nets rather than trawls (MacKenzie and Stehlik, 1996; Box and Bonilla Salgado, 2009; Heyman and Granados-Dieseldorff, 2012), discarded bycatch is minimal.

2.5.1.2.4 Subsistence fisheries

Subsistence fisheries catches were calculated following the procedures described for the Caribbean, except that the majority of subsistence catch was based on the incidental fish bycatch from the shrimp fishery (see above). In this case the anchor point for the number of artisanal fishers was 1,600 in 2004 (Soto, 2012).

2.5.1.2.5 Recreational fisheries

We could not find any records of recreational fishing in the Gulf of Fonseca, and local experts had no knowledge of any commercial enterprises engaged in recreational fisheries. We assumed that all landed catch would be consumed and therefore consider any domestic recreational fishing that may occur to actually count as subsistence fishing, whose catch was estimated above.

2.5.2 Fisheries economics

Economic data (i.e., landed value) for the fisheries of Honduras, Mexico, Belize, and Guatemala were provided by the *Sea Around Us*. The landed value of the catch is based on the ex-vessel price data which represent the prices in real 2010 US$ paid to fishers at the first point of sale, combined with catch volumes, represent the landed value of the catch (Sumaila, Marsden, Watson, & Pauly, 2007; Swartz, Sumaila, & Watson, 2013; Tai, Cashion, Lam, Swartz, & Sumaila, 2017). We examined the landed value data for the four countries that make up the Mesoamerican reef ecoregion (Honduras, Mexico, Guatemala, and Belize), and using reconstructed landed catch data – discards were not included – data were downloaded from the *Sea Around Us* data portal (http://www.seaaroundus.org/data/#/search).

2.5.3 Statistical analysis

Reported and unreported data from both the Atlantic and Pacific coasts were combined to generate a total Honduran reconstructed catch time series for 1950-2015. Trends of catches tonnages and trends of reconstructed economic values (landed value of catches) over time, from reported and unreported catches of the industrial and artisanal sector were analyzed using segmented linear regressions, in the R-package SEGMENTED (Muggeo, 2008), and changes in the slope were evaluated applying Davies tests in the same package. Segmented regression models determine regression break point years that indicate a significant change in trend over time, and segmented line slopes. Prior to analysis, all data were evaluated for normality, all data were identified to be within the boundaries of normal distributions.

2.6 Results

The total reconstructed catches as estimated here for 1950-2015 were 2.9 times greater than the data reported to FAO by Honduras (Figure 2.2a). Official records reported total landed catches of approximately 500 t in 1950 increased to 11,079 t by 2015. This compares to our reconstructions that estimated total catches of around 5,000 t in 1950 and 32,000 t in 2015 (Figure 2.2a). Catches from the Caribbean Sea in the Atlantic Ocean (FAO Area 31) comprised the greatest contribution to total Honduran catches, with approximately 80% in 2015. For the Caribbean side (FAO Area 31), official catch records reported approximately 500 t in 1950, which increased to just under 9,000 t in 2015, while the catch reconstruction estimated 5,000 t in 1950, which increased to over 26,000 t in 2015 (Figure 2.2b). Catches from the Pacific Ocean (FAO Area 77) have increased in importance, in 1950 they accounted for less than 0.01% of the total catch, while by 2015 they comprised over 20% of the total reconstructed catch. No official records were identified for this area in 1950, while the reconstruction suggested catches of 23 t in 1950 (Figure 2.2c). By 2015, official records reported catches of 2,000 t, while our reconstruction estimated catches of nearly 6,000 t (Figure 2.2c).

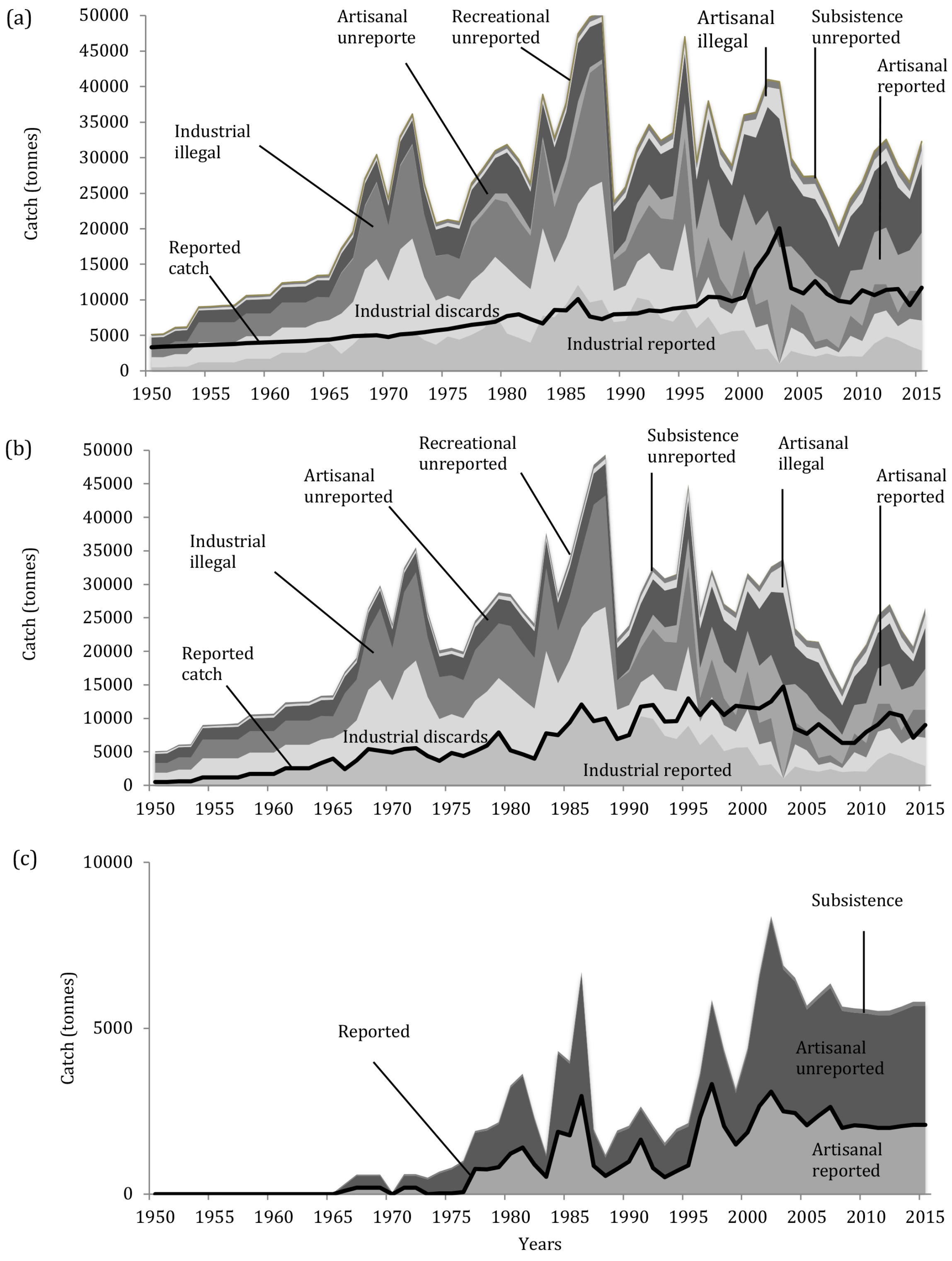

Figure 2.2. Honduran catch reconstructions for the period of 1950-2015. (a) Total combined catch from Areas 31 and 77 (Note: official reported catch black line); (b) Catch reconstructions for Area 31; and (c) Catch reconstructions for Area 77 (note different Y-axis scale).

Differences in trends between reported and reconstructed catch time series were observed (Figure 2.3). Reported total catches suggested a continuous period of growth from 1950 to 2000, after which catches began to decline (Figure 2.3a, Table 2.1). Our reconstruction estimates followed a similar trend; however, the period of growth is shorter, 1950 to 1986, after which time catches declined (Figure 2.3a, Table 2.1). In the industrial fishery, reported and reconstructed estimates followed the same trend; a period of growth from 1950 to 1986 was observed, followed by a significant decline (Figure 2.3b, Table 2.1). However, reconstruction estimates suggested a much stronger decline in industrial catches (which include discards) after 1986 (Figure 2.3b, Table 2.1). While unreported industrial landings drove much of this difference, unreported discards from this sector also contributed (Figure 2.2a). Reconstructed and reported estimates for the artisanal fisheries followed matching trends, with a period of relatively gradual growth followed by a period of more rapid growth, starting in the early and late 1970s, respectively (Figure 2.3c, Table 2.1). The growth of artisanal fisheries is associated with an increased contribution of this sector to total landed catches of the country, and by 2015 artisanal catches accounted for approximately 61% (nearly 20,000 t) of the total catch (Figure 2.2a).

Table 2.1. Results of segmented regressions and Davies tests for total, industrial and artisanal reconstructed and reported catches of Honduras for the time period 1950-2015, and for reconstructed economic landed value (2010 US$) of the industrial and artisanal fisheries.

Catch sector	Landed catch time series	Segmented regressions			Davies test
		Breakpoint (year)	Line	Slope (t. yr^{-1})	
Total	Reconstructed	-	1	951.8	-
		1986	2	-407.8	**0.0001**
	Reported	-	1	284.5	-
		2000	2	-276.4	**0.0001**
Industrial	Reconstructed	-	1	706.3	-
		1986	2	-909.2	**0.0001**
	Reported	-	1	226.6	-
		1986	2	-261.9	**0.0001**
Artisanal	Reconstructed	-	1	105.4	-
		1972	2	456.5	**0.04**
	Reported	-	1	4.9	-
		1979	2	261.8	**0.0002**

Catch sector	Landed value time series	Segmented regression			Davies test
		Breakpoint (year)	Line	Slope (US$million yr^{-1})	
Industrial	Reconstructed	-	1	1.2	-
		1986	2	-2.4	**0.0001**
Artisanal	Reconstructed	-	1	0.2	**-**
		1996	2	0.8	**0.0001**

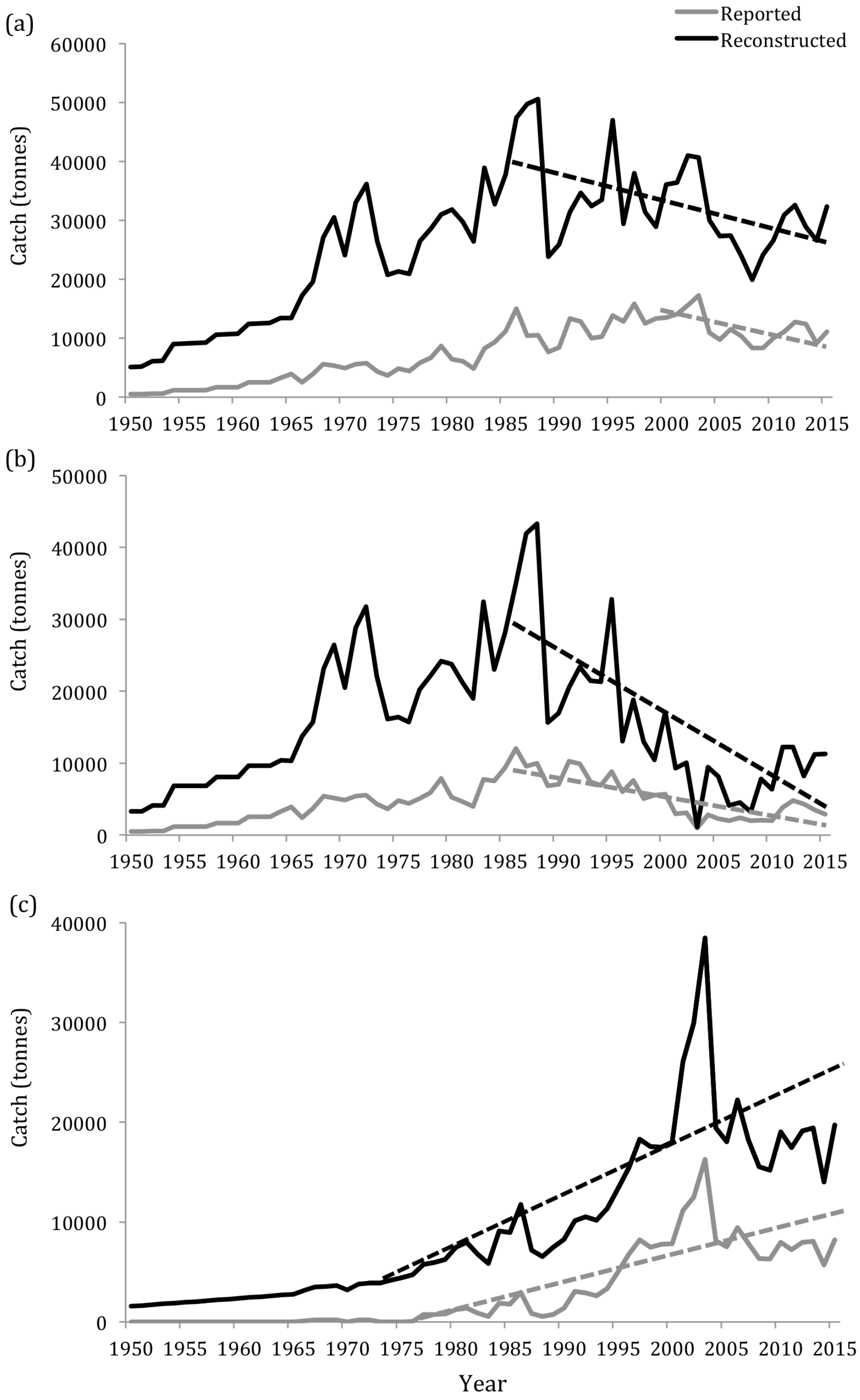

Figure 2.3. Reported catches (grey) and total reconstructed catch estimates (black) for total catches of (a) all Honduran fisheries, (b) industrial fisheries, and (c) artisanal fisheries (note different Y-axis scale). The regression trend lines (dashed lines) represent periods of catch decline or increase (identified as a breakpoint by segmented regression analyses).

Historically the industrial fishery was the fishery of greatest value; however, as catches declined in this fishery and increased in the artisanal fishery, the artisanal fishery increased in value and surpassed the landed value of the industrial fishery in 2000. The industrial fishery peaked in landed value in 1987, at US$ 59 million and declined to just under US$ 13 million by 2015 (Figure 2.4a). The Caribbean (Area 31) artisanal fisheries from the same period show an increasing value in the fishery since 1950, in 1996 a significant increase in the value of the fishery is observed with a peak value of US$ 35 million in 2003 (Figure 2.4a). The pattern of artisanal fisheries being of greater economic value is found in all four countries of the Mesoamerican reef region (Figure 2.4). In Mexico and Belize artisanal fisheries have been of greater value since 1950; however, this gap has only increased over time (Figure 2.4b & c). In Guatemala, as in Honduras, artisanal fisheries became more valuable around 2001 (Figure 2.4d).

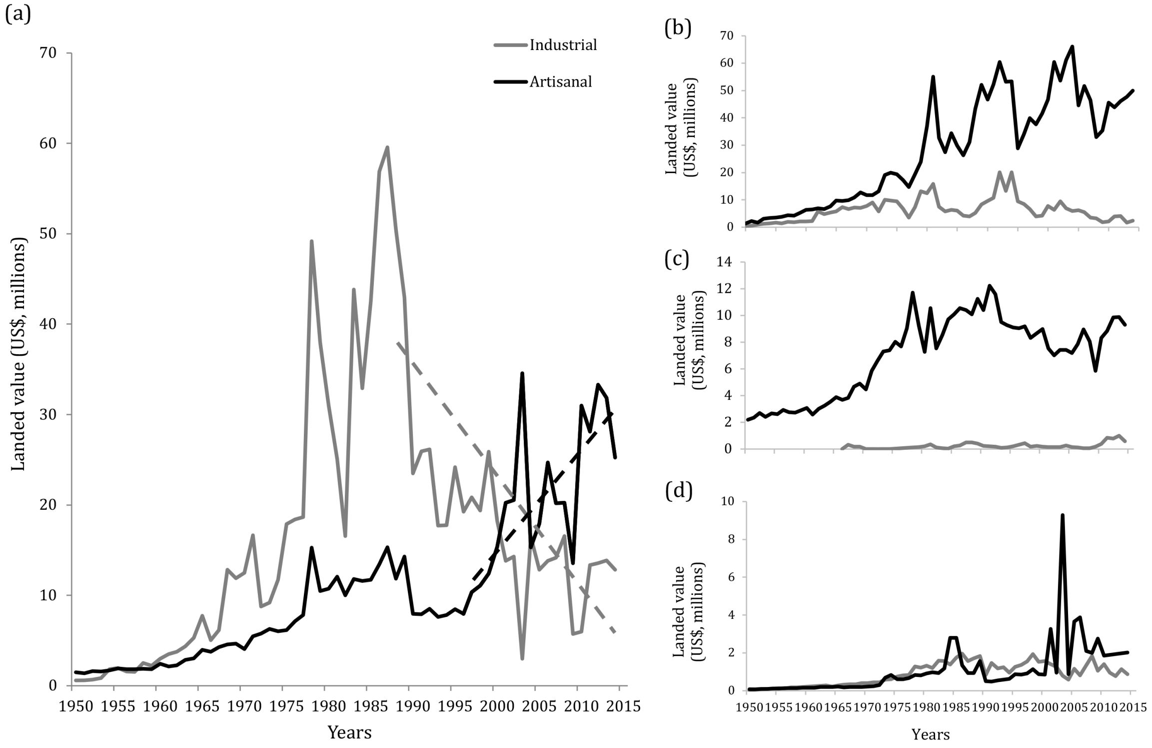

Figure 2.4. Mesoamerican reef ecoregion fishery valuations, based on reconstructed landed data (discards are not included) from the Caribbean Sea fisheries of (a) Honduras, (b) Mexico, (c) Belize, and (d) Guatemala (note different Y-axis scale). Landed catch values are of reconstructed catches, data for all countries were downloaded from the Sea Around Us online database. The regression trend lines (dashed lines) represent periods of catch decline or increase (identified as a breakpoint by segmented regression analyses) in the Honduran fishery.

2.7 Discussion

The reconstructed catches for the Honduran fisheries in the Atlantic (FAO Area 31) and Pacific (FAO Area 77) EEZs were 2.9 times greater than the catches (landings only) reported by FAO on behalf of Honduras. Our reconstruction illustrated that contrary to the official reported data, which implied a period of continuous growth from 1950 to 2000, total reconstructed catches suggested that the Honduran catches have actually been in decline since 1986. This decline, driven by strongly declining industrial catches was masked by significant increases in artisanal catches starting in the early 1970s. The growth in artisanal catches meant that by 1996, catches by the artisanal sector exceeded the catches of the industrial fishery, and by 2015 accounted for approximately 61% of the total reconstructed catches. Associated with the change in the dominance of landed catch from the industrial to the artisanal sector is a distinct shift in economic importance since 2000, with the artisanal fishery worth more annually than the industrial fishery. There is lag of approximately four years between landed catch and the economic value of the artisanal fishery surpassing the industrial fishery. This is due to the high value species associated with the industrial fishery, e.g. spiny lobster; in contrast to the lower priced finfish, which contribute a greater proportion of artisanal fishery catches. A similar trend is observed in Guatemala; while artisanal fisheries have been more economically valuable than industrial catches in Mexico and Belize since 1950. These economic data highlight the importance of artisanal fisheries within the Mesoamerican reef ecoregion, which supports over 2 million coastal people (Kramer & Kramer, 2002), and highlights the need for focused management within this important fishing sector.

This shift in sector emphasis from industrial to artisanal fisheries has important implications for fisheries management, as artisanal fisheries have a greater potential for sustainable use of coastal resources (Pauly, 2006), and to ensure the resilience of coastal communities through food security (Golden et al., 2016) and employment (Beltrán Turriago, 2013). These findings highlight the critical importance of disaggregating data to fisheries sectors to identify important trends and patterns within a country's fishery (Pauly & Zeller, 2016a) and for investing in data collection systems for artisanal fisheries (Pauly & Charles, 2015). The majority of artisanal fisheries in Honduras are within the informal sector and therefore no official records of catches or the associated value exist, which proliferates the underestimation of their importance to coastal communities and their economies.

The reported data for Honduras suggested mistakenly that the country's fisheries were growing until 2000, whereas the reconstruction illustrated that the growth period ended much earlier, in 1986, followed by a much stronger decline in catches. The disparity in trends between these two data sets has important implications for fisheries management and data collection from all fisheries sectors. Our results highlight that the aggregation of data from different fisheries sectors can mask important changes within a country's fishery (Pauly & Charles, 2015). By disaggregating the industrial and artisanal sectors, we were able to show how the industrial fisheries have been in decline since 1986, whilst catches from artisanal fisheries, from both the Atlantic and Pacific Oceans, have increased. The combined catches from the Atlantic and Pacific are greater than the industrial fishery landings. Although a lack of consistent fishing effort data prevented us from assessing if the decline in industrial catches was related to a shift in fishing effort from the industrial sector to the artisanal sector, it is likely that the artisanal fishery has undergone independent growth in parallel, rather than in response to a decline in the industrial fleet. This has been mirrored in the economic growth in the artisanal sector and provides further evidence for the need of comprehensive management of artisanal fisheries to maintain food security and livelihoods in coastal communities.

The general results of our catch reconstruction for Honduras are comparable to other reconstructions for Central American countries, with reconstructed data being higher than reported data, 1.4 times for Panama (Harper, Guzman, Zylich, & Zeller, 2014), 2.6 times for Costa Rica (Trujillo, Cisneros-Montemayor, Harper, Zylich, & Zeller, 2012), 3.4 times for Nicaragua (Haas, Harper, Zylich, & Zeller, 2015) and 3.5 times for Belize (Zeller, Graham, & Harper, 2011), and about 1.5 globally (Pauly & Zeller, 2016a, 2016b). Additionally, artisanal fisheries are of greatest economic importance in the Caribbean fisheries of the four countries of the Mesoamerican reef ecoregion, Mexico, Belize, Guatemala, and Honduras. Interannual variability on the reported and reconstructed catches trend is commonly found in all catch reconstruction analysis (e.g. Harper, Zylich, & Zeller, 2012; Trujillo, Cisneros-Montemayor, Harper, Zylich, & Zeller, 2012; Harper, Guzman, Zylich, & Zeller, 2014; Haas, Harper, Zylich, &

Zeller, 2015), this could be a phenomenon based on the natural species fluctuations, or a result of changing fishing pressure due to externalities such as fuel prices.

While the estimates of catches improved in terms of tonnages, the taxonomic resolution of these reconstructions is low, and for effective management, the collection of data with greater taxonomic resolution is required. Greater investment needs to be made in collecting such improved data, which should also include fishing effort data across all fisheries sectors. There have been important advances to address the complex task of collecting fisheries data from widely dispersed artisanal fisheries, which are characterized by geographical remoteness, the diversity of supply-chain participants (commercial fish buyers, markets and restaurants) and fishing gears used. Specifically, in Honduras and Belize a novel freeware application, *OurFish* (https://ourfish.org/), is being implemented which records transactions between fishers and fish buyers, including restaurants, using widely available and extensively used cellphone and Wi-Fi technology. This application is connected to national fisher licensing databases, which links each transaction to individual fishers, thus allowing for fisheries data at the individual, community, region and national level to be collated and used for management. This initiative has been a collaborative effort between multiple institutions, including government departments, non-government organizations, and local communities. The system supports the aim to provide managers with up-to-date, comprehensive fisheries data on an on-going basis, which can be used to develop local, regional and national fisheries management plans, and directly include and link principle stakeholders (i.e., local artisanal fishers and fish buyers) within the data collection and data use process. With the advent of these digital platforms that can be used directly by fishing communities, the onus is now on those involved in fisheries management and governance to help scale-up the adoption of these systems to transform fisheries data collection to support data for decision making around the status and use of marine fisheries. Finally, these fisheries management and governance participants need to also ensure that these new data are seamlessly incorporated in all national and international (i.e., FAO) data reporting schemes.

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Chapter 3

Fisheries spatial management tools

3.1 Evaluating tools for the spatial management of fisheries

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Keywords: *Ocyurus chrysurus*, fisheries tools, morphometrics, otoliths, genetics, small-scale fisheries.

Contribution: Within this chapter, alongside Stephen Box, I designed the experiment. I conducted all of the fieldwork, collecting genetic material, otoliths and measurements on all fish. I processed the morphometric data, and conducted the statistical analyses for all three data sets. I wrote the first draft and revised the manuscript based on comments and inputs from the other authors, sections of the methodology were written by co-authors, genetic analyses by Nathan Truelove, and otolith analyses by Simon Chenery and Matthew Horstwood.

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Evaluating tools for the spatial management of fisheries

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3.3 Abstract

1. The ability to define the spatial dynamics of fish stocks is critical to fisheries management. Combating illegal, unreported and unregulated (IUU) fishing and the implementation of area-based management through physical patrols and port side controls are growing areas of management attention. Augmenting the existing approaches to fisheries management with forensic techniques has the potential to increase compliance and enforcement success rates.
2. We tested the accuracy of three techniques (genotyping, otolith chemistry and morphometrics) that can be used to identify geographic origin. We used fish caught from three fishing grounds separated by a minimum of 5km and a maximum of 60km to test the accuracy of these approaches at relatively small spatial scales.
3. Using nearest-neighbor analyses, morphometric analysis was the most accurate (79.5%) in assigning individual fish to their fishing ground of origin. Neither otolith microchemistry (54.0%) or genetic analyses (52.4%) had sufficient assignment accuracy at the spatial scales we examined.
4. The combination of accuracy and minimal resource requirements make morphometric analyses a promising tool for assessing compliance with area-based fishing restrictions at the scale of kilometers and have promising application especially in small-scale fisheries through to community-based management approaches where technical and financial resources are limited.

3.4 Introduction

Fisheries stock management aims to manage exploited fish populations, based on estimating maximum sustainable yield or maximum economic yield, and managing catch limits around these targets to maximize catches and profits (Christensen, 2010). The financial investment and technical expertise required to conduct fish stock assessments is significant as are the resources required to implement harvest control rules and effectively limit total allowable catch. Therefore, the majority of the world’s fish stocks remain unassessed and largely unmanaged. To address declines in fish stocks, managers have a suite of input and output controls over fishing activities including limiting entry, harvest control rules and area based management approaches, such as marine protected areas (MPA’s), no-take zones (NTZ’s), and territorial user rights fisheries

(TURF's), (Selig *et al.*, 2017). MPA's and NTZ's aim to reduce or eliminate fishing pressure across defined areas, which allow for fish populations to increase and then spill-over into surrounding waters to replenish the exploited areas and/or populations (Gaines *et al.*, 2010). TURF's link area based management to explicit access rights of a geographically-defined fishing area or areas to which an individual fisher or fishing community have been granted exclusive access (Nguyen *et al.*, 2017). To effectively manage MPA's, NTZ's and TURF's and combat illegal, unreported and unregulated (IUU) fishing, a combination of increased compliance and effective enforcement of regulations is required. Current top down enforcement strategies focus on physical patrols, onboard monitoring and port side measures, however these can be prohibitively expensive to conduct routinely (Arias *et al.*, 2014; Dhanjal-Adams *et al.*, 2016). Additionally fishers have been observed to alter their behavior when they know patrols are in operation or when enforcement vessels come into view, resulting in diminishing returns of physical patrols (Dhanjal-Adams *et al.*, 2016). Shortfalls in enforcement personnel and financial stability have been identified as primary factors which undermine the effectiveness of area based management including MPAs (Gill *et al.*, 2017). Alternative cost-effective tools are required to help improve management efficacy. We evaluated the potential of three approaches currently used to identify the geographic origin of individual fish; microsatellite genetic analysis, otolith elemental analysis, and morphometric analysis, all of which have successfully been used to delineate fish stocks (Cadrin, 2000). The ability to assign individual fish to their fishing ground of origin via forensic methods could provide evidence to either confirm compliance or identify fishing infractions, e.g. fishing within an NTZ or in an area outside a fishers designated fishing area, providing an additional tool to fisheries managers to verify origin or identify illegal fishing activity. Additionally, the ability to independently verify the origin of landed catch is key for fisheries management. Fishing grounds are often shared between multiple communities each of which have individual names for their fishing ground (personal observations), therefore local and regional management plans may underestimate fishing pressure at a single fishing ground. Here we looked at three appropriate methods for identifying origin and compared them on accuracy, cost, time versus technical difficulty and applicability at small spatial scales – kilometers to tens of kilometers.

3.4.1 Genetic analysis

Previous studies have used these approaches at large spatial scales 10’s-100’s kilometers. Yet many reserves and community-based management approaches often established under TURF and managed access initiatives operate at smaller scales (less than 10’s km). Many of these fisheries are also relatively low value and any management operates under severe resource constraints. Genetics analyses use the variation of allele frequencies within and among sample groups to identify stocks or populations. Microsatellites (Simple Sequence Repeats) produce comparable estimates of population structure to other molecular markers (Powell *et al.*, 1996; Nybom, 2004). Microsatellites offer some specific advantages over other markers, which include; the selective neutrality of loci (Meloni *et al.*, 1998), and very high levels of allelic polymorphism (Bhargava and Fuentes, 2010). High levels of allelic polymorphism is useful when assessing species which exhibit very low levels of variation (Bhargava and Fuentes, 2010), and thus may be more indicative when sampling at fine spatial scales (less than 100km). Microsatellite markers have important applications in fisheries management and conservation strategies (Abdul-Muneer, 2014) and have successfully been used to discriminate fish stocks at spatial scales varying from 100’s to 1000’s km (e.g. Gold et al. 2009; Saillant et al. 2012).

3.4.2 Microchemistry

Otoliths provide an archive of environmental conditions of fish habitats through elemental deposits. Otoliths are acellular and metabolically inert; elements constantly accrete onto the growing (outer) surface from surrounding waters throughout the life cycle of the fish, and dietary derived inorganic elements are minimal (Hoff and Fuiman, 1995). The accreted elements provide a permanent record of the environment which they inhabit (Campana and Neilson, 1985), and can be used to identify and classify individuals to specific stocks or populations. Otolith microchemistry can be analyzed through laser ablation inductively coupled plasma mass spectrometry (ICP-MS) which is costly and time consuming. Otolith element signatures have successfully distinguished fish stocks across different geographies and spatial scales of 10’s-1000’s km (e.g. Wells, Rooker and Prince, 2010; Bickford and Hannigan, 2005; and Sohn, Kang and Kim, 2005).

3.4.3 Morphometrics

Morphometric analyses use a series of standard anatomical features to create a truss network, which provides a representation of an individual fish's body shape via inter-landmark distances (Strauss and Bookstein, 1982). A variety of environmental variables can influence fish morphology, including diet (Wimberger, 1992), water temperature (Lõhmus *et al.*, 2010), predation pressure (Scharnweber *et al.*, 2013), habitat structure (Willis, Winemiller and Lopez-Fernandez, 2005), depth (Mwanja *et al.*, 2011), and water currents (Franssen, Stewart and Schaefer, 2013). These environmental differences can vary geographically. Morphometric analyses have been used successfully to discriminate fish populations at spatial scales of 100's to 1000's km (e.g. Vasconcellos et al. 2008; Turan 2004) .

Here, we compared the accuracy of genetic, otolith and morphometric analyses at assigning individual fish to three fishing grounds separated by 5-60km, using the yellowtail snapper (*Ocyurus chrysurus*) as a model species. Yellowtail snapper is an important fishery within the Wider Caribbean especially for small-scale fisheries (Claro et al. 2009). Our model fishery was the Honduran small-scale fishery, where yellowtail snapper contributes a significant proportion to the total catch for local fishing communities (Box and Canty, 2010).

3.5 Methods

Our study was based on samples from three distinct fishing grounds, separated by 5-60km, and fished by communities based on the Utila Cays (N16.06°; W086.96°) and Chachahuate (N15.96°; W086.47°), Honduras (Figure 3.1). A total of 149 individuals, 93 adults (≥250mm fork length (FL)) and 56 juveniles (150-249mm FL) from the fishery, caught by local fishers were collected (Summary statistics in Figure 3.2). Sampling was conducted from August 2011 through March 2012, fish were caught using hook and line and the fishing ground georeferenced. For complete descriptions of methodologies of genetic and otolith analyses see supplementary materials (S2).

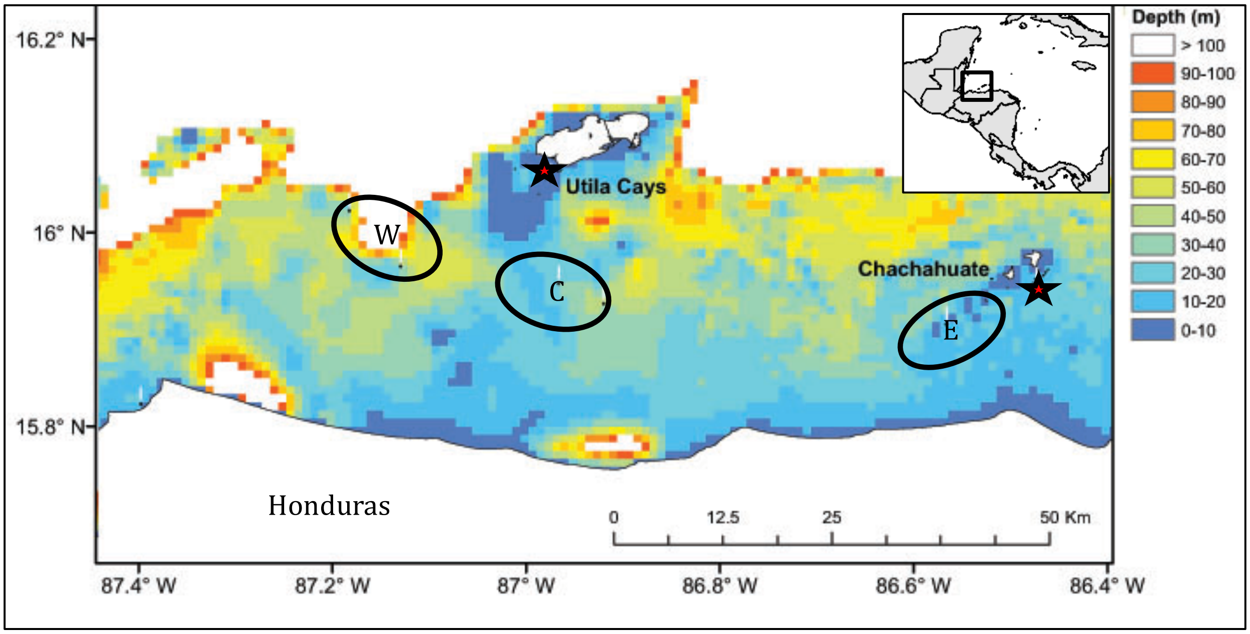

Figure 3.1. Map of the Honduran north shore, highlighting the fishing communities of the Utila Cays and Chachahuate, Cayos Cochinos, and the eastern (E), central (C) and western (W) fishing grounds. Color is the depth profile produced from an interpolation of Gebco data (Bathymetric map created by Iliana Chollett). Inset map is of Central America, highlighting area of interest in this study.

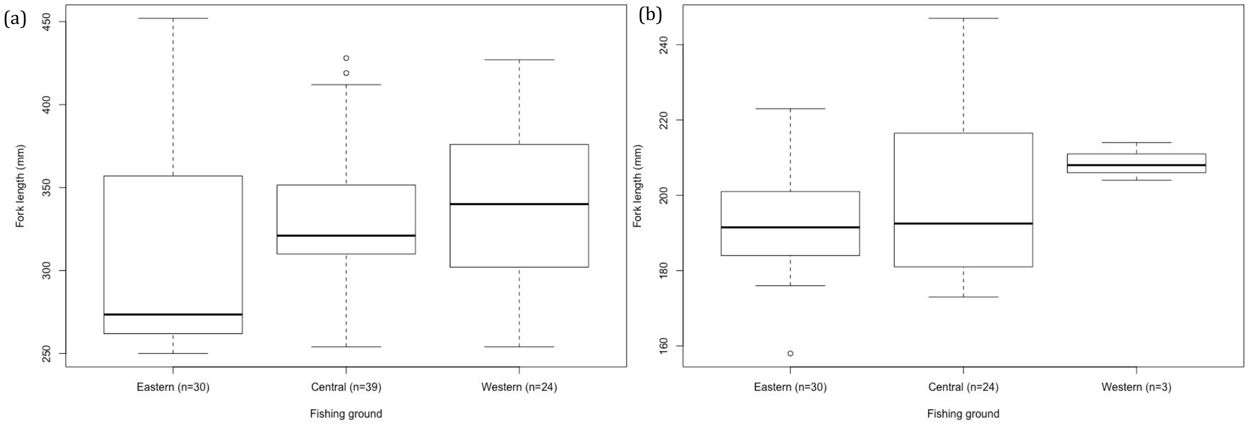

Figure 3.2. Summary statistics of adult (a) and juvenile (b) yellowtail snapper used in the testing of the genetic, microchemistry and morphometric analyses.

3.5.1 Fishing grounds

The eastern fishing ground is part of the Chachahuate small-scale fishery, located within the Cayos Cochinos archipelago, and the central and western fishing grounds are part of the Utila Cays small-scale fishery (Figure 3.1). Each of the fishing grounds are associated with different bathymetries, and terrestrial and oceanic inputs (Table 3.1). We assume these will have a differential effect on otolith element signatures and morphometrics of fish found within each of the fishing grounds. Despite the close proximity of two of the fishing grounds (5km) we assume that deep water (60-70m) separating the shallow banks would preclude the mixing of individuals across the different fishing grounds, due to the association of yellowtail snapper with reef habitats.

Table 3.1. Abiotic characteristics of the three fishing grounds within the Honduran small-scale fishery.

	Fishing grounds		
	Eastern	Central	Western
Depth range (m)	1-30	10-60	60-100
Depth profile*	Shallow	Medium	Deep
Distance to mainland (km)	12.7	19.7	28.6
Terrestrial input*	High	Medium	Low
Distance to continental shelf drop-off (km)	15.1	16.0	0.0
Oceanic input*	Medium	Medium	High

* Relative scales in respect to characteristics of the three fishing grounds.

3.5.2 Genetic analysis

All 149 fish were used in the genetic analyses. A 1cm^2 caudal fin clip was taken from each individual and stored in alcohol at -20°C prior to DNA extraction, which was conducted using a Qiagen DNeasy Blood and Tissue Kit. We used fifteen previously described microsatellite markers; seven for yellowtail snapper (*och2, och4, och6, och9, och10, och13, och14*), five for lane snapper (*lsy2, lsy5, lsy7, lsy11, lsy13*) and three for mutton snapper (*lan3, lan5, lan11*), all of which have been validated as polymorphic and easy to score for yellowtail snapper (Renshaw, Karlsson and Gold, 2007), we used the scored genotypes for statistical analyses.

3.5.3 Otolith elemental analysis

Only adults (≥250mm FL) were used in the otolith elemental analyses. Due to breakages during sectioning and the cost associated with laser ablation a total of 71 individual otoliths were analyzed. Otoliths were sent to the British Antarctic Survey for sectioning prior to elemental analysis at the British Geological Society. A total of fifteen elements, strontium, manganese, barium, lithium, boron, sodium, magnesium, potassium, copper, tin, lead, aluminium, iron, zinc and rubidium, were measured with ^{42}Ca used as the internal standard to correct for ablation volume differences. The elemental signatures of the outer two ablations, which we consider to be the most recent accretions by the adult fish, produce a mean elemental ratio which comprised the signature for each otolith.

3.5.4 Morphometric analysis

Only adults were used in the morphometric analyses (n=93). Juveniles were not included in the morphometric analysis due to allometric growth differences (Huxley, 1932). Additionally, individuals that have not fully recruited to the fishing ground would not have been subjected to the environmental conditions which influence fish morphology, and therefore may not have a true signal for the ground. Ten truss points, that provided a truss network with 21 discrete measurements, were used in the morphometric analysis (Strauss and Bookstein 1982; Figure 3.3). Measurements were taken with callipers of 1.0mm precision, using methods adapted from Vasconcellos et al. (2008). Each measurement was transformed to a proportion of the total length (TL) of the individual to remove bias of size differences, making inter-landmark measurements directly comparable among individuals.

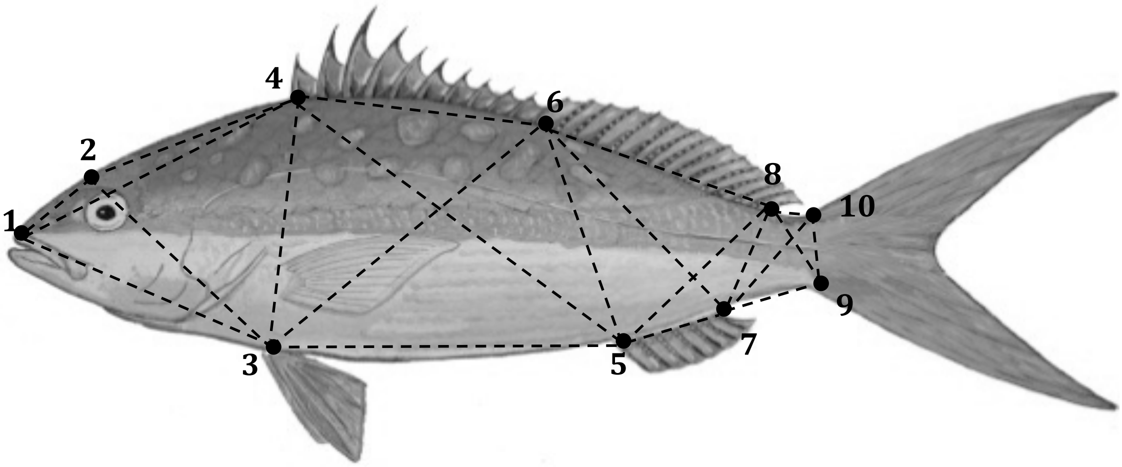

Figure 3.3. Ten morphometric truss points overlaid on a yellowtail snapper used for the canonical correspondence analysis (adapted from Strauss and Bookstein, 1982; portrait of yellowtail snapper by Javier Maradiaga).

3.5.5 Statistical analysis

We conducted pairwise permutational analyses of variance (PERMANOVA) tests between the fishing grounds using the ADONIS function in the R-package VEGAN, using 999 permutations.

The PERMANOVA test does not assume normal data distributions. We conducted nearest neighbor analyses, a non-parametric test, on microsatellite genotypes, otolith elemental signatures, and morphometric truss ratios, using the R-package kknn. Data were normalized along a scale of 0-1, where 0 is the minimum value and 1 the maximum value of a variable, to reduce bias associated with large numbers. Original K values were assigned based on the square root of the number of observations, however once the model was run an optimal K value was provided by the model, this value was subsequently selected for each permutation of the model (Table 3.2). Each model was trained using 10% of the associated data set, which was randomly selected for each of the 100 iterations of the model, from which we calculated a mean assignment accuracy for each of the tools.

Table 3.2. Management tool nearest neighbor analysis parameters and assignment accuracies to their correct fishing ground.

				Assignment accuracy		
Management tool	**N**	**Initial K**	**Optimal K**	**Minimum**	**Maximum**	**Mean***
Microsatellite genotypes	149	11	7	26.7%	80.0%	52.4%
Otolith chemical signatures	71	8	5	12.5%	87.5%	54.0%
Morphometric truss ratios	93	9	8	50.0%	100.0%	79.5%

*Mean is calculated from 100 permutations

Sample sizes were relatively small, in particular for otolith analyses (n=71), however our sample sizes are comparable with those for discrete sampling sites in similar studies that used microsatellite genetic analyses (e.g. Davies et al. 2011) and otolith analyses (e.g. Carlson, Fincel and Graeb, 2016). Our sample size conformed to minimum samples sizes recommended for morphometric analyses (Kocovsky, Adams and Bronte, 2009; Cardini, Seetah and Barker, 2015). We therefore consider our sample sizes sufficient to provide robust statistical analyses.

3.5.6 Tool comparisons

We tabulated the different steps required to get from initial sampling to data interpretation for each of the tools we tested. We constructed a relative scale for the expertise, a time requirement and a cost per sample to conduct each of the analyses, based on obtaining initial samples (i.e. genetic material, otoliths, and truss measurements) through to data interpretation (useable data outputs). We assumed that fishers would provide access to fish for genetic and morphometric measurements free of charge, whilst due to the otolith extraction process the purchase of individual fish is required for otolith analyses. For each of the analyses we reviewed the costs associated for each analysis that are required to fulfil each procedural step, we did not include the costs of basic equipment (e.g. thermocycler, mass spectrometer, callipers), nor did we include estimates of labour costs.

3.6 Results

Of the three techniques morphometric analysis was the most accurate. Pairwise PERMANOVA analyses of morphometric truss ratios identified highly significant differences between all pairs of fishing grounds (eastern and central, *F*=10.29, *p*=0.001; eastern and western, *F*=6.63, *p*=0.001; central and western, *F*=9.37, *p*=0.001). Significant differences of genotypes were observed between all three fishing grounds, (eastern and central, *F*=4.06, *p*=0.014; eastern and western, *F*=5.46, *p*=0.009; central and western, *F*=5.31, *p*=0.004). With otolith microchemistry, significant differences were only observed between central and western fishing grounds (*F*=5.67, *p*=0.011), and no significant differences were observed between central and eastern (*F*=1.17, *p*=0.31) or eastern and western fishing grounds (*F*=1.58, *p*=0.183; Table 3.3).

Table 3.3. Fishing ground pairwise PERMANOVA analyses of microsatellite alleles, otolith chemistry signatures and morphometric truss ratios.

Microsatellite genotypes (n=149)	*F-static*	*p*
Eastern - Central	4.06	**0.016**
Eastern - Western	5.46	**0.009**
Central - Western	5.31	**0.004**
Otolith chemical signatures (n=71)	*F-static*	*p*
Eastern - Central	1.58	0.183
Eastern - Western	1.17	0.310
Central - Western	5.67	**0.011**
Morphometric truss ratios (n=93)	*F-static*	*p*
Eastern - Central	10.29	**0.001**
Eastern - Western	6.63	**0.001**
Central - Western	9.37	**0.001**

Significant results are highlighted in bold.

Nearest neighbor assignment accuracy was greatest for morphometric truss ratios, with a mean accuracy of 79.5%. The mean assignment accuracies for otolith element signatures and microsatellite genotypes were 54.0% and 52.4%, respectively (Table 3.2).

Morphometric truss ratio analysis requires a lower level of technical expertise has the fastest turnaround time from data collection to interpretation, and the lowest cost per sample. Microsatellite genotyping and otolith chemical signature analyses require high levels of technical expertise and an average turnaround time of 2 months from data collection to data interpretation.

Of these two laboratory-based approaches microsatellite genotyping was cheaper than otolith chemical signature analysis (Table 3.4).

Table 3.4. Processes required for each of the three analyses tested, including level of expertise and time required to conducts each analysis and a typical cost per sample

Process	Microsatellite genotyping	Otolith chemical analyses	Morphometric truss ratios
1	Tissue collection	Otolith removal	Fish measurements
2	DNA extraction	Sectioning and mounting	Data analysis
3	PCR reactions	Laser ablation	Data interpretation
4	Sequencing	Data analysis	
5	Data analysis	Data interpretation	
6	Data interpretation		
Technical expertise and specialized equipment	High	High	Medium
Time requirement	2 months	2 months	Hours
Typical cost per sample[a]	US$ 20	US$ 35	US$ 0

[a]Costs were based on processing costs only, i.e. reagents and costs of running specific equipment. The purchase of any specialized equipment and/or labour was not included in the cost estimate.

3.7 Discussion

Our study found that measuring the truss points of a fish and using those to provide a morphometric profile provided the highest accuracy of assigning individual fish to their fishing ground of origin (79.5%), at spatial scales of 5-60km compared with laboratory-based microchemistry or genetic approaches. Importantly, measuring fish post capture has low cost other than labor, with no specialized equipment or installations required. Results are available within a day, requiring a medium level of technical expertise and analyses. The low-cost and high accuracy of morphometric analyses make it an appropriate method for use by fisheries managers but also accessible to management groups focused on low value, or community-based fisheries. In addition to minimal equipment requirements, data analyses are simple and the short turnaround time from sampling to results, make morphometric nearest neighbor analyses a powerful tool and relatively easy to adopt. Forensic methods can augment physical patrols, with sampling possible at fish landing sites or at sea. To improve the accuracy of the tool a greater number of individuals should be used to provide the baseline morphometric signature of each fishing ground. Based on the current accuracy level morphometric analyses are best paired with physical patrols, the tool can be used to support in situ observations of fishing infractions. Whilst tested on the yellowtail snapper, there is the potential for morphometric analyses to be appropriate for other fisheries, for example: groupers (Serranidae); snappers (Lutjanidae); grunts (Haemulidae) and spiny lobsters (Palinuridae). However, applicability of this methodology to these species within these families requires explicit testing. An important caveat is morphometric analyses is not a "one size fits all" management tool, it may not be a useful tool for fish species with large home ranges or low residency rates or in areas with very homogeneous environmental conditions. However, the potential for morphometric analyses to be a useful management for species with high residency times and in areas where the spatial unit of management is tens of kilometers.

Otolith element signatures and microsatellite genotypes assignment accuracies were low (54.0% and 52.4%, respectively). Significant genetic differences were observed between the three grounds, however these differences were not sufficient to accurately assign individuals to their fishing ground of origin. Significant differences in otolith element signatures were only observed between central and west fishing grounds. Fishing ground assignment accuracy for otolith measures were slightly greater than for the genetic analyses, however the range of assignment accuracy was highly variable. We therefore do not consider otolith element signatures and microsatellite genotypes suitable tools to assist in fisheries management for this species at these spatial scales. Assignment accuracy could be improved by the analysis of additional elements for otolith element signatures, testing genomic analyses (Single-nucleotide polymorphisms (SNPs)), and increasing sample size. Additionally, pairwise analyses of genetic, otolith and morphometric analyses could have increased assignment accuracy, however the high costs of laboratory-based tools and the slow turnaround time from sample collection to final analysis reduces the utility of both otolith and genetic analyses for fisheries managers with limited resources and therefore the adoption of the management tool. However, both genetic and otolith analyses have important roles in fisheries management (e.g. Ferguson, Ward, and Gillanders 2011; Truelove et al. 2017). None of the tools examined in this study are stand-alone tools, they constitute options that need to be incorporated where appropriate for specific parts of fisheries management and monitoring strategies.

Our findings suggest the presence of three distinct body shapes in yellowtail snapper, each distinct to one of the three fishing grounds and detectable over small-spatial scales (5-60km). Our results do not however show where the boundaries between these differences occur or explain causation.

Vasconcellos et al. (2008) had similar findings within the yellowtail snapper fisheries of Brazil but at larger scales. In their study, morphometric analyses differentiated yellowtail snapper among four areas separated by hundreds of kilometers where genetic analyses lacked discriminatory power. We hypothesize that the environmental conditions at each of the three fishing grounds in our study influenced the body shape of individuals which provides additional evidence of a limited home range of yellowtail snapper (Farmer and Ault, 2011). Medina et al. (2008) identified morphometric differences in the African hind (*Cephalopholis taeniops*) that were directly correlated with geographical distance of sampling sites and depth. Bathymetry of each of our sampling sites suggest a range of depth gradients, thus depth could be an environmental driver of morphology within the Honduran yellowtail snapper fishery. Local hydrology may also be a driver of morphometric differences, for example differences have been observed in the northern pike (*Esox lucius*) as a result of flow variations in different streams (Senay *et al.*, 2017). There are likely to be differences in local hydrological conditions at each of the fishing grounds in this study based on their proximity to the continental shelf and Honduran mainland where riverine inputs will impact hydrological patterns, salinity and sediment load. Local hydrology and bathymetry influence water temperature, which is another known driver of body shape (Lõhmus *et al.*, 2010). Additional research is required to untangle which environmental factor or factors are driving the morphology of yellowtail snapper in the Honduran fishery, and to identify the extent of similar morphology on a continuum.

3.8 Conclusion

Accurate and robust tools to support evidence-based management are critical to achieving sustainable fisheries. Expensive and highly technical management tools are constrained in their applicability through financial and technical limitations. Morphometric analyses offer a cost-effective and accurate tool to assist in site-based management approaches, with the potential application to fisher compliance of no-take zones and/or territorial user right fisheries. Importantly, it would be possible to automate this approach using off the shelf digital technology and a digital image of the sampled fish. Incorporating these data into user-friendly systems with outputs that are easily interpreted by mangers, fishers, and other stakeholders can increase the availability of data for decision making.

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3.10 Contributions

SWJC, conducted research design, fieldwork, statistical analyses, and provided the main input into the writing of the manuscript. *NKT*, conducted genetic analyses through allele scoring, wrote relevant methods section and provided editorial input. *RFP*, assisted with genetic and statistical analyses, and provided editorial input. *SC and MASH*, conducted the laser ablation of otoliths, wrote the relevant methods section, and provided editorial input. *SJB,* conducted research design and provided editorial input.

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Chapter 4

Fine-scale genetic analysis of an endangered species of coral

4.1 Genetic structure of a remnant *Acropora cervicornis* population

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Keywords: *staghorn coral; Acropora; population genetics; restoration*

Contribution: Within this chapter experimental design was conceived by myself and Richard Preziosi. I conducted all of the fieldwork, collecting genetic material, all of the laboratory work from DNA extraction through amplification. Marker scoring and subsequent statistical analyses were conducted by me. I lead the writing of this paper from draft to final manuscript, with input from co-authors on various drafts.

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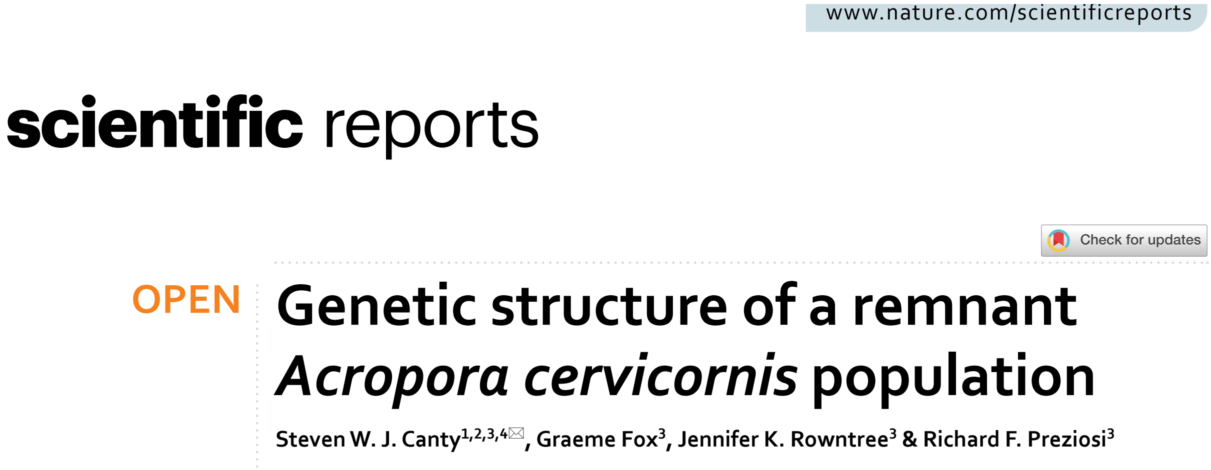

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Genetic structure of a remnant *Acropora cervicornis* population

Steven W. J. Canty[1,2,3,4✉], Graeme Fox[3], Jennifer K. Rowntree[3] & Richard F. Preziosi[3]

4.3 Abstract

Amongst the global decline of coral reefs, hope spots such as the Cordelia Bank, Honduras, have been identified. This site contains remnant dense thickets of the endangered species *Acropora cervicornis*, which are viewed, by local managers and conservation organizations, as a potential source population for coral restoration projects. The aim of this study was to determine the genetic diversity of colonies across three banks within the protected area. We identified low genetic diversity ($F_{ST} = 0.02$) across the three banks, and genetic similarity of colonies ranged from 91.3 to 95.8% between the banks. Clonality rates were approximately 30% across the three banks, however, each genotype was identified unique to each bank. Despite the low genetic diversity, subtle genetic differences within and among banks were demonstrated and these dense thickets were shown not to be comprised of a single or a few genotypes. The presence of multiple genotypes suggests *A. cervicornis* colonies from these banks could be used in restoration projects. Management of hope spots, such as Cordelia Bank, and the incorporation of genetic information into restoration projects to ensure genetic diversity within out-planted populations will be critical in the ongoing challenge of conserving and preserving coral reefs.

4.4 Introduction

Coral reefs are under severe threat from global climate change. Particular issues include increases in sea surface temperature[1,2], ocean acidification[3], as well as localized stressors such as overfishing[4] and eutrophication[5]. Coral reefs are reaching a tipping point, with phase shifts from coral to algal dominance becoming increasingly prevalent[6,7], and potentially irreversible. As the biological and physical structure of coral reefs change, the resilience and ecosystem service provision of these systems to future stresses is reduced[8]. The loss of ecosystem services is of concern for coastal populations, who rely on them both directly, e.g. for fisheries[9], and indirectly, e.g. for storm protection[10]. To abate phase shifts and conserve coral reef biodiversity, urgent management is required at both global and local scales.

Within the Caribbean, average coral cover declined from 34.8% in 1970 to 16.3% in 2012[11]. Of significance during this time period was the loss of approximately 80% of Caribbean Acroporid corals, which was triggered by outbreak of white band disease in combination with multiple climatic events, including hurricanes[12]. During the intervening decades there has been little to no recovery of these populations, and both *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral) have been listed as critically endangered by the International Union for Conservation of Nature[13,14]. However, remnant Acroporid populations have been documented throughout the Caribbean, e.g. in Mexico and Belize[15], Honduras[16], Guadeloupe[17], U.S. Virgin Islands, St. Vincent and the Grenadines, Bonaire and Curacao[18].

Low genetic diversity and high clonal frequency can be common within Acroporid populations[17]. Asexual or clonal reproduction strategies are associated with maintaining and preserving existing genetic diversity during periods of population decline and poor recruitment from sexual reproduction, a particular concern in fragmented and remnant populations[19]. Critically, remnant populations have the potential to become sexually extinct after prolonged periods of clonal growth, if recruitment of sexually reproduced individuals from other populations is low[20]. Which may be attributed to the Allee effect, as fertilization success in broadcast spawning corals, such as Acroporids, is density dependent[21]. Caribbean Acroporid populations are generally considered to be dominated by clones, and thus non-sexual reproduction, however there are exceptions to this; high levels of genetic diversity have been observed in populations of *A. palamata* in Mexico, Belize[15], and the Eastern Caribbean[22], and *A. cervicornis* populations along the Florida Reef Tract[23]. Higher levels of genetic diversity suggest a greater prevalence of sexual reproduction and within the Eastern Caribbean this has been considered to be related to habitat characteristics[22]. Sexual reproduction has the potential to promote genetic diversity and, therefore, the ability to respond to environmental change within a species, increase resilience in the face of environmental stresses[24], and may enhance species diversity at the community level[25]. Further, areas with high genetic diversity have been associated with higher coral cover[26]. Within *A. cervicornis* clumping of genets, or clonal genotypes, has been observed across the reef scape[22,27]. This suggests low genetic diversity at the micro-scale and increased genetic diversity at the macro-scale, therefore greater allelic diversity is observed in larger populations.

Whilst the presence of remnant populations of threatened species is a cause for hope, there is a realization that coral reefs are unlikely to return to past configurations in terms of community assemblage. The challenge, therefore, for both the scientific and management communities, is to maintain ecosystem function in these critical systems[28]. There is concern that recovery by natural processes may not be sufficient, for example, if coral recruit settlement is inhibited by algae[29], in which case, interventions such as anthropogenic restoration may also be required[30]. In light of this, initiatives are focusing on remnant populations as potential seed populations[31], at least at the local scale.

Remnant populations of *A. palmata* and *A. cervicornis* have been observed in Honduras[16], and Guadeloupe[17] and there are suggestions that corals from these populations have the potential to seed the recovery of Caribbean Acroporid populations[31]. The Cordelia Bank Site of Special Importance to Wildlife, is one such area. The reef system, located in the Honduran Caribbean, was identified to contain extensive *A. cervicornis* colonies[16] . Due to the prevalence of colonies, the area is being considered as the potential source of colonies for use in local restoration projects. Knowledge of the genetic composition of colonies prior to restoration is essential[32–34], but to date no genetic studies have been conducted on the colonies within Cordelia Bank Site of Special Importance to Wildlife. It is not known if a single, or multiple genotypes are found within these populations. We used microsatellite markers to assess the genetic diversity of individual sexually mature colonies of *A. cervicornis* across three banks within Cordelia Bank Site of Special Importance to Wildlife. Our aim was to provide a genetic baseline of colonies within the protected area prior to the implementation of restoration projects that plan to use these colonies as a source population.

4.5 Materials and methods

4.5.1 Study site and sample collection

Cordelia Bank (N 16.30°; W 086.52°) was officially declared a site of special importance for wildlife in 2012, by the Honduran government[35]. The area consists of four off-shore banks, Cordelia Shoal, Smith Bank, Big Cay and Little Cay, that are located approximately one mile south west of the island of Roatan, Bay Islands, Honduras (Fig. 4.1). The area was given protective status due to the abundance of *A. cervicornis*, with colonies estimated to extend over an area of 63,440m^2, across three primary banks[36].

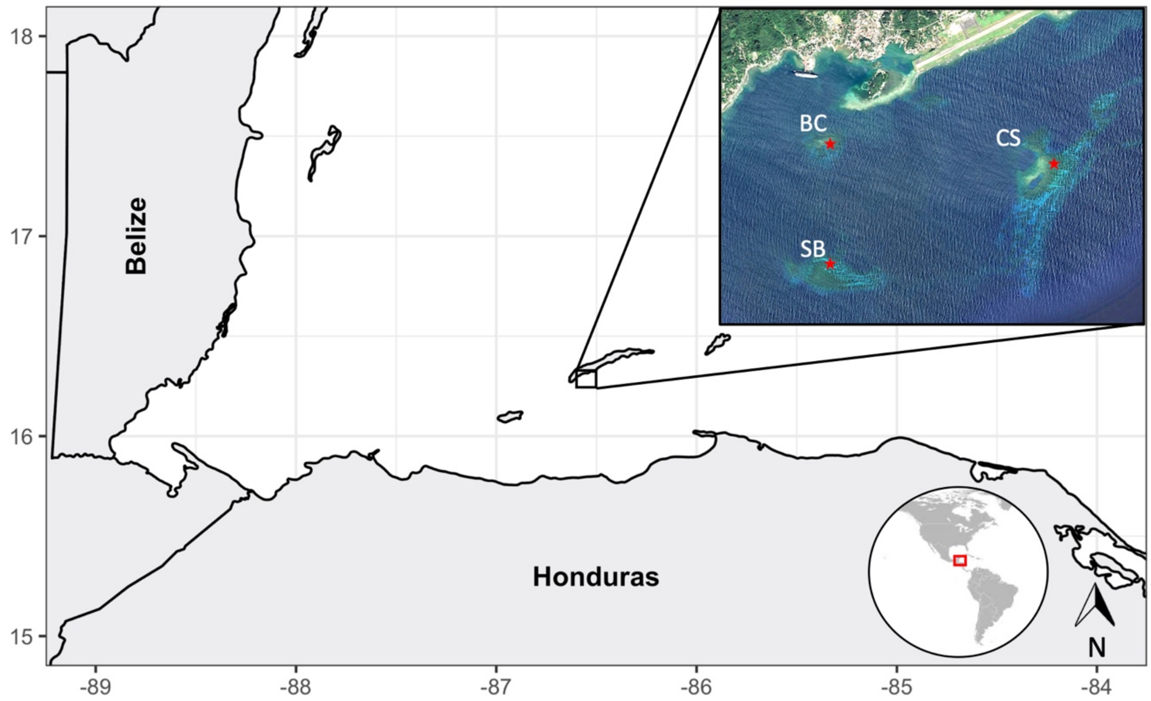

Fig. 4.1. Map of the Honduran north shore, highlighting the location of Cordelia Bank Site of Special Importance to Wildlife, and the three banks with dense thickets of *Acropora cervicornis*, BC – Big Cay, CS – Cordelia Shoal, SB – Smith Bank, approximate sampling locations are indicated by red stars (Map was created in the ggmap[37] in R studio v1.2.5042 (https://rstudio.com/).

Sampling was conducted in April 2014 on three of the four banks: Big Cay; Cordelia Shoal and Smith Bank, based on the presence of high densities of *A. cervicornis,* as identified by Riegl et al.[36]. Sampling was not undertaken on Little Cay due to weather constraints. In-water observations were first conducted to confirm the suitability of sampling areas and ensure that the selected locations had close to 100% *A. cervicornis* coral cover. For each bank, 100 5m x 5m sampling cells were initially established across a 50m x 50m grid. Due to inclement weather and the risk of causing damage to the reef, the sampling grid was modified on the shallowest banks: Big Cay to 50m x 25m and on Cordelia Shoal to 50m x 30m. This provided a combined area of 5,250m^2, providing representation of over 8% of the total estimated combined cover of *A. cervicornis* cover across the three banks.

The sampling grid was laid out on the reef using four 50m measuring tapes, to demark the sampling area. Three additional measuring tapes were used to make horizontal internal lines at 5m intervals, to create two adjacent rows. Flagging tape placed at 5m intervals along the measuring tapes was used to demark individual sampling cells of 5m x 5m. Once sampling was completed for these two rows, measuring tapes were moved further up the reef to create two subsequent rows and repeated until the sampling was complete. Sampling started at the deepest part of the reef, working up to the shallows.

Corals were sampled by taking a small cutting, 2-3cm long, from the branch of a single *A. cervicornis* colony within each of the sampling cells. Cuttings were placed into individually labelled bags containing seawater, taken ashore and then transferred to 100% ethanol and frozen for storage prior to genetic analyses. Sampled colonies were chosen if: 1) they were the dominant colony within the grid that had basal attachment, and had not been sampled in a previous grid; and 2) they had a minimum branch length of 17cm, to ensure they were sexually mature[38]. If the dominant colony had been sampled previously, the next largest colony in the grid was sampled instead. Sampling mature colonies was a specific strategy to detect the full genetic composition of the potential reproductive stock of *A. cervicornis* within the protected area. Each sample was geo-referenced, with G.P.S. coordinates recorded by a snorkeler at the surface, and depth recorded to 0.1m accuracy using a Matrix dive computer (Mares, Rapallo, Italy). A total of 205 samples were collected and successfully genotyped from across three offshore banks, Big Cay n = 50, Cordelia Shoal n = 57, Smith Bank n = 98 (Table 4.1).

Table 4.1. Description of ramet and clonal diversity of *Acropora cervicornis* within the Cordelia Bank Site of Special Importance to Wildlife.

						Ramets per genet			Percentage
	N	N_g	N_g/N	C_g	C	Maximum	Minimum	Mean	clones
Big Cay	50	42	0.84	7	15	3	2	2.1	30.0%
Cordelia Shoal	57	44	0.77	4	17	10	2	4.3	29.8%
Smith Bank	98	75	0.77	10	33	8	2	3.3	33.7%
Combined	205	161	0.79	21	65	10	2	3.1	31.7%

N, is the total number of colonies sampled; N_g, is the number of unique genotypes identified; N_g/N is the genotype to colony ratio; C_g is the number of genets identified; and C is the total number of ramets identified across genets.

No significant differences were observed in the number of genets per bank (chi-squared=1.348 p=0.510), the number of ramets identified per bank (chi-squared=4.125 p=0.127), or the mean number of ramets per genet (chi-squared=0.392 p=0.822).

4.5.2 Genotyping

Fragments of approximately 1cm length of coral were used for DNA extraction. These were crushed using a 0.5” chisel and transferred to a microcentrifuge tube, to which Qiagen DNeasy

Blood and Tissue ATL buffer and Proteinase K were added. Samples were then placed in an Eppendorf thermomixer (Hamburg, Germany) at 56°C and 600rpm for 4 hours. Once digestion was completed, DNA extractions followed the Qiagen DNeasy Blood and Tissue protocol. DNA concentration was calculated using a BioTek Epoch Microplate Spectrophotometer (Winooski Vermont, United States), and where necessary, DNA was concentrated to ensure that 20ng of DNA was used in each reaction.

Individual *A. cervicornis* colonies were genotyped using fourteen polymorphic microsatellite loci: 0166, 0181, 0182, 0192 & 0207[39] and 0513, 0585, 1195, 1490, 2637, 5047, 6212, 9253 & 0007[40]. Polymerase chain reactions were carried out on BIO-RAD T100 Thermal Cyclers (Hercules California, United States), with an initial denaturation step at 95°C for 5 min followed by 35 cycles of 95°C for 20 s, 51-55°C for 20 s, 72°C for 30 s, and a final extension of 30 min at 72°C, with the exception of 0007. This marker required an initial denaturation step at 95°C for 5 min followed by 31 cycles of 95°C for 15 s, 55°C for 15 s, 72°C for 30 s, and a final extension of 30 min at 72°C. Genotyping was performed using an ABI 3730xl automatic DNA sequencer (Applied Biosystems, Waltham, Massachusetts, United States). An internal size standard (GeneScan 500-Liz, Applied Biosystems) was used for accurate sizing. Electropherograms were analyzed using GeneMapper v.5.0 and alleles were subsequently binned with the R-package Msatallele version 1.02[41]. Genotyped colonies with more than 20% missing data (missing three or more loci) were removed from subsequent analyses. The locus 0192 did not genotype evenly across samples and therefore was removed from the analysis. All of the laboratory and computer work were conducted in and with the support of the Laboratories of Analytical Biology facilities of the Smithsonian's National Museum of Natural History (Washington, D.C., United States).

4.5.3 Data analysis

Clones were identified as genetically identical to another individual, a ramet, these individuals were then assigned to a genet, using a stepwise mutation model of the corrected Nei's diversity index statistic with the randomize alleles over individual colonies of all three banks, using 999 permutations in GenoDive[42]. These outputs were cross-checked in GenAlEx 6.5, which allows for the inclusion of colonies with missing data, using the matching function where all data is considered as a single population and alleles are codominant[43]. Through this step an additional three colonies were identified as ramets and assigned to corresponding genets. Where clones were corroborated, a single representative of the genet was used in further analysis. Summary data of each locus (number of alleles, expected and observed heterozygosity) were calculated for each population and pairwise F_{ST} and Nei unbiased genetic identity tests were conducted in GenAlEx 6.5[43].

Population structure of *A. cervicornis* colonies was analyzed using the software *STRUCTURE*[44], using an admixture model with allele correlation. The Burn-in period length was set at 100,000, and the number of Markov chain Monte Carlo replications after Burn-in was set at 100,000. We ran the model with K values of 1 through 10, and with 10 permutations for each K value. To identify the optimal K, the model outputs were analyzed in STRUCTURE HARVESTER[45], with the highest delta K value used to identify the optimal K value. Mantel tests were conducted to test for correlations between genetic distance and geographic distance, and genetic distance and depth, and a partial Mantel test to test for partial correlations among all three, these analyses were conducted using the *vegan* package[46]. Additional Chi-squared analyses of clonal diversity across the three banks were also conducted in R 3.6.0[47] using R Studio 1.2.1335[48].

4.6 Results

4.6.1 Clonal genetic analysis

A total of 65 clones, belonging to 21 genets, were identified across the three banks, and were unique to individual banks (Fig. 4.2, Table 4.1). Approximately one third (31.7%) of all colonies sampled were identified as a clone. Ranging from 29.8% to 33.7% across the three banks, no significant differences in the occurrence of colonies identified as clones were observed (chi-squared, $p = 0.846$). Across all alleles, the number of genets varied among banks, as did the mean number of ramets per genet, neither were significant (chi-squared, $p = 0.654$, chi-squared, $p = 0.132$ respectively), nor was there an interaction between the number of genets and the number of ramets, per bank (chi-squared, $p = 0.654$) (Table 4.1).

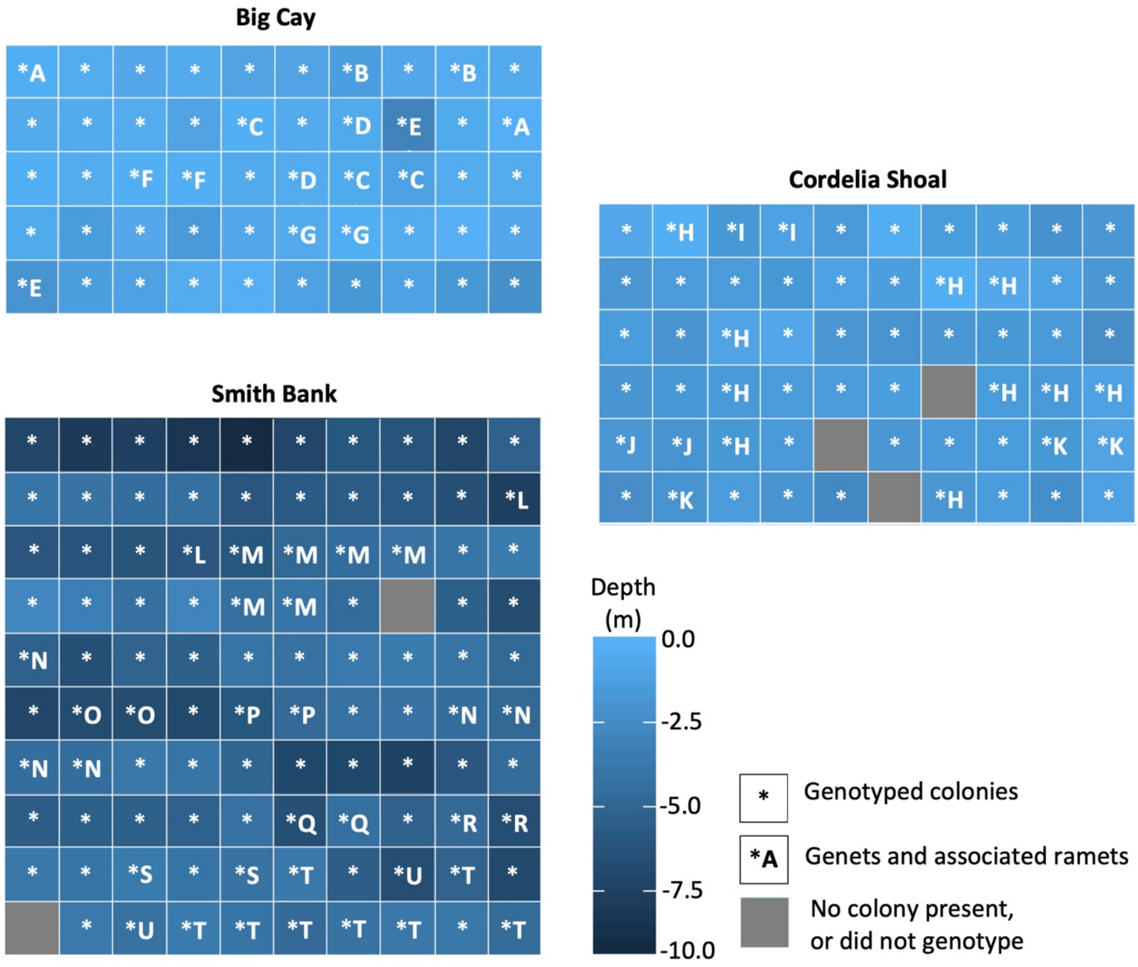

Figure 4.2. Depth profiles of sampled *Acropora cervicornis* colonies and location of clones within the three banks of Cordelia Bank Site of Special Importance to Wildlife, each letter represents a unique genet (clonal genotype). A weak significant relationship was observed between genetic distance and geographic distance (Mantel test, r = 0.108, p = 0.002). No significant relationship was observed between genetic distance and depth (Mantel test, r = -0.038, p = 0.909), nor between geographic distance and depth (Partial mantel, r = -0.089, p=0.993). Depth profiles were created using the lattice package in R studio v1.2.5042 (https://rstudio.com/).

4.6.2 Genetic structure

Genetic diversity across the Cordelia Bank Site of Special Importance to Wildlife was low, F_{ST} = 0.020, varying from F_{ST} = -0.032 – 0.102 across the individual banks (Table 4.2). Pairwise F_{ST} analyses suggested low genetic differentiation among the colonies sampled across the three banks, with values ranging from 0.014 to 0.025. Nei's unbiased genetic identity analyses corroborate these findings, indicating limited genetic differentiation among the three banks, ranging from 0.913 to 0.958, with greatest similarities observed between Big Cay and Smith Bank (Table 4.3).

A weak significant relationship was observed between genetic distance and geographic distance (Mantel test, r = 0.108, p = 0.002), no relationship was observed between genetic distance and depth (Mantel test, r = -0.038, p = 0.909) or between genetic distance and a combination of geographic distance and depth (Partial mantel, r = -0.089, p = 0.993). Population structure analyses highlight the similarities in genetic structure of *A. cervicornis* colonies within and across the sampling locations, with individual colonies having both K clusters well represented and no individual colony fully assigned to either cluster (Fig. 4.3.a). However, subtle differences in cluster allocation were observed at the bank level. Individual colonies on Big Cay (~56%) (Fig. 4.3b) and Smith Bank (~55%) (Fig. 4.3c) have greater proportions of cluster 2, whereas colonies on Cordelia Shoal (~51%) have a slightly greater proportion of cluster 1 (Fig. 4.3d).

Table 4.2. Genetic diversity at 13 microsatellite loci for *Acropora cervicornis* for the three sample sites of Cordelia Bank Site of Special Importance to Wildlife. Only one representative of each clonal genotype is included within the analysis. N_a –number of alleles; F_{ST} – Fixation coefficient.

	Big Cay		*Cordelia Shoal*		*Smith Bank*		*All sites*	
Loci	$\mathbf{N_a}$	$\boldsymbol{F_{ST}}$	$\mathbf{N_a}$	$\boldsymbol{F_{ST}}$	$\mathbf{N_a}$	$\boldsymbol{F_{ST}}$	$\mathbf{N_a}$	$\boldsymbol{F_{ST}}$
0166	7	-0.086	6	0.017	7	0.021	9	0.024
0181	8	-0.081	12	0.026	12	0.064	13	0.015
0182	10	-0.124	11	0.006	14	0.031	16	0.013
0207	8	-0.094	7	-0.060	8	0.014	9	0.034
0513	6	-0.088	8	0.009	8	-0.190	10	0.009
0585	7	0.020	7	0.146	4	-0.013	7	0.004
1195	4	0.071	5	0.242	6	0.372	6	0.021
1490	5	0.220	3	0.634	5	0.404	6	0.065
2637	7	0.012	6	-0.178	10	0.030	10	0.005
5047	7	-0.159	7	0.293	7	-0.068	9	0.023
6212	12	-0.026	10	0.120	13	0.122	15	0.006
9253	2	-0.024	3	-0.018	4	-0.030	6	0.047
0007	10	-0.060	12	0.093	12	0.063	13	0.017
Overall		-0.032		0.102		0.063		0.020

Table 4.3. Pairwise F_{ST} and Nei unbiased genetic identity values of *Acropora cervicornis* colonies from three banks within the Cordelia Bank site of special importance to wildlife.

Pairwise F_{ST}

	Big Cay	Cordelia Shoal	Smith Bank
Big Cay	-		
Cordelia Shoal	0.025	-	
Smith Bank	0.014	0.017	-

Nei unbiased genetic identity

	Big Cay	Cordelia Shoal	Smith Bank
Big Cay	-		
Cordelia Shoal	0.913	-	
Smith Bank	0.958	0.939	-

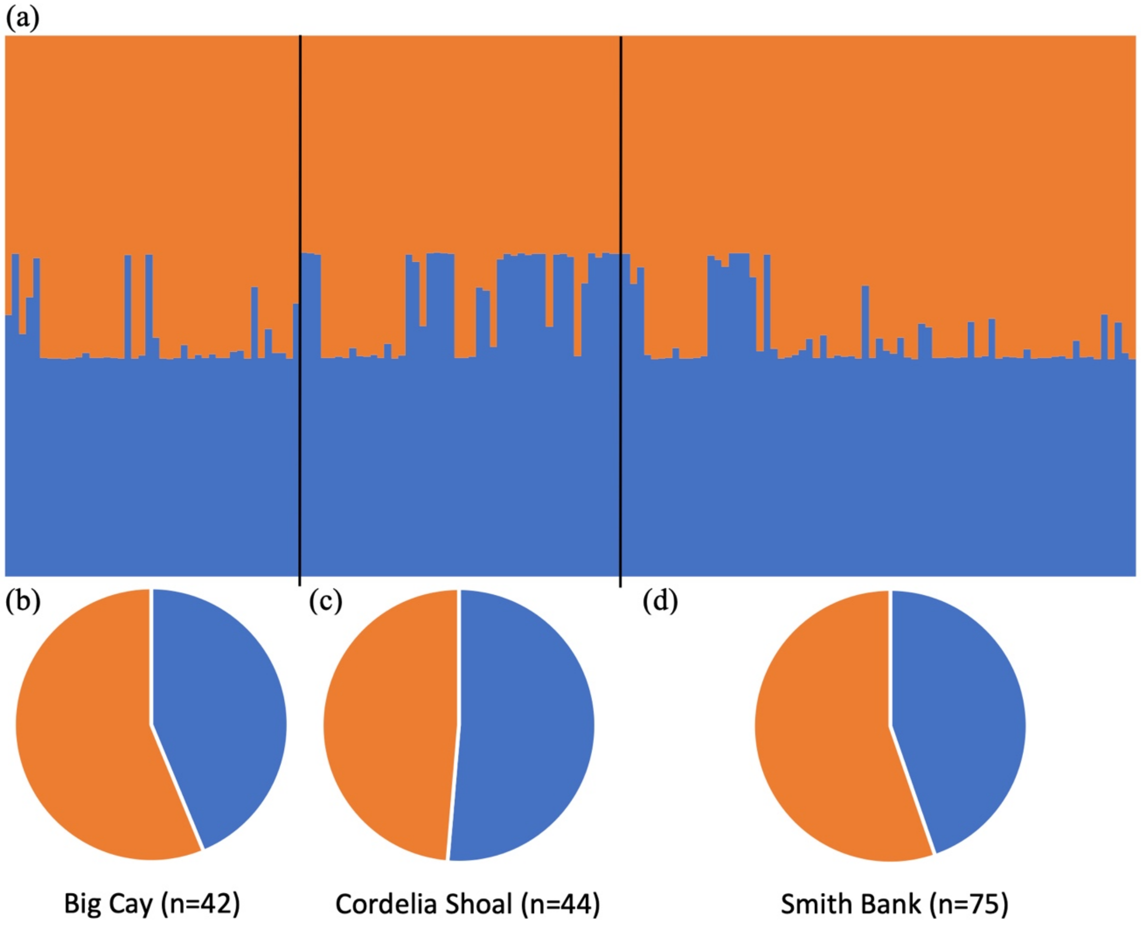

Fig. 4.3. STRUCTURE outputs for all genotypes (K=2), mean of 10 permutations, for each colony within each banks (a); and the mean cluster classifications of all colonies within Big Cay (b); Cordelia Shoal (c); and Smith Bank (d). Blue – Cluster 1; and Orange – Cluster 2.

4.7 Discussion

The extensive thickets of *Acropora cervicornis* colonies within the Cordelia Bank Site of Special Importance to Wildlife are comprised of numerous genetically distinct colonies, however genetic diversity within and among the three banks was low. Clones were observed in each of the three banks, with mean clonality across the three banks at 31.7%. However, genotypes were unique to individual banks suggesting spatial structuring between the banks, which has been observed in other populations[22,27]. The high number of unique genotypes which was observed (mean $N_g/N = 0.79$) differs from how *Acropora* reefs are generally considered and what has been observed in other populations, e.g. Florida ($N_g/N = 0.33$), Belize ($N_g/N = 0.39$)[49] and Guadeloupe ($N_g/N = 0.01$)[17]. The systematic sampling methodology used in this study, which ensured that multiple sexually mature colonies were sampled, has the potential to maximize the genetic diversity observed. This may have contributed to the lower prevalence of clonality than that observed in other studies. However, similar to this study, high frequencies of unique genotypes and low clonality have been observed in *A. cervicornis* populations, e.g. the Bahamas ($N_g/N = 0.64$), Turks and Caicos ($N_g/N = 0.65$), and Panama ($N_g/N = 0.66$). The high frequency of distinct, but similar, genotypes within and across the three banks of Cordelia Bank Site of Special Importance to Wildlife provide a small, but potentially significant, reservoir of genetic diversity. Whilst genetic diversity may be low within and across *A. cervicornis* populations, significant, but weak, genetic differences driven by geographic distance were observed. This research did not address the drivers of genetic differentiation, and therefore we can only postulate that the genetic differentiation observed is as result of natural selection or a founder effect. These subtle genetic differentiations could be key in allowing individual colonies to adapt to future stressors and therefore it is critical that this diversity is protected and conserved, this will become more important if these reefs, and others, are not restored through sexual recruitment.

Maintaining this genetic diversity will be important if sexual reproduction events are triggered in the future, such events provide the opportunity to increase genetic diversity within populations[50]. Spawning activity within Acroporid populations has been observed in the Florida Keys, Panama and Belize, July through October[51], and spawning in Belizean *A. plamata* has been observed most years from 2010-2019 (Personal communication, M. Scott Jones, Smithsonian Marine Station). Monitoring for spawning activity of *A. cervicornis* in Cordelia Bank Site of Special Importance to

Wildlife was last conducted during the full moons of June, July and August 2013. No spawning was observed in *A. cervicronis* colonies during this period, however spawning of *Orbicella annularis* and *O. faveolata* was observed during the August full moon (Personal observations, SWJC). Spawning in multiple *A. palmata* colonies in Tela Bay, Honduras, was observed during the same August 2013 full moon (Personal communications, Andrea Rivera, Universidad Nacional Autónoma de México). These observations suggest that environmental cues to trigger spawning are present in the region. Whilst the potential for natural recovery exists, even where spawning has regularly been observed, the overall cover of Acroporids has remained low[52]. It is therefore likely that further intervention is required to assist in the recovery of Caribbean Acroporid populations.

Restoration is becoming an increasingly popular tool for conservation and management of marine habitats[53,54] and within the Caribbean over 150 projects in more than 20 countries have been implemented[55]. Coral gardening, a preferred technique in the Caribbean, inherently limits genetic diversity as the technique focuses on the growing and out-planting of clones[56]. Despite genetics being an important factor that complements traditional restoration ecology methodologies[57], and ensures ecological and evolutionary processes are incorporated into the restoration process[58]. Genetic diversity provides colonies with the potential to respond to changing environmental conditions, and where no genetic variation exists, responses are limited to phenotypic plasticity to deal with these stressors. During restoration there is the potential for the loss or reduction of fitness in the restored population, driven by founder effects, genetic swamping and inbreeding or outbreeding depression[32]. Greater attention needs to be given to genetic diversity when restoring systems[59], especially when projects are dominated by a single species, as in these cases, the genetic diversity represents the primary biodiversity of the habitat. Genetic composition of out-planted colonies, is one of many important criteria that should be considered within a best practices approach to restoration[60].

Understanding the drivers of existing genetic structure and environmental conditions will be important in the successful management and conservation of these populations, and of restoration projects that use colonies from these populations. If a restoration project using colonies from Cordelia Bank Site of Special Importance to Wildlife is to be implemented, then the genetic diversity across the banks observed in this study should be considered. Careful selection of colonies during the restoration process can ensure representation of a range of genotypes maximizing the potential for evolutionary adaptation of corals within a restored area. There is an important caveat that underlies this potential and the future of the corals within Cordelia Bank, the Caribbean, and globally. Understanding and reversing the ultimate localized drivers of reef decline (e.g. overfishing and eutrophication) must be part of comprehensive local and regional management strategies. The coral populations of the Mesoamerican barrier reef system, which encompasses Cordelia Bank, are under pressure from ocean acidification, hurricanes, pollution and fishing, and at high risk from mass bleaching over the next decades, and the ecosystem has been categorized as critically endangered by the IUCN[61]. In the specific case of Cordelia Bank, fishing and recreational activities have been excluded from highly sensitive areas, however urban runoff and untreated effluents from Coxen Hole, and the proximity of two major cruise ship docks and an international airport, represent potential major threats[62]. If coral reefs are to have sufficient resilience to climate change, and continue to provide critical ecosystem services to the coastal communities that depend on these resources, the drivers of their decline must be reduced. Whilst management cannot prevent the damaging effects of major disturbances, it can provide protection to reefs that have the greatest potential to be resilient and contribute to recovery through natural processes[63]. Natural regeneration promotes more complex and resilient systems than active restoration[64], therefore restoration should be considered as one of a multitude of management tools in the conservation of coral reefs.

4.8 Acknowledgements

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4.9 Author contributions

S.W.J.C. & R.F.P. conceived the study. S.W.J.C. conducted the fieldwork, laboratory analyses and genotyping. G.F. produced the bioinformatics pipeline. S.W.J.C. & G.F. conducted the statistical analysis. S.W.J.C. produced the first draft. S.W.J.C., J.K.R., R.F.P. & G.F. contributed to writing and editing the manuscript.

4.10 Additional information

Competing interests. The authors declare no competing interests.

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Chapter 5

Genetic structure within a mangrove forest

5.1 Seeing the trees within the forest, a fine-scale genetic analysis of a mangrove forest.

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Contribution: Experimental design was conceived by myself, Jennifer Rowntree, and Richard Preziosi. Fieldwork was led and conducted by me, as was the laboratory work, were I conducted all of the DNA extractions, and worked with Kenan Matterson to assemble the libraries and conduct the amplifications. Statistical analyses, with the exception of the spatial auto-correlation, were conducted by me., and the first drafts of the paper were primarily written by me, with input on the methodologies from the appropriate co-author.

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5.2 Abstract

Mangrove stands are thought to have relatively low genetic diversity, due to proportionally higher frequency of self-recruitment and self-pollination rates. To test the hypothesis of low genetic structure in mangrove forests at fine spatial scale, we conducted a genetic analysis of the dominant trees within a 400m^2 parcel of a *Rhizophora mangle* forest on a small cay in Honduras. A total of 182 trees were successfully genotyped using a panel of 575 SNPs. We identified moderate levels of genetic differentiation within the parcel (G_{ST} = 0.23), with significant spatial autocorrelation observed at 2m spatial scales. High numbers of half- and full-siblings were detected, with the majority concentrated along the seaward fringe of the parcel. K-means clustering analyses identified three significantly different clusters (F_{ST} = 0.098 – 0.430). We interpret that these clusters are associated with successful recruitment events from different sources at a range of unknown spatial scales. Within each of the clusters, canopy sizes ranged from covering single to multiple 1m^2 sampling cells, which we suggest reflects successful recruitment within this parcel of forest over different, but at unknown temporal scales. These findings highlight that there is greater genetic structure within mangrove forests than previously considered. Our results also suggest that understanding how recruitment events influence forest structure over different spatial and temporal scales has important implications for protected area management and restoration initiatives. We provide recommendations to improve sampling efforts of future mangrove population genetic studies, and to promote genetic diversity within restoration projects.

5.3 Introduction

Mangroves provide critical ecosystem services to coastal communities and neighboring habitats (Lee et al. 2014). Despite their importance, mangrove forest cover has been severely reduced, and there was real concern that we faced a world without mangroves if deforestation rates continued at the rate observed through the 1990s and early 2000s (Duke 2007). Positively, global mangrove deforestation rates have slowed over the past decade, although certain areas such as South East Asia and West Africa remain areas of concern (Friess et al., 2019). Critical to reducing deforestation rates has been the increased awareness of the ecosystem services provided by mangroves, driving mangrove conservation measures at the global scale (e.g. IPCC 2014; UNEP 2014). Ecosystem services of particular importance include reduction of climate driven events, such as hurricanes, storms (del Valle et al. 2020; Zhang et al. 2012) and floods (Menendez et al. 2020), and the mitigation of drivers of climate change, through carbon sequestration (Macreadie et al. 2019). Specific strategies to manage and conserve mangroves include, establishing protected areas, community-based management, regulatory management, and restoration and rehabilitation (Suman 2019). Schmitt and Duke (2015) provide an overview of the requirements for effective mangrove management, focusing on integrated coastal zone management, directed by multi-stakeholder integration and participation, ecosystem-based management, adaptive management, and transboundary collaboration. Managed areas, such as Ramsar sites, or conservation zones, which include marine protected areas, have been used as a tool to protect and conserve mangroves. Within the design of managed areas and spatial planning it is critical to understand connectivity of mangrove populations across the seascape (Canty, Preziosi, and Rowntree 2018). Ensuring that benefits of protection not only help to build resilience in the area of mangrove being protected, but areas outside of protection also receive benefits, such as maintain gene flow between populations (Palstra and Ruzzante 2008).

Numerous studies have assessed the genetic connectivity of mangrove populations across various spatial scales, including at the estuary (Ngeve et al. 2017), seascape (Cisneros-de la Cruz et al. 2018), regional (Kennedy et al. 2016) and biogeographic scale (Wee et al. 2017). Population connectivity and structure is mediated by dispersal of gametes and propagules followed by successful recruitment (Sousa et al. 2007; Hodel et al. 2018). Mangrove species may be either insect or wind pollinated, but high self-pollination rates have also been reported (Kennedy, Sammy, et al. 2020; Lowenfeld and Klekowski 1992), which can lower genetic diversity. Additionally, habitat discontinuities can form strong barriers to gene flow (Binks et al. 2019). However, buoyant propagules provide the potential for long distance dispersal (Rabinowitz 1978), yet high self-recruitment is more common in established mangrove stands, particularly in species that produce large propagules (Hamilton, Osman, and Feller 2017; Van Der Stocken et al. 2015). Whilst dispersal is key for the movement of propagules, recruitment rates of propagules to a mangrove forest or stand is what determines forest structure (Sousa et al. 2007). Recruitment success is influenced by numerous biotic and abiotic factors, which include propagule predation rates (Cannicci et al. 2008), sediment conditions (Krauss et al. 2008), and the presence of canopy gaps (Clarke 2004; Ross et al. 2006).

Successful repeated recruitment events contribute important genetic diversity to the forest, which is critical to population persistence and ecosystem processes (Reynolds, McGlathery, and Waycott 2012). Of particular importance is the introduction of uncommon or rare alleles which can be crucial in promoting survival through adaptation (Browne and Karubian 2018). In mangroves, population that colonize new areas and experience limited subsequent gene flow have been shown to have lower within population genetic diversity than mature stands, which may be attributed to founder effects (Kennedy et al. 2017). Over the next 50 years, it is predicted there will be increased occurrences of high intensity hurricanes (Murakami et al. 2018; Sobel et al. 2016; Walsh 2004), unprecedented changes in sea-level (Saintilan et al. 2020), and increased temperatures (Alexander et al. 2018), all of which have significant implications for mangroves, such as physical damage, drowning, and growth rates and productivity (Alongi 2015). Maintaining high genetic diversity within mangrove systems allows for adaptation to these changing environmental condition (Reynolds et al. 2012), and therefore should be a key component of management and restoration frameworks (see Mijangos et al. 2015).

Whilst large-scale genetic studies are important to understand connectivity of populations across seascapes, fine-scale analyses provide insights into genetic diversity and structure within a population. For example, fine-scale analyses of the scleractinian coral *Acropora cervicornis* (staghorn coral) using microsatellites (Canty et al. 2020 – Chapter 4) and fine-scale analysis of three species of bulrush, *Bolboschoenus maritimus*, *Schoenoplectus acutus* and *S. americanus* using amplified fragment length polymorphisms (Kettenring et al. 2019), revealed higher levels of genetic diversity than previously expected, which has major implications for spatial management and restoration practices of these species. With the increased interest in mangrove management, understanding genetic structure and connectivity at a range of spatial scales is critical to inform protected area design. Moreover, the planting of mangroves to restore forests is being adopted throughout their entire geographical range. However planted forests do not resemble the genetic structure of natural populations (Jordan et al. 2019), and loss of genetic diversity within planted forests has been observed (Granado et al. 2018). To better inform spatial management and restoration practices, we need a more comprehensive understanding of the genetic structure of mangrove forests. In this study, we conducted a fine-scale population genetic analysis of a 400m^2 parcel of *Rhizophora mangle* forest on a small cay in Honduras.

5.4 Materials and methods

5.4.1 Sample collection and DNA extraction

The red mangrove, *Rhizophora mangle*, is the iconic mangrove species along the Atlantic shores of Latin American, Caribbean and African countries, occupying the most seaward area of land. High levels of self-fertilization and self-recruitment within this species are assumed to reduce genetic structure at the forest scale (DeYoe et al 2020). An isolated *R. mangle* forest was selected to test the hypothesis of limited genetic differentiation at fine scales within forests of this species. A mature *R. mangle* forest was identified on Fort Cay which is separated from the island of Roatan, Honduras by a minimum of 1km. A parcel of the forest was selected, and delineated using a 20x20m sampling grid, individual 1x1m sampling cells were constructed in the forest using measuring tapes and ropes (sampling cell A1 – N 16.404045, W -86.282116; Figure 5.1). Sampling was conducted over a three-day period between 24th – 26th April 2016. Two to three leaves were collected from the dominant tree within each of the sampling cells. Dominant trees were characterized as either the tree with the largest trunk within the sampling cell, or with the greatest canopy cover of the cell. Young leaves were preferentially sampled, due to lower concentrations of polyphenolics and other secondary metabolites compared to older leaves (Kandil et al. 2004), as secondary metabolites can cause shearing of DNA during extraction (Sahu, Thangaraj, and Kathiresan 2012). Upon collection, petioles were removed and leaves were broken in half to facilitate desiccation, and stored in individually labeled bags containing a 0.06 – 0.80mm granular mix silica gel with cobalt indicator, prior to DNA extraction. Samples were collected for each cell, however, where a tree dominated two or more cells only one sample, from the first cell occupied by the tree was used in the analysis.

Prior to extraction approximately 1cm^2 of leaf tissue sample was placed in individually labeled 2.0ml microcentrifuge tubes, and bathed in 500µl of 100% ethanol for 3-4 days and dried under fume hood for an additional two days. This process aided in the removal of secondary metabolites within leaves, and provided an additional dehydration step. Once dry, a single 5mm stainless steel ball-bearing (Qiagen, Venlo, Netherlands) was added to each tube and samples were lysed using a Retsch (Düsseldorf, Germany) MM440 mixer mill (also known as a Tissuelyser). Samples were placed in one of two Tissuelyser adapter sets and lysed at 30Hz for 1min. Samples were flipped and swapped between Tissuelyser arms and lysed at 30Hz for a further 1min to facilitate consistent lysing across samples. DNA extraction from lysed tissue was conducted using the DNeasy 96 Plant Kit (Qiagen) following the manufacturers' protocol.

5.4.2 RADseq library preparation

Libraries were prepared using a modified version of the Wang et al. (2012) restriction site associated DNA (RAD) protocol which utilizes type IIB restriction enzymes that cut both upstream and downstream of the enzyme's target site, resulting in the production of RAD tags of uniform length. Briefly, approximately 50–100 ng of high-quality genomic DNA (thin bright band on gel, with no smearing) from each sample was digested with the enzyme BcgI (New England BioLabs, Ipswich, USA), producing uniform 36bp length fragments with random overhangs. Genomic digests were then ligated to a pair of partially double-stranded adaptors targeting a reduced subset of BcgI sites through a different reduction scheme depending on organism genome size. RAD tags were then amplified with sample-specific 5,6bp or 6,6bp dual-barcodes and Illumina adaptors. PCR products were visualized on a 2.0% agarose gel to verify the presence of the expected 160-170 bp target band (i.e., fragment, barcodes and adaptors included). Gel purification of the target band was carried out following protocols outlined in Guo et al. (2014). Amplification products were pooled at equimolar concentrations and sequenced on an Illumina HiSeq 3000 (San Diego, USA) at the Center for Genome Research and Biocomputing at Oregon State University.

5.4.3 SNP calling and quality control

Raw reads were downloaded from the Oregon State University online portal. Libraries for three trees failed to amplify. Successfully amplified libraries from the remaining 182 trees were processed using ipyrad 0.9 (Eaton and Overcast 2020) on the Smithsonian Institution High Performance Computing Cluster (https://doi.org/10.25572/SIHPC). The genome of *R. apiculata* (Xu et al. 2017), a close relative of *R. mangl*e, was used as the reference genome. In ipyrad, all parameters were set to default, except for the following: data type = 2brad; restriction overhang = 'TGCAG'; cluster threshold = 0.85; maximum barcodes mismatch = 0; filter adapters = 2; filter minimum trim length = 20; maximum alleles consent = 2; minimum samples per locus = 4; and, trim read = 0; and trim loci = 0. An initial panel of 113,626 SNPs was generated. Screening for null alleles, deviation from Hardy-Weinberg equilibrium and linkage disequilibrium were conducted in R packages adegenet (Jombart and Ahmed 2011), poppr (Kamvar, Tabima, and Grünwald 2014), and genepop (Rousset 2008). After post filtering and quality control, a panel of 575 informative SNPs was identified.

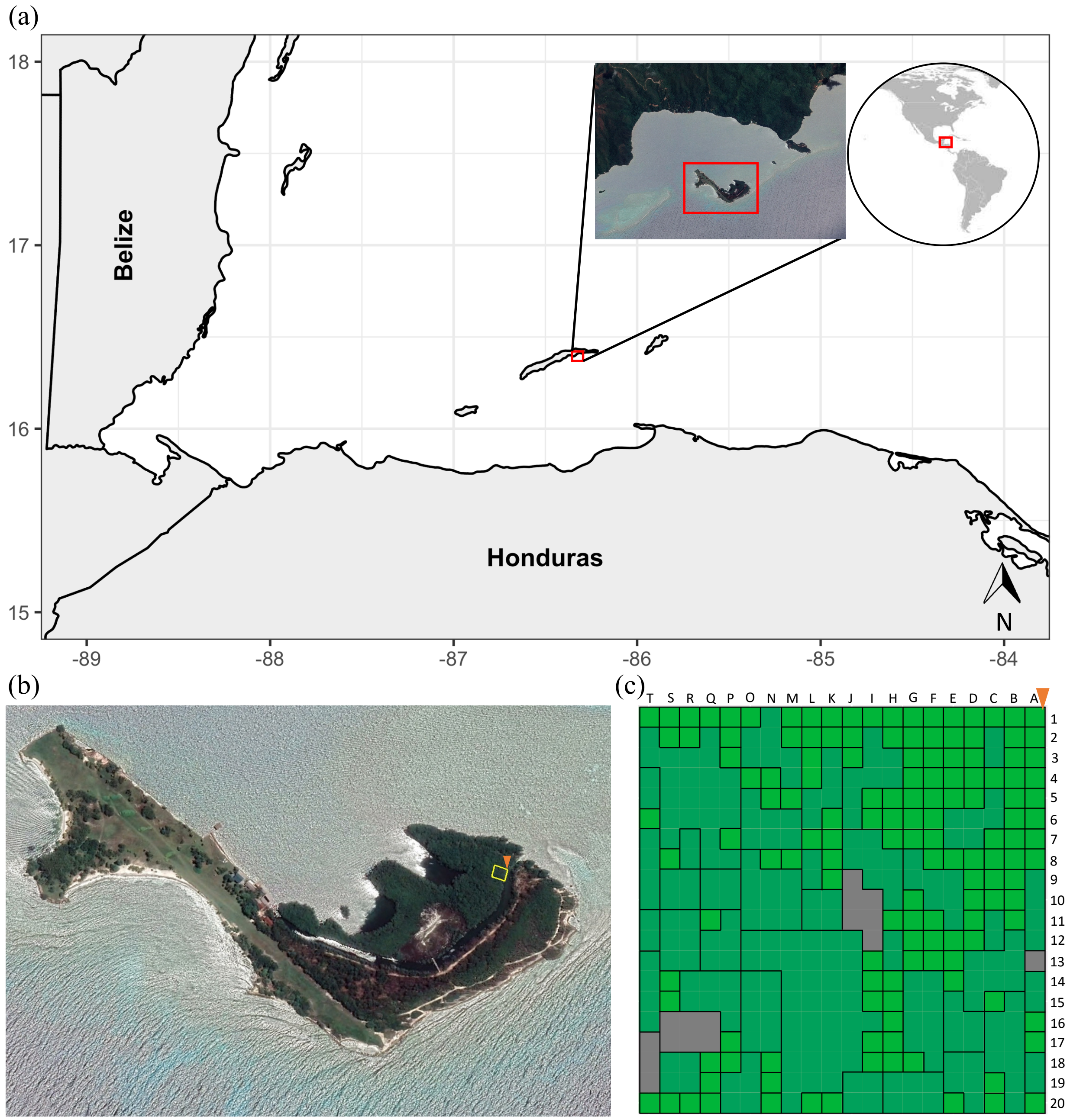

Figure 5.1. Map of Fort Cay in relation to the island of Roatan, within the Bay Island Archipelago, Honduras (a), and the location of the sampling area on Fort Cay (b), the orange peg indicates the initial sampling square A1. Map of individual *Rhizophora mangle* trees within 400m^2 parcel of forest sampled (c). Black outlines demark individual trees;

Light green – trees dominant within a 1m^2 area; Dark green – trees dominant in 2m^2 or greater; Gray represents no tree present (A13) or samples collected that did not sequence (I10, Q16, T17).

5.4.4 Statistical analyses

Genetic differentiation of the forest was assessed in GenoDive (Meirmans 2020), using Nei's diversity index. A Mantel test and spatial autocorrelation to assess fine-scale genetic structure within the area of forest sampled were conducted in GenAlEx 6.5 (Peakall and Smouse 2012). We calculated pairwise inter-individual genetic distances (outlined in (Smouse and Peakall 1999)) and geographic distances (measured between the grid locations of individual trees) to evaluate the extent of genetic differentiation between pairs of individuals at specified distance classes across the sampled area. Consistent with our systematic sampling design, we performed this analysis with even distance classes (10 total classes, each encompass 2 m intervals) which maintained large numbers of sample pairs (565 – 2,204) at each distance class. An autocorrelation coefficient (r) was calculated for each distance class and plotted as a spatial genetic correlogram. Null 95% confidence intervals at each distance class were generated via 999 random permutations of all samples and 95% confidence intervals around each r value were generated via 10^3 bootstrap replicates of the samples at the respective distance class. As described in (Peakall, Ruibal, and Lindenmayer 2003), we accepted statistical significance of spatial autocorrelation at a distance class when (1) the r value exceeded the null confidence interval and (2) the confidence interval around the r value did not overlap with zero. These analyses were conducted across the entire data set.

K-Means clustering analyses were conducted in GenoDive using the settings: cluster = individuals; method = Amova; run from 1 to 20 clusters. Convergence type was simulated annealing using 50,000 steps with 20 algorithm repeats, best clustering according to Clinsku & Harbasz' pseudo-F were used in this analysis. Iterations of these analyses were conducted using "Bayesian Information Criterion", "Aikaike's Information Criterion" and "within-groups sum of squares", statistics. Pairwise F_{ST} analyses of K clusters (as populations), using 50,000 permutations, were conducted in GenoDive. K-Means clustering analyses on a subset of data, trees assigned to cluster 2, and pairwise F_{ST} analyses of all K clusters (as populations) identified, were subsequently conducted in GenoDive, using the same parameters as above.

A map was constructed using the sampling grid squares as they related to the leaf collection from the tree with the dominant canopy cover of individual squares. This provided us with estimates of canopy cover for individual trees, age structure is inferred from canopy dominance, with smaller canopy size associated with younger trees and greater canopy size with older individuals.

Relatedness analyses were conducted in the R package Demerelate (Kraemer and Gerlach 2017). Single locus similarities were averaged over loci for each pairwise comparison using 1000 bootstrap iterations of F_{IS} calculations, with no reference population. Outputs of the model were pairwise genetic similarity estimates, which are translated in to relatedness through the generation of relatedness assignment thresholds: full-sibling (≥ 0.793) and half-sibling (≥ 0.702 and < 0.793) or no relation (< 0.702). The high threshold value of a full-sibling could indicate a parent-offspring match.

5.5 Results

5.5.1. Genetic differentiation and spatial structure

Moderate levels of genetic differentiation were observed within the area of forest sampled (G_{ST} = 0.23), suggesting the presence of genetic structuring within the 400m^2 area. There was a significant relationship between genetic and geographic distances (Mantel test, r = 0.13, p = 0.01), indicating weak isolation by distance within the parcel. Genetic spatial autocorrelation analysis identified significant positive autocorrelation that progressively declined in intensity for the first four distance classes (2 - 8m), followed by significant negative autocorrelation at the next five distance classes (10 - 18m). No significant genetic spatial autocorrelation was observed at the last distance class of 20m (Figure 5.2).

K-Means clustering analyses identified the presence of two clusters dispersed throughout the parcel, trees assigned to cluster 1 dominate the first 8m from the seaward fringe into the forest, and are replaced by a band of trees, approximately 6m wide, that traverses the parcel from the northwest corner to the south of the parcel (Figure 5.3). Pairwise analysis identified significant genetic differentiation between the two clusters (F_{ST} = 0.353; p = 0.0001). A second K-Means clustering analysis of cluster 2, based on the relatedness analysis, identified two sub-groups, clusters 2a and 2b. Pairwise analysis identified significant genetic differentiation between all three clusters, with greatest differences observed between clusters 1 and 2b (Table 5.1).

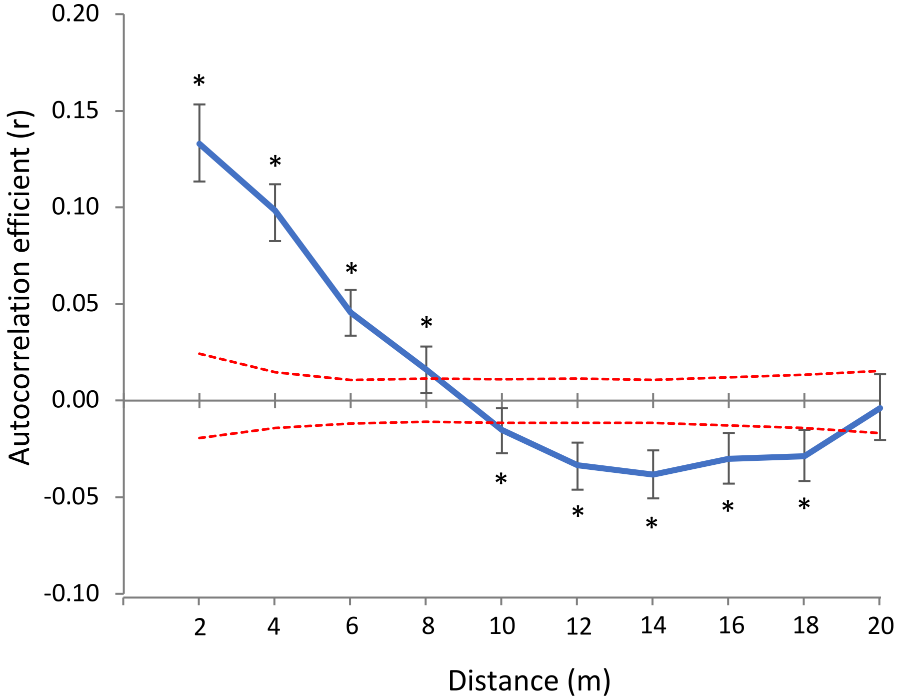

Figure 5.2. Spatial autocorrelation analysis, at a 2m spatial scale, of all data. Red dashed lines denote the upper and lower null confidence interval. Asterix denote significant interactions.

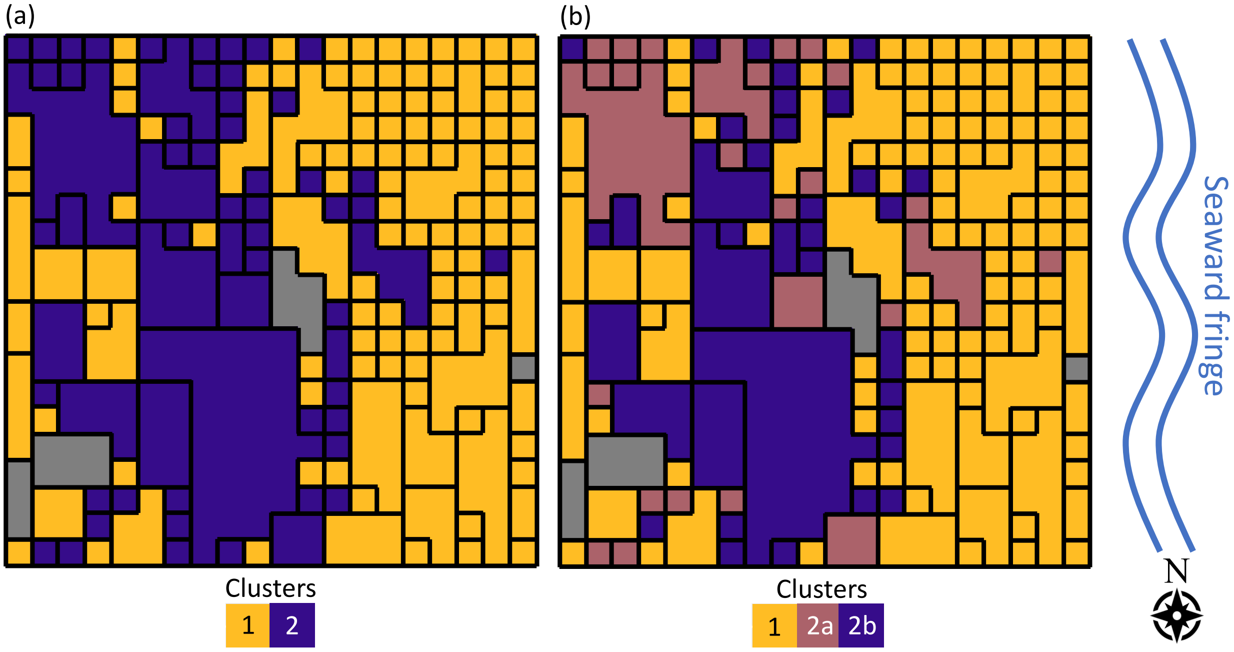

Figure 5.3. K-Means clustering assignment of (a) K=2 and (b) sub-analysis of cluster 2, within the 400m2 parcel of *Rhizophora mangle* forest on Fort Cay, seaward fringe of the parcel is located to the east. Black outlines demark individual trees, and gray represents no tree present or the sample collected did not sequence.

Table 5.1. Pairwise F_{ST} analysis of clusters identified by K–Means clustering analyses, (a) Optimum K = 2, (b) Sub-analysis of cluster 2.

(a)

		p	
	Clusters	**1**	**2**
F_{ST}	**1**	-	**0.0001**
	2	0.353	-

(b)

			p	
	Clusters	**1**	**2a**	**2b**
F_{ST}	**1**	-	**0.0001**	**0.0001**
	2a	0.292	-	**0.0001**
	2b	0.430	0.098	-

5.5.2 Forest structure

The parcel of forest is primarily comprised of trees assigned to cluster 1. These account for approximately two-thirds of the trees, and just over half of the canopy cover of the parcel (Table 5.2; Figure 5.3). Trees assigned to cluster 1 had a mean canopy cover of 1.8 ±0.2 squares and were the smallest trees within the parcel and trees assigned to cluster 2 a mean canopy cover of 2.8 ±0.7 squares (Table 5.2). Within each of the clusters a range of size, and therefore ages, are observed (Table 5.2; Figure 5.3). Mean canopy cover of trees assigned to clusters 2a and 2b were 2.5 ±0.9 and 3.0 ±1.0, respectively, and are larger and therefore assumed older than trees assigned to cluster 1 (Table 5.2). To present the relatedness data we identified 15 of the largest trees within the parcel (B12, B15, C1, D18, E9, F14, H3, H8, I16, M3, M6, M9, N14, P4 and P14 – identified by the coordinates of the first grid square they occupy), that provide a good representation of the geographic positions of trees, and their assignment to one of the three clusters identified.

Table 5.2. Summary data of trees assigned to each of the K – Means clusters identified within the parcel of *Rhizophora mangle* forest.

	Clusters		
	1	**2a**	**2b**
Minimum number of squares per tree	1	1	1
Maximum number of squares per tree	9	22	37
Mean number of squares per tree	1.8	2.5	3.0
Standard error	0.2	0.9	1.0
Number of trees per cluster	120	26	36
Proportion of assigned trees in the parcel* (%)	64.9	14.1	19.5
Number of squares covered	211	65	108
Proportion of squares covered§ (%)	52.8	16.3	27.0

*Includes three trees which did not sequence. §Proportion of the total area of the parcel (400m^2), includes the area of the three trees which did not sequence and the empty space of A13.

5.5.3 Genetic relatedness

Full- and half-siblings were identified throughout the parcel, with some individual larger trees exhibiting high levels of relatedness to smaller surrounding trees, whilst in other larger trees limited to no relatedness to other trees in the parcel were identified (Figure 5.4). The greatest number of sibling trees were associated with the large trees assigned to cluster 1 (B12, B15, C1, D18, F14, H3, & H8), with concentrations of siblings located along the seaward fringe to the east of the parcel, and a smaller band to the west of the parcel (Figure 5.4). No siblings were assigned to trees that formed a band from the northwest corner to the south of the parcel, which correspond to the area occupied by trees assigned to cluster 2. Within this band full- and half-siblings were assigned to larger trees assigned to cluster 2 (I16, M6, M9, N14, & P14), specifically cluster 2b (Figure 5.4). Lower levels of relatedness, 0 – 7 half-siblings were assigned to trees E9, M3, & P4, which on further analysis were assigned to cluster 2b (Figure 5.4).

Figure 5.4. Relatedness analysis of all trees to a selection of 15 large trees in the parcel (shown in dark green) that provide a spatially representative distribution of the parcel (cluster assignment in brackets). Seaward fringe of the parcel is located to the east. Black outlines demark individual trees, and gray represents no tree present or the sample collected did not sequence. Relatedness assignment based on thresholds from the R package Demerelate.

5.6 Discussion

Fine-scale analysis of a small (400m^2) parcel of *Rhizophora mangle* forest identified moderate levels of genetic differentiation among the 182 trees. Significant positive genetic spatial autocorrelation was observed across the parcel at 2 – 8m distances, at spatial scales of 2m. K-means clustering analyses identified a total of three clusters within the forest, all of which were significantly different from each other, suggesting recruitment of propagules from three distinct sources. Additionally, we infer that trees with larger canopies, those occupying more than one 1m^2 cell, are older than trees which dominate a single cell, and the presence of a range of sizes of trees within each of the three clusters suggests that recruitment has occurred multiple times, rather than each cluster representing a single recruitment event. Whilst the source populations of these clusters are unknown, our findings emphasize the important role of recruitment events to genetic structure at fine spatial scales and indicate that genetic diversity of mangrove forest at fine-scales is greater than previously considered. Defining the spatial and temporal scales of recruitment events is critical to understanding the connectivity of *R. mangle* populations and managing this important ecosystem at the correct spatial scales. The hypothesis of low genetic structure at fine-scales in *R. mangle* forests is therefore rejected.

5.6.1 Genetic structure

Contrary to the idea that mangrove forest lack genetic structure, our findings show the presence of three genetically distinct and spatially discrete groups within a small area of mangrove forest. Within the parcel we observed significant positive genetic spatial autocorrelation at 2m spatial scales, at 2 – 8m distances, and significant negative genetic spatial autocorrelation at 10 – 18m distances, these patterns are best explained by the distribution of the three clusters throughout the parcel. These results suggest that individual clusters have a spatial dominance of 2 – 8m in size, and trees outside of this boundary are significantly different genetically. The significant genetic differences observed, both in genetic spatial autocorrelation and pairwise F_{ST} analyses, suggest the existence of at least three different sources of propagules which have dispersed and recruited into this section of forest. The range of tree canopy sizes observed within each of the clusters, suggest that propagule dispersal into this forest from the sources of the three clusters has occurred at various different times, we infer that the largest tree, I16 in cluster 2b, with an estimated canopy size of 36m^2 is part of a much earlier recruitment event than smaller trees within the same cluster with estimated canopy sizes of 7m^2, for example M9, or 1m^2, for example H11. Our findings suggest the presence of sustained recruitment from three distinct sources at a range of spatial and temporal scales.

These findings do not refute mass dispersal or recruitment events of highly related individuals (e.g. (Kennedy, Dangremond, et al. 2020)), rather our study provides evidence to support such events. For example, we suggest that trees assigned to cluster 1 are part of a more recent recruitment event, in particular the northeast corner of the parcel. This section of the parcel has a concentration of highly related, both full- and half-siblings, trees of a similar size, which is indicative of rapid growth as a result of an opening within the forest canopy (Clarke 2004). High levels of genetic similarity and the presence of half-siblings in cluster 2b, suggest a similar event may have occurred in the past, based on larger tree size within the cluster. Fewer individuals of cluster 2b may be present in the forest due to the natural thinning of trees as they develop (Berger, Hildenbrandt, and Grimm 2004). Recruitment to mature mangrove forests is facilitated by the creation of a light gap, potentially from a hurricane (Fickert 2018) or a lightning strike (Amir 2012). Which allows for the exploitation of available space by local gene pools, saplings or propagules already present in the understory (Hasan et al. 2018; Proffitt, Milbrandt, and Travis 2006; Ross et al. 2006), potentially occurring in cluster 1 where numerous smaller highly related trees surround larger more established trees, or via an influx of propagules by storm waters (Kennedy, Dangremond, et al. 2020). We suggest that when recruitment events do occur, they do not dominate established forests, instead numerous post-colonization events occur, and are associated with various source populations occurring over different temporal scales, the success of recruitment is dependent upon available space (Amir 2012; Clarke 2004). The result of which is a patchwork of trees assigned to different clusters, and a number of related individuals in clusters 1 and 2b, recruiting to the forest from different sources, which significantly influences the genetic structure of the forest. Whilst defining the drivers and spatial and temporal scales of recruitment events are beyond the scope of this study, our results identify the influence of recruitment events, from either proximal or distal sources, on genetic diversity and structure at fine scales. Recruitment events from distant sources provide the opportunity for the introduction of uncommon or rare genotypes which can be critical in promoting survival, of individuals and populations, through adaptation (Browne and Karubian 2018). Moreover, genetic structure has implications to ecosystem function and the composition associated biodiversity (Binks et al. 2019; Haddad et al. 2015; Jump and Peñuelas 2006), which is of increasing importance during an era of unprecedented climate change. Within the Caribbean region an increased frequency of high intensity hurricanes (Murakami et al. 2018) and sea level rise of 0.3 – 1.0m are predicted (Saintilan et al. 2020). Maintaining genetic diversity to build resilience and adaptive capacity will be important in mangrove populations, and should be an essential component of management and restoration frameworks (Jalonen et al. 2014; Mijangos et al. 2015; Pacioni et al. 2020).

5.6.2 Management implications

Whilst fine-scale population genetics studies may be cost prohibitive across seascapes and at every restoration project, it is essential that representative genetic structure is included within assessments. Previous population genetic studies have increased our understanding of dispersal mechanisms and connectivity of mangrove populations (see Van der Stocken et al. 2019). To avoid sampling the same individual or close relatives sampling scales among trees in such studies generally range from 5 – 30m (Bologna et al. 2019; Cerón-Souza et al. 2012; Cisneros-de la Cruz et al. 2018; Ngeve et al. 2017), and up to 100m (Núñez-Farfán et al. 2002). When stated, most studies conduct sampling along the fringe of the mangrove (Bologna et al. 2019; Cerón-Souza et al. 2012; Núñez-Farfán et al. 2002). Our findings suggest that such sampling ranges are adequate, but based on the genetic structure observed here, positive spatial autocorrelation up to 8m, we recommend sampling at similar spatial scales, 5 – 30m, into the mangrove forest or stand. Sampling within, not just along, a mangrove forest will provide greater representation of the genetic structure within a population. Sampling at broader scales can be used to monitor and evaluate the genetic diversity and structure of forests and provide comparisons to local extant forests. Which in turn can inform the spatial-scale required for effective management of mangroves across seascapes, and to monitor the effectiveness of restoration projects in maintaining genetic diversity, which are fundamental to the success of forest management (Jalonen et al. 2014; Pacioni et al. 2020), and restoration frameworks (see Mijangos et al. 2015).

5.6.3 Implications for restoration

Mangrove restoration initiatives are increasingly being implemented as a management action to reverse the decline in mangrove cover which has been observed in many countries (Friess et al.

2019). It is important to note, Lewis (2009) identified five steps to facilitate successful mangrove restoration: (1) Understand the mangrove species ecology at the site, in particular the patterns of reproduction, propagule distribution, and successful seedling establishment; (2) Understand the natural hydrology of the area, this controls the distribution and successful establishment and growth of recruiting propagules; (3) Assess modifications or barriers to the mangrove environment which prevent natural secondary succession; (4) Select sites based on the application of steps 1-3 and the resources available to implement any actions; and (5) Design the restoration project at appropriate scales, ensure the appropriate hydrology is restored, and utilize natural volunteer mangrove propagule recruitment. Only if mangroves fail to establish is a sixth step, the planting of propagules or cultivated seedlings, required. However, mass plantings of propagules or seedlings are common place, despite their low success rates (Kodikara et al. 2017; Lee et al. 2019). Additionally, planted forests rarely resemble natural forests (Jordan et al. 2019), and lower genetic diversity has been documented in restored mangrove forests (Granado et al. 2018). Our findings suggest that to best emulate genetic structure of natural populations restoration initiatives should not plant propagules or seedlings *en masse*. Colonization of new areas has been shown to be a gradual process comprised of the establishment of vagrant trees and then subsequent recruitment events expand the population (Kennedy et al. 2017, 2020). This study supports these findings and suggests that continued recruitment occurs to more mature forests in a similar incremental pattern. Therefore, if restoration initiatives require planting, we recommend a phased approach to emulate natural recruitment events. Each phase would comprise of a 5-10m band of planted propagules or seedlings, in suitable habitat preferably close to the fringe of an extant forest, subsequent phases would source propagules or seedlings from appropriate local, and diverse, populations. Source population selection and the monitoring and evaluation of restoration outcomes can be enhanced through the implementation of genetic and genomic tools (Breed et al. 2018, 2019). The sourcing of propagules and seedlings may have regulatory and ethical issues which would need to be addressed (Breed et al. 2019). Maintaining genetic diversity and gene flow of restored forests is a critical step in building resistance, resilience and adaptation of restored mangroves to future environmental conditions (Coleman et al. 2020).

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5.9 Author contributions

S.W.J.C., J.K.R., and R.F.P. were responsible for the experimental design, and S.W.J.C. conducted the fieldwork. S.W.J.C and K.M. conducted laboratory components of the study. S.W.J.C., J-P. K. G.F., V.G., and K.M. worked on the bioinformatic pipeline and data analyses. J.K.R. and R.F.P supervised the research. S.W.J.C., J.P.K., G.F., V.G., and K.M. wrote their respective components of the methods. S.W.J.C. wrote the final manuscript with input from all coauthors.

Chapter 6

Mangrove governance and management

6.1 Dichotomy of mangrove management: A review of research and policy in the Mesoamerican reef region.

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Keywords: Mangroves, Management, Conservation, Research foci, Mesoamerica, Threats.

Contribution: I conducted the literature review, collating all of the peer-reviewed articles, management plans and grey literature. I analyzed the collated materials to identify mangrove coverage estimates, mangrove legislation and research themes. I wrote the first drafts of the paper, other authors provided edits to drafts.

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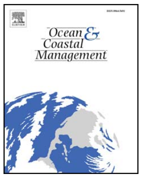

Dichotomy of mangrove management: A review of research and policy in the Mesoamerican reef region

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6.3 Abstract

Mangroves are declining globally at faster rates than tropical forests and coral reefs, with primary threats including, aquaculture, agriculture and climate change. Mangroves provide ecosystem services to coastal communities of Mexico, Belize, Guatemala and Honduras, which comprise the Mesoamerican Reef (MAR) ecoregion. Over the past two decades mangroves within the MAR have declined. Current estimates of mangrove cover in the region suggest that mangroves cover 239,176 ha of the MAR, equivalent to 1.7% of the world's mangroves. Concerted efforts to manage, conserve and protect mangrove forest are apparent in all four countries. Comprehensive laws that prohibit the cutting and clearing of mangroves have been implemented in Mexico, Guatemala and Honduras. Belize has a permitting system to regulate mangrove alterations. In addition, a total of seven international and regional agreements have been ratified. Across the ecoregion, forty-three protected areas have been designated that contain mangroves, providing protection to 111,396 ha of mangroves (47% of the total). However, our findings suggest a lack of transparency in the governance framework, a disconnect between management and research, and geopolitical differences have all played a role in reducing management efficacy. A key finding of our study reveals a distinct division in the perceived major threats to mangroves between Ramsar site managers and researchers. Ramsar site managers identify anthropogenic disturbances as key threats, while in contrast, the bulk of research focuses on natural disturbances. To promote the inclusion of evidence-based research within mangrove management plans, greater efforts to connect these important stakeholders are required.

6.4 Introduction

Mangroves are a diverse group of halophytic plant species, which form highly productive forests in the area between mean sea level and the highest spring tide mark along tropical and sub-tropical coastlines and estuaries (Tomlinson, 1994). Once perceived as mosquito infested wastelands, mangroves have now been recognized as highly productive and ecologically important ecosystems. Providing ecosystem services to marine and terrestrial environments, and human societies (Gilman *et al.*, 2008; Nagelkerken *et al.*, 2008), which are valued at US$9,900–35,900 $ha^{-1}yr^{-1}$ (Costanza *et al.*, 1997; Sathirithai and Barbier, 2001; Barbier, Hacker, Kennedy, Kock, Stier, 2011). Some of the most important mangrove ecosystem services include: coastline protection (in particular storm, hurricane and tsunami protection); waste water treatment; production of extractable materials; and provision of cultural sites (Rönnbäck, Crona and Ingwall, 2007; Warren-Rhodes *et al.*, 2011). Despite the known value of these forests, mangroves are highly threatened. Deforestation estimates suggest mangrove cover has declined by 30-86% since the mid 1990's (Duke *et al.*, 2007), and mangroves continue to decline globally at unprecedented rates (FAO, 2007). Globally, the main threats to mangrove forests include: coastal development; logging for timber and fuel; aquaculture; salt extraction; and agriculture (Valiela, Bowen and York, 2001; Alongi, 2002; Rönnbäck, Crona and Ingwall, 2007). The additional threats of climate change, e.g. sea-level rise, are also of concern (Schaeffer-Novelli *et al.*, 2016; Short *et al.*, 2016). Understanding if or how mangroves can adapt to such changes is of particular relevance to already threatened ecosystems, e.g. in the Caribbean (Godoy and De Lacerda, 2015; Sasmito *et al.*, 2016).

The majority (over 70%) of mangroves are located within developing countries (Giri *et al.*, 2011), where limited resources and capacity can inhibit effective management. At the international level, a number of treaties and conventions afford some protection to mangroves (Macintosh and Ashton, 2002), for example: the Ramsar Convention (1974); the Cartagena Convention (1983); and the International Tropical Timber Agreement (2011). However, few of these treaties provide any effective legal protection and none of them address the conservation, preservation, or management of a particular mangrove species (Polidoro *et al.*, 2010). National legislation pertaining to mangrove management in the 1960's was primarily focused on mangrove exploitation (Carter, Schmidt and Hirons, 2015). However, over the past five decades management has progressed and has led to the integration of mangroves into coastal zone management plans (Carter, Schmidt and Hirons, 2015).

Common tools for the preservation and management of mangrove and other marine ecosystems include: marine protected areas (MPA's); nature reserves; wilderness areas; national monuments and national parks. Since 1974, increasing protection has been provided through Ramsar site designation. To date, 281 Ramsar sites (12.5% of all Ramsar sites) are intertidal forested wetlands, which includes mangrove forests (www.ramsar.org). Although increased recognition of mangroves in management plans is encouraging, the majority of plans associated with MPA's and Ramsar sites are based on generalized characteristics and threats, with limited reference to prior scientific research. In fact, there appears to be no effective mechanism for creating links between management activities for, and scientific research on, mangroves, thus research is rarely incorporated into management plans. Similar observations have been made in the management of coral reef ecosystems, where a mere 14% of information cited in management plans for the reefs of Australia, Kenya and Belize was primary research (Cvitanovic *et al.*, 2014). In this case, research was deemed to be inaccessible to managers due to, long publication times, subscription only access to research and poor articulation of management implications of the research (Cvitanovic *et al.*, 2014). Yet, for effective management to take place, evidence based decision-making is critical (Christensen *et al.*, 1996; Ruckelshaus *et al.*, 2008).

In this article we use the Mesoamerican reef (MAR) ecoregion as a case study, to examine the current status of mangroves, the legislation implemented to protect, manage and conserve mangroves, and review peer-reviewed scientific outputs from the region. The aim of this paper is to understand the current management paradigms within the MAR and identify threats to mangroves within the region. We compare the foci of management strategies and research programs in order to determine where overlap occurs and where there are gaps in the knowledge base.

6.5 Methods

6.5.1 Study area

We have chosen to focus on the Mesoamerican Reef (MAR) ecoregion because the majority of mangrove research is concentrated in South-East Asia, where larger and more diverse stands of mangroves are located (Saenger, 2002). Much less is known about these ecosystems in Latin America and the Caribbean (but see, Ellison and Farnsworth, 1997; Núñez-Farfán *et al.*, 2002; Ellison, 2004). The MAR ecoregion extends over 1000 km from the Yucatan peninsula, Mexico (21.56°N; 087.09°W) to the east coast of Honduras (14.97°N; 083.16°W), encompassing the Caribbean coastlines, open-ocean, networks of cays, and offshore banks of Mexico, Belize, Guatemala and Honduras (Kramer and Kramer, 2002) (Figure 6.1). It is home to the largest barrier reef in the western hemisphere and supports the livelihoods of approximately two million people (Kramer and Kramer, 2002), of particular importance are the fishing (Box and Canty, 2010) and tourism industries (Doiron and Weissenberger, 2014). Considerable attention has been given to coral reefs in the region, however seagrass and mangrove ecosystems have often been overlooked.

In this review we consider the entire Honduran north shore as part of the MAR ecoregion, due to potentially high levels of connectivity between the Honduran east coast and the MAR (Butler *et al.*, 2011; Truelove *et al.*, 2015; Chollett *et al.*, 2017). The boundaries of the ecoregion were originally defined by the presence of several physiogeographic boundaries, these include the Gulf of Mexico, strong oceanic currents between the Yucatan peninsular, Mexico and south west Cuba, the shallow waters of the Nicaraguan rise, Honduras, in addition to a number of terrestrial environmental variables, e.g. rainfall. The ecoregion was officially declared in 1997 as part of the Tulum agreement, where all four countries came together recognizing the importance of the region and the need to jointly manage a shared marine resource (Kramer and Kramer, 2002).

6.5.2 Mangrove cover estimations

First, we estimated mangrove forest cover for each country across the region. The three true mangrove species: *Rhizophora mangle; Avicennia germinans* and *Laguncularia racemosa* are considered as part of the mangrove forest system in all four countries. However, the mangrove associate *Conocarpus erectus* (Buttonwood mangrove) is only defined as part of the mangrove forest in Guatemala and Honduras. Regardless of a country's definition of the mangrove complex, mangrove cover estimates herein include all four species. Country specific estimates of mangrove cover were taken from the most recent estimates available (Mexico (Rodríguez-Zúñiga *et al.*, 2013), imagery from 2010; Belize (Cherrington *et al.*, 2010), imagery from 2010; Guatemala (MARN, 2013), imagery from 2010; and Honduras (Carrasco and Caviedes, 2014), imagery from 2008-2010).

6.5.3 Mangrove management plans

To ascertain the level of management and protection directly focused on mangroves in each country, we first reviewed national environmental legislation, using Google searches and accessing management plans. We subsequently identified which international and regional conventions and agreements relating to mangroves each country has signed or ratified. Within the Caribbean, protected areas that contain mangroves include Ramsar sites and Marine Protected Areas (MPAs). Ramsar sites that contain mangroves were identified through the American Ramsar Secretariat (Pers. Comms.) and the Ramsar website (www.ramsar.org). The Healthy Reefs for Healthy People Initiative (HRI; www.healthyreefs.org) provides the names of all of the MPAs within the MAR, which have marine territory, and provides the associated management plan. If a management plan was not available on the HRI website a wider web search was conducted, if after the search we did not identify a management plan we assumed that one did not exist or is not publicly available. Web searches (in English and Spanish), were used to identify management plans for each of the named protected areas. Management plans for protected areas, where available, were downloaded and searched using the keywords mangroves (mangr*) in English, and manglar (mangl*) in Spanish to find explicit references to the management of mangroves. It must be noted that the most recent management plans were used in this review and that management plans within the region are generally designed for a five-year period. In many cases the management period had expired, but we assume that current management strategies are based on the most recent plans.

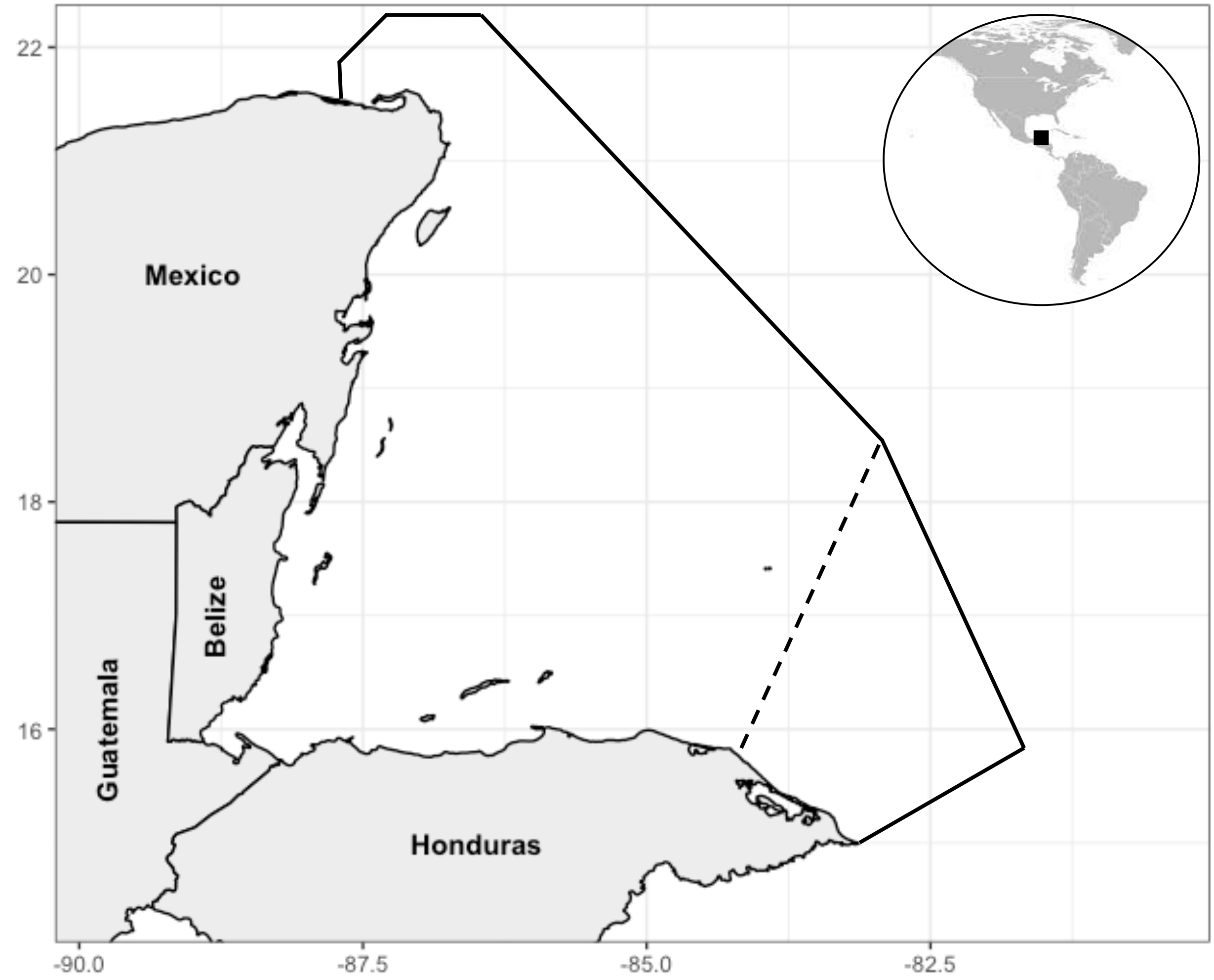

Figure 6.1. Map of the Mesoamerican Reef Eco-region. Solid line highlights the area included within the study, the official boundary of the MAR (dotted line) does not include the eastern north shore of Honduras.

6.5.4 Scientific literature review

To determine the focus of scientific research on mangroves in the MAR, peer-reviewed scientific publications were searched for using the Boolean search methodology. Multiple combinations of the following keywords (and their equivalents in Spanish) were used in the search: ‘Mangrove’; ‘*Rhizophora*’; ‘*Avicennia*’; ‘*Laguncularia*’; ‘*Conocarpus*’; ‘Mesoamerica’; ‘MBRS’; ‘MAR’; ‘Caribbean’; ‘Mexico’; ‘Belize’; ‘Guatemala’; and ‘Honduras’. Only articles published from 1997 to date were used, as this date coincides with the declaration of the MAR as an ecoregion by all four countries, and therefore to the direct management of the ecoregion. Books or book sections were not used, as we could not be sure of the peer-review process, and reviews were not included. Methodologies of articles were examined to ensure that research occurred in at least one of the four MAR countries and within the boundaries of the MAR ecoregion, as we delimited it. A total of 81 peer-reviewed publications (see supplementary materials for a full list of publications) were identified and the research undertaken in each country was tallied. Where research occurred in multiple countries in a single paper, each country received a tally.

6.5.5 Identification of threats

A fine scale analysis of articles that were identified to focus on threats to mangroves was conducted to categorize the type of threat. Eight different threats were identified, a total of 29 times, and each threat was categorized as either natural or anthropogenic disturbances. *Natural disturbances* were: hurricanes; sea-level change; light gaps; seismic activity; tsunamis; and subsidence. *Anthropogenic disturbances* were: commercial development and deforestation. Threats identified were tallied and a proportion of each threat category was calculated based on the total number of threats identified.

A list of threats to Ramsar sites was obtained from the American Ramsar Secretariat. The threats were identified by future managers of Ramsar sites from a list of 51 options supplied by Ramsar (see supplementary materials for the full list of threats and their definitions) during the Ramsar site application process. The list of threats provided was pre-defined, and as a result not all threats reported may be relevant to the protected area, e.g. in Guatemala ‘agriculture and aquaculture’ was a reported threat. However, aquaculture is currently not present in the Guatemalan Caribbean, in contrast agriculture is present and is considered a threat to mangroves.

Thirty-seven different threats were identified by Ramsar managers, across the four countries, a total of 236 times, with a maximum of twenty-two at a single site. We categorized threats as either natural disturbances or anthropogenic disturbances. *Natural disturbances* were: storms and flooding; fire and fire suppression; problematic native species; invasive and other problematic species and genes; climate change and severe weather; and invasive non-native/alien species. *Anthropogenic disturbances* were: biological resource use; human settlements (non-agricultural); tourism and recreation areas; housing and urban areas; fishing and harvesting aquatic resources; natural system modifications; agriculture and aquaculture; pollution; logging and wood harvesting; human intrusions and disturbances; hunting and collecting terrestrial animals; vegetation clearance/land conversion; recreational and tourism activities; gathering terrestrial plants; transportation and service corridors; water regulation; household sewage; livestock farming and ranching; urban waste water; agriculture and forestry effluents; drainage; dams and water management/use; energy production and mining; unspecified development; wood and pulp plantations; mining and quarrying; industrial and military effluents; water abstraction; garbage and solid waste; shipping lanes; and air-borne pollutants. Individual threats that were reported were tallied as either natural or anthropogenic disturbances, a proportion of each threat category was calculated from the combined number of threats identified.

6.6 Results

6.6.1 Mangrove cover

Mangrove cover in the MAR is estimated at 239,176 ha, cover has declined across the region since the 1990's, where mangroves covered approximately 350,000 ha (Figure 6.2), a loss of over 110,000 ha in a twenty-year period. Proportional cover of mangroves in the MAR region varies considerably between and within the four countries. The majority of mangrove cover within the MAR is located along the Yucatan Peninsula, Campeche and Quintana Roo regions of Mexico (53.5%; 128,049 ha; Figure 6.2), however Mexico has significantly greater mangrove cover in the Gulf of Mexico and on the Pacific coastlines. Belize is the only country to have its entire coastline in the MAR, and approximately one third of mangrove cover of the MAR is found in Belize (31.2%; 74,684 ha; Figure 6.2). Only a small fraction of the total mangrove cover of the region is located in Guatemala (0.5%; 1,170 ha; Figure 6.2), the majority of Guatemalan mangroves are located on the Pacific coast. Despite the size of its coastline, mangrove cover in Honduras is a small proportion of the MAR total (14.7%; 35,273 ha; Figure 6.2). Mangrove cover in Honduras is almost equally divided between the Caribbean and Pacific coasts.

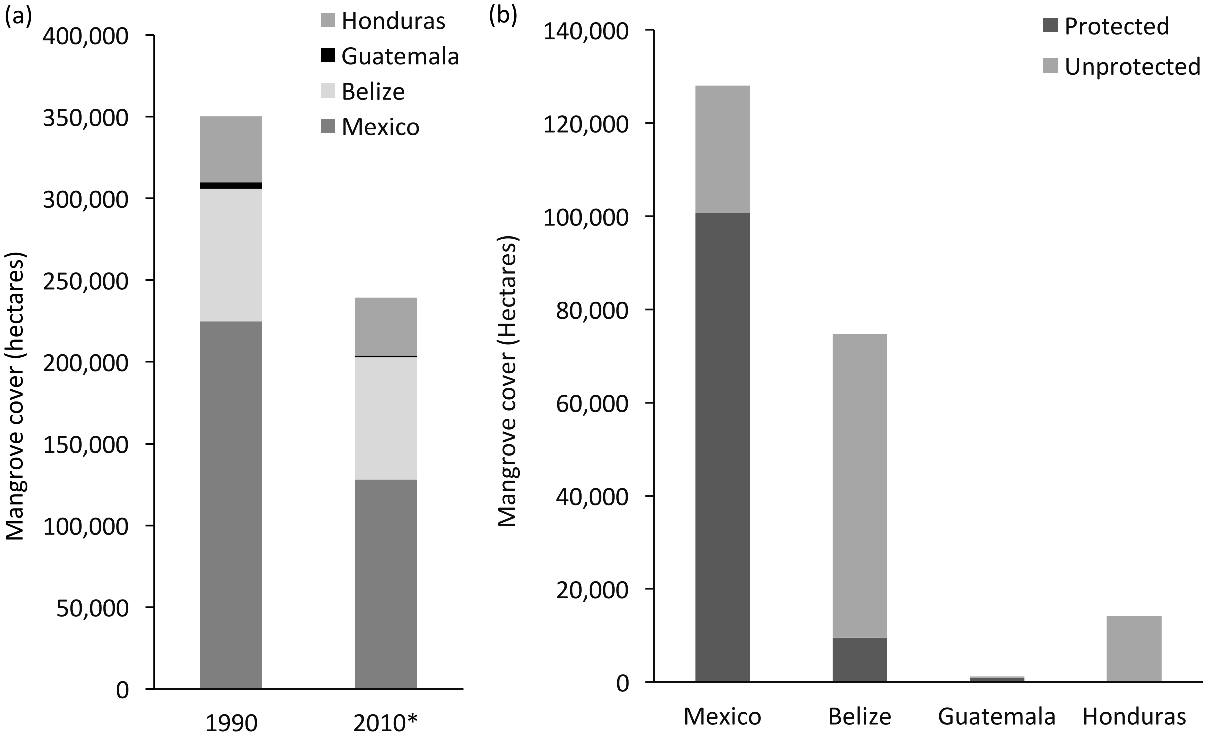

Figure 6.2. Mangrove cover within the MAR region**.** (a) Historical (Kramer and Kramer, 2002) and recent estimations of mangrove cover. (b) Total mangrove cover in each of the four MAR countries, with hectares of protected and unprotected mangrove highlighted. (Mexico (Rodríguez-Zúñiga *et al.*, 2013); Belize (Cherrington *et al.*, 2010); Guatemala (MARN, 2013); Honduras (Carrasco and Caviedes, 2014). *Some data from Honduras is from 2008.

6.6.2 Legislation and management

Comprehensive legislation exists within the region to protect mangroves. In Mexico, Guatemala and Honduras, mangroves are property of the state and stringent laws exist which prohibit the removal and cutting of mangroves and prevent changes in land use (Table 6.1). In contrast, the majority of Belizean mangroves are privately owned and only 30% are state owned. However, national legislation in Belize is applicable to all mangroves regardless of ownership. Within Belize, the cutting and clearance of mangroves is controlled by a permitting system, however the dredging and landfill of mangroves is only permitted under exceptional circumstances.

At the international level, the four countries of the MAR have ratified a total of seven international conventions and agreements to promote the management and sustainable use of marine and wetland resources (Table 6.1). The most important of these for mangroves is the Ramsar (wetlands) convention. Geopolitical differences influence regional cooperation, e.g. Mexico, a North American country, is excluded from Central American agreements, and Belize with a British rather than Spanish colonial heritage exhibits preferences with Caribbean Community agreements. All four countries are parties of the two main international conventions that are relevant to environmental protection: the Cartagena convention and Ramsar convention (Table 6.1). Honduras is the only country not to have ratified the Cartagena convention, but is a signatory to the convention. Additionally, all four countries ratified the Tulum declaration and the subsequent Mesoamerican barrier reef system project (www.mbrs.doe.gov.bz).

We identified a total of 43 protected areas in the MAR which have mangroves within their borders (Table 6.2), and estimate that just under half (46.6%; 111,396 ha) of the mangroves in the MAR are within the boundaries of a protected area. Over two thirds (31) of the protected areas have management plans (Table 6.2), although implementation of these plans may vary. The majority of management plans had no specific management strategies for mangroves, other than a reference to the national legislation, in the few instances where strategies were stated they were related to mangrove restoration, e.g. Shipstern Conservation and Management Area, Belize.

In Mexico, mangroves are the responsibility of the Department of Ecology and Environment, and the Institute for Flora, Fauna and Culture within the Secretariat of the Environment and Natural Resources. In addition, the National Commission for Natural Protected Areas (CONANP) assumes responsibility for mangroves when they are located within a protected area. CONANP may co-manage protected areas with a local non-governmental organization (NGO). We identified 13 protected areas that contain mangroves in Mexico, these areas provide protection to approximately 80% (100,764 ha) of Mexican mangroves forests in the MAR (Table 6.2; Figure 6.2).

In Belize, the Forestry Department within the Ministry of Agriculture and Fisheries is responsible for managing Belizean mangroves. The Coastal Zone Management Authority and Institute and Fisheries Department may also assume a management role. NGO’s co-manage a number of protected areas in Belize and therefore assume a direct role in the management of mangroves.

Private protected areas are increasingly popular, and these areas are coordinated by the Belize Association of Private Protected Areas. We were not able to identify any private protected areas that provided protection to mangroves. Only a small proportion (12.9%) of the total mangrove cover of Belize is located within the 15 protected areas (Table 6.2; Figure 6.2).

Mangroves in Guatemala are the responsibility of the National Forest Institute within the Ministry of the Environment and Natural Resources. The National Council for Protected Areas (CONAP) has a role in mangrove management when mangroves are located in protected areas (Table 1). Protected areas are co-managed by CONAP and local NGO's and these organizations assume the day to day responsibilities of the protected areas. The majority of mangroves within Guatemala (88.2%) are located within the two protected areas (Table 6.2; Figure 6.2).

The responsibility of mangroves in Honduras resides with the Department of Fisheries under the Secretariat of Energy, Natural Resources, Natural Environment and Mines, and local municipal environmental units have a role in mangrove management within their jurisdiction. Within protected areas, mangroves receive additional management from the Conservation and Forest Development, Protection and Wildlife Institute and local NGO's. The NGO's assume the day-to-day responsibilities of the protected areas. A total of 13 protected areas have been declared that have mangroves within their boundaries, however limited mangrove cover data is available, which precludes an accurate estimation of mangrove coverage within Honduran protected areas (Table 6.2).

Table 6.1. Legislation, Agreements and Protection of Mangroves in the Mesoamerican Reef Region.

Mangrove Legislation		**Mexico**	**Belize**	**Guatemala**	**Honduras**
Legislation		General Wildlife Act 2000, Article 60.	Forestry Act 1989, Article 52. Forests Act Chapter 213, revised in 2003	Forestry Act 1996, Article 35.	Fisheries Act 1959, Article 52.
		It is prohibited to remove, transplant, prune or conduct any work or activity that may affect the integrality of the hydrological flow of mangroves.	Dredging and landfill is strictly prohibited unless there is significant benefit to the general population. Three types of permits can be issued for the alteration of mangroves, depending on the area of mangrove to be altered. Permits can be denied.	Change of land use of mangrove ecosystems is prohibited. By-law Resolution No. 01.25.98, Article 15 allows family consumption to a maximum of $5m^3.yr^{-1}$	The removal and cutting of mangroves is prohibited.
State ownership of mangroves		100%	30%	100%	100%
Government Agencies					
Government hierarchy for the management of mangroves	*Ministry*	Secretariat of the Environment and Natural Resources	Ministry of Agriculture and Fisheries	Ministry of the Environment and Natural Resources	Secretariat of Energy, Natural Resources, Natural Environment and Mines
	Department	Department of Ecology and Environment; Institute for Flora, Fauna and Culture	Department of Forestry	National Forest Institute	Fisheries department
	External departments		Coastal Zone Management Authority and Institute; Department of Fisheries	National Council for Protected Areas	Institute for Conservation and Forest Development, Protected Areas and Wildlife
	Other Agencies	National Commission for Protected Natural Areas		National Council for Protected Areas	Local Municipal Environment Units
	Non-government organizations	e.g. Comunidad y Biodiversidad Asociacion Civil; Amigos de Sian Ka'an	e.g. Belize Association of Private Protected Areas; Toledo Institute for Development Environment	e.g. Fundación para el Ecodesarrollo y la Conservación	e.g. Bay Island Conservation Association; Roatan Marine Park
International and Regional Agreements					
Cartagena Convention (*Signatory only)		1985	1999	1989	1983*
Wetlands Convention (Ramsar[2]*)*		1986	1998	1990	1993
Tulum Agreement		1995	1995	1995	1995
Mesoamerican Barrier Reef System Project		1997	1997	1997	1997
Central American Policy for the Conservation and Rational Use of Wetlands		N/A	2002	2002	2002
Ramsar Regional Initiative for the Integral Management and Wise use of Mangroves and Coral Reefs		2009	-	2009	2009
Ramsar Caribbean Wetlands Initiative		-	2009	-	-

Table 6.2. Protected areas of the Mesoamerican Reef ecoregion with mangroves within their borders.

	MPA /NP	Ramsar site	Management plan	Reference
Mexico (n=13)				
Área de Protección de Fauna y Flora Yum Balam	X	X	Y	(CONANP, 2013)
Parque Nacional Isla Contoy	X	X	Y	(SEMARNAT & CONANP, 2015b)
Manglares de Nichupte		X	Y	(SEMARNAT & CONANP, 2014)
Parque Nacional Arrecifes de Puerto Morelos	X	X	Y	(SEMARNAP, 2000a)
Manglares y humedales del norte de la isla Cozumel		X	Y	(SEMARNAT, 2014)
Parque Marino Nacional Arrecifes de Cozumel	X	X	Y	(SEMARNAP, 1998a)
Playa Tortuguera X'Cacel-X'Cacelito		X	-	
Reserva de la Biósfera de Sian Ka´an	X	X	Y	(SEMARNAT & CONANP, 2015a)
Reserva de la Biósfera Banco Chinchorro	X	X	Y	(SEMARNAP, 2000b)
Parque Nacional Arrecifes de Xcalak	X	X	Y	(CONANP, 2004)
Parque Marino Nacional Punta Occidental Isla Mujeres, Punta Cancun y Punta Nizuc	X		Y	(SEMARNAP, 1998b)
Área Marina y Costera Protegida Actam Chuleb	X		-	
Zona Sujeta de Conservación Ecologica Santuario Manati Bahia Chetumal	X		-	
Total:	*10*	*10*	*10*	
Belize (n=14)				
Bacalar Chico National Park and Marine Reserve	X		Y	(BFD, 2004)
Laughing Bird Caye National Park	X		Y	(BFoD, 2010)
Payne's Creek National Park	X		-	
Sarstoon-Temash National Park	X	X	Y	
Shipstern Conservation & Management Area	X		Y	(PACT, 2016)
Corozal Bay Wildlife Sanctuary	X		-	
Swallow Caye Wildlife Sanctuary	X		-	
Half Moon Caye Natural Monument	X		Y	(BAS, 2007)
Caye Caulker Marine Reserve	X		Y	(BCZMIA & BFD, 2004)
Gladden Spit and Silk Cayes Marine Reserve	X		Y	(BFD, 2010a)
Glover's Reef Marine Reserve	X		Y	(BFD, 2007)
Hol Chan Marine Reserve	X		Y	(BFD, 2002)
Port Honduras Marine Reserve	X		Y	(BFD, 2012a)
Sapodilla Cayes Marine Reserve	X		Y	(BFD, 2010b)
South Water Caye Marine Reserve	X		Y	(BFD, 2009)
Turneffe Atoll Marine Reserve	X		Y	(BFD, 2012b)
Total:	*15*	*1*	*12*	
Guatemala (n=2)				
Reserva de usos multiples rio Sartsun	X	X	Y	(CONAP, 2009)
Punta de Manabique	X	X	Y	(CONAP, 2011)
Total:	*2*	*2*	*2*	
Honduras (n=13)				
Parque Nacional Sistema de Humidales de Cuyamel – Omoa	X	X	-	
Parque Nacional Jeannette Kawas	X	X	Y	(ICF, 2012a)
Refugia de Vida Silvestre Punto Izopo	X	X	Y	(ICF, 2012b)
Sistema Humedales Laguna de Zambuco		X	-	
Refugio de Vida Silvestre Cuero y Salado (Barras de Cuero y Salado)	X	X	Y	(ICF, 2011)
Parque Nacional de las islas de la Bahia	X		Y	(IHT y ICF, 2015)
Zona de Proteccion Especial Marina Turtle Harbour – Rock Harboury el Sistema de Humedales de la Isla de Utila	X	X	Y	(IHT y ICF, 2012)
Zona de Protección Especial Marina Sandy Bay West End	X		-	
Parque Nacional Port Royal	X		-	
Monumento Natural Marino Archipielago Cayos Cochinos	X		Y	(CMCC, 2009)
Refugio de Vida Silvestre Laguna de Guaimoreto	X		-	
Reserva de la Biósfera del Rio Platano	X		Y	(ICF, 2013)
Laguna de Bacalar		X	-	
Total:	*11*	*7*	*7*	
Grand totals **43**	**38**	**18**	**31**	

6.6.3 Threats to mangroves

A total of 81 peer-reviewed articles focusing on mangroves were identified within the MAR region. The majority of the research was conducted in Belize (68.2%), the remaining studies were conducted in Mexico (22.0%) and Honduras (9.8%). No peer-reviewed primary mangrove research identified from Guatemala. Of the 81 peer-reviewed articles identified, 15 of these address threats to mangroves (Ellison and Farnsworth, 1997; Feller *et al.*, 1999; Cahoon *et al.*, 2003; Piou *et al.*, 2006; Mckee, Cahoon and Feller, 2007; McKee, Rooth and Feller, 2007; Taylor *et al.*, 2007; Vaneslow, Kolb and Fickert, 2007; Granek and Ruttenberg, 2007; Carrillo-Bastos, Elizalde-Rendón, Erika Marcela Torrescano Valle and Flores Ortiz, 2008; Islebe *et al.*, 2009; Macintyre *et al.*, 2009; Mckee and Vervaeke, 2009; Hirales-Cota *et al.*, 2010; McCloskey and Liu, 2013),, a total of 8 different threats were classified. A total of 37 different threats, were identified from the 20 Ramsar sites, the majority of which were anthropogenic (90.7%), e.g. 'logging', 'aquaculture and coastal development' (Figure 6.3). The majority of peer-reviewed mangrove research from the MAR region has focused on natural disturbances (71.4%) of mangrove systems (Figure 6.3). These trends are not just a regional trend, but hold for each of the individual countries, where researchers and managers foci are on natural and anthropogenic disturbances, respectively (Figure 6.3). Primary research interests include hurricanes and sea-level change, and Ramsar managers across the region are concerned with deforestation, agriculture, and development.

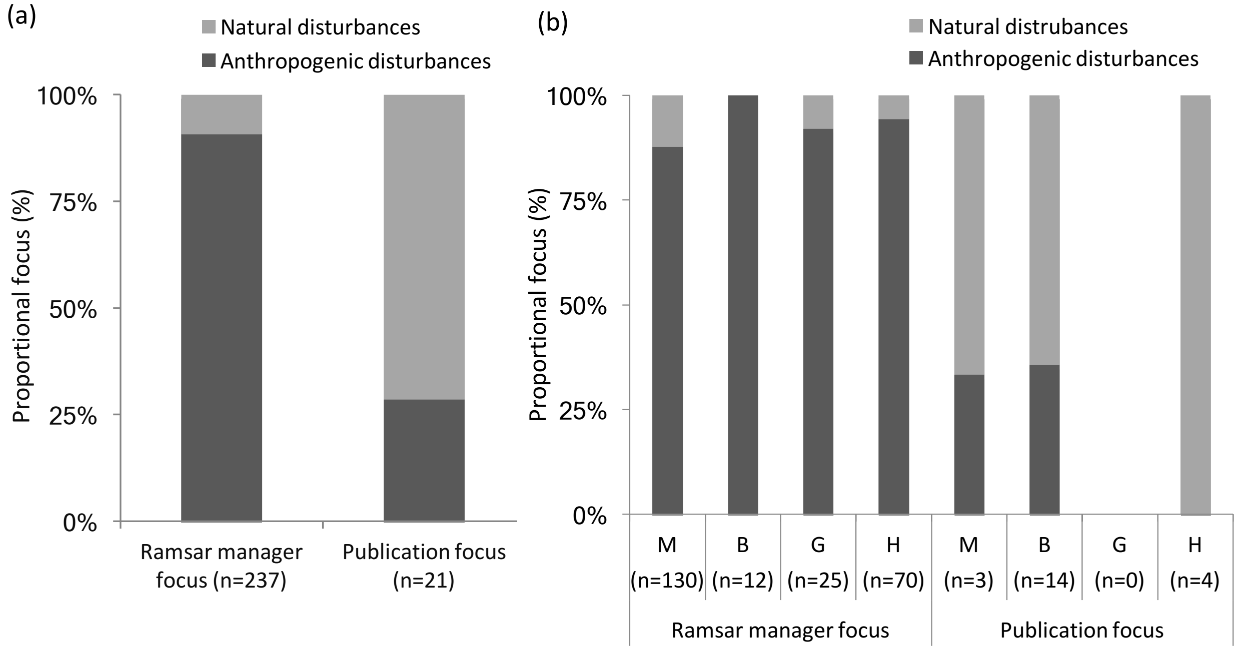

Figure 6.3. Threats to mangroves of the MAR as identified by Ramsar managers and within peer-reviewed publications (a) throughout the MAR; and (b) individual countries: M – Mexico; B – Belize; G – Guatemala; and H - Honduras.

6.7 Discussion

Despite the stringent national legislation and international agreements which provide protection to mangrove forests, and the additional protection provided by the 43 protected areas (which contain mangroves), mangrove cover in the MAR declined by over 110,000 ha from 1990-2010, with an estimated current cover of 239,176 ha, equivalent to 1.7% of the world's mangroves (Giri *et al.*, 2011). The greatest losses were observed in Mexico and Honduras. The decline in mangrove cover suggests a problem with enforcement. We suggest a lack of resources for enforcement, transparency within the governance framework, and lack of political will as potential reasons for the failure in the enforcement of mangrove legislation. The number of organizations responsible for the management and protection of mangroves in each country varies and causes confusion, with the exact role of each party unclear. Each country has a specific government department responsible for mangrove protection, with additional oversight from external agencies and non-government organizations (NGO's) when mangroves are located in protected areas. It must be noted that such discrepancies are not unique to mangrove systems or to this region (Rife *et al.*, 2013). Limited national budgets of the four countries reduce governmental institutional capacity, which has resulted in civil society in the form of NGO's filling the void in the management of protected areas. NGO's assume an important role as co-managers of protected areas, fulfilling the day-to-day management duties. However, a lack of authoritative power and a lack of human capacity to physically patrol often large and remote areas, inhibits the ability of NGO's to enforce environmental legislation (Cudney-Bueno *et al.*, 2009; Rife *et al.*, 2013). In essence many of the protected areas in each of the four countries could be considered "paper parks", as they provide no greater protection or management to mangroves than national legislation (Rife *et al.*, 2013). It is important not to be too critical of these institutions, however, all of which are operating on limited resources. The focus should be on how to support and build capacity of these organizations to allow them to improve mangrove and natural resource management efficacy.

Geopolitical interests of the different countries have reduced collaborative efforts of mangrove protection. Despite the four countries sharing an ecoregion, significant geopolitical divisions exist. This is exemplified by Belize ratifying a separate Ramsar initiative to the other three countries. The paradox is that despite having the same or very similar objectives, the four countries are not working together to achieve these goals. A lack of collaboration and harmonization in how management strategies are developed and implemented can reduce mangrove protection, especially in forests that straddle international borders (McCallum, Vasilijević and Cuthill, 2015). Belize is the only country where all of mangroves are within the boundaries of the MAR. In contrast Mexico and Guatemala have significantly greater mangrove cover on other coastlines, and a little more than half of the mangrove cover of Honduras is concentrated within the Gulf of Fonseca, on the Pacific coast. Threats to mangroves may vary significantly on the different coasts, and therefore influence how national mangrove legislation is developed, and how governments prioritize limited management resources. Regardless, greater collaborative efforts, such as the Mesoamerican Barrier Reef System Project, need to be established to promote the protection of marine resources, and facilitate transboundary initiatives that recognize that ecological populations do not align with geopolitical boundaries. There is a high probability that mangrove forests within the region are connected as recent studies have shown high levels of ecological connectivity in the MAR region for lobster, fish and corals (Butler *et al.*, 2011; Truelove *et al.*, 2015; Chollett *et al.*, 2017).

Evidence based decision-making has been well documented as an important component of resource management (Christensen *et al.*, 1996; Ruckelshaus *et al.*, 2008). However, in the papers we reviewed there appears to be no discernible link between researcher recommendations and resource manager decision-making or actions. Concluding statements within articles may make some reference to conservation or management, but usually included no advice on how to apply research findings directly to management. Additionally, our study identified a disconnection between Ramsar site managers and the scientific community. Managers were primarily focused on localized anthropogenic threats (e.g. Macintyre *et al.*, (2009)), while researchers focused on natural disturbances, such as hurricane events (Vaneslow, Kolb and Fickert, 2007) and the impact of sea-level change (Mckee, Cahoon and Feller, 2007). Both anthropogenic and natural threats have either had, or have, the potential to negatively affect mangrove cover, but the different foci of researchers and managers is likely to hinder progress in mitigating threats from either source.

It is crucial that researchers and managers increase their communication and work together to understand the full complexity of the threats to mangrove forests. Combining these different priorities could bring important benefits. For example, the identification of areas of mangrove forests resilient to climate change can focus management efforts and create local priority conservation zones where anthropogenic disturbances should be minimized. Both groups are focusing on important issues, however the assumed lack of dialogue between stakeholders precludes the integration of science into mangrove management plans. Cvitanovic et al. (2014) have reported similar disconnects in the management of coral dominant marine protected areas. They proposed knowledge brokers, boundary organizations, knowledge co-production and management-orientated summaries in research articles as potential solutions to provide managers access to scientific outputs. The HRI program has put some of these in place within the MAR primarily focused on coral reefs, but these could be adapted to facilitate greater communications between managers to promote science lead mangrove management. In addition, discussion forums exist, such as the mangrove list (majordomo@essun1.murdoch.edu.au). Listservs provide a forum where individuals can pose questions to experts in an array of different fields and can provide useful dialogue between practitioners and researchers.

These potential solutions provide important links between peer-reviewed conservation science and conservation managers, but the dichotomy of researcher and manager foci must also be addressed.

Combining current research interests of natural disturbances with local management concerns of anthropogenic stresses, in particular the understanding of local drivers of deforestation, is critical. However, if institutional capacity is lacking, then the implementation of management strategies will always be problematic. Building capacity within and among government departments and NGO's to ensure the effective enforcement of legislation and promote links with the scientific community to facilitate science-based decision-making is vital for the management of mangroves in the MAR, and elsewhere. It is important that managers have access to and make use of current research, especially when developing management plans (Adeel and Pomeroy, 2002; Iftekhar and Islam, 2004; Schmitt and Duke, 2015). There is also an onus on researchers to increase the availability of their research to management authorities, not just government agencies, potentially through regional online archives or data repositories. Additionally, researchers should engage managers prior to conducting their research to foster a dialogue that can promote mangrove management and conservation efforts. Promoting public awareness to garner political will is also important, and a greater understanding of the ecosystem services provided by mangroves to local communities and their inclusion in management has the potential to increase the protection and conservation of mangroves (Shunula, 2002; Sudtongkong and Webb, 2008; Datta, Chattopadhyay and Guha, 2012).

We propose the following recommendations to promote management of mangroves within the region:

(1) Coordinated and detailed mapping projects in Belize and Honduras to provide more recent estimates of mangrove cover that can be used to set baselines from which management actions can be monitored and assessed;
(2) The implementation of a systematic, harmonized, mangrove monitoring protocol throughout the region that will facilitate comparisons of mangrove forest status;
(3) A program of work to increase understanding of the connectivity of mangrove populations throughout and beyond the MAR ecoregion, which can then be used to identify areas where greater collaborations are needed;
(4) The creation of a repository of scientific literature of the region to which researchers can submit their research, making it available for practitioners in the region and providing

another step towards an increased dialogue between managers and the scientific community.

Our proposals require coordination and management of resources and information across the MAR. The HRI program already brings together stakeholders from across the region, but at present is heavily coral reef focused. Mangrove coverage was an key indicator within the original HRI guide (McField and Kramer, 2007), and therefore could become part of the biennially produced report card, which provides stakeholders an update on the status of marine resources. Our suggestion is that the network of contacts and collaborations within this program could be used to facilitate more coordinated monitoring and assessment of mangroves and seagrass ecosystems in the region.

6.8 Conclusion

The stringent national legislation and international agreements which should provide protection to mangrove forests within the MAR are ineffective. A number of local anthropogenic stressors threaten mangrove forests, and despite comprehensive legislation, mangrove cover has declined in all four countries. Capacity building of government and non-government institutions is required, as a lack of capacity has reduced environmental regulation enforcement. Local anthropogenic stressors are of greatest concern to managers of protected areas, whilst scientific research is focused on natural disturbances, primarily climate change. These different focuses can be advantageous if they can be linked effectively. For example, the identification of climate change resilient mangrove forests can channel mangrove management efforts to maximize effectiveness of limited resources. Greater understanding of drivers of local anthropogenic threats to mangroves is required to provide managers with the necessary tools to reduce these threats and promote mangrove forests and the ecosystem services they provide. To promote successful management, we suggest the reinforcement of institutional capacity, enhance links between government departments and civil society and increase science-based decision-making within protected areas management plans.

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Chapter 7

General discussion

7.1 Discussion

Globally widespread declines in coral (Hughes et al. 2017), mangrove (Friess et al. 2019) and seagrass (Unsworth et al. 2019) cover and degradation of these ecosystems have been reported, as have declines in fish stocks (Pauly and Zeller 2014; Sale and Hixon 2015). This has important implications not only for the future of these ecosystems and the biodiversity they support, but also for the coastal communities that rely on these resources (Diaz et al. 2019). The Mesoamerican reef (MAR) ecoregion is a microcosm of these global trends, and in 2017 the MAR was designated as a critically endangered ecosystem (Bland et al. 2017). However, there are positives within the region, as greater collaboration is being observed and greater efforts to promote management of marine resources is increasingly evident. To reverse the observed trends in ecosystem declines, greater conservation and management strategies have been enacted to protect coral reefs, mangroves and seagrasses *in situ*, and ambitious restoration projects are being implemented (Boström-Einarsson et al. 2020; GMA 2019). Whilst there is significant merit in restoring ecosystems, it is critical that restoration is forward looking and ensures that these ecosystems are resilient and able to cope with future environmental conditions (Hughes et al. 2017).

7.1.1 Fisheries

Meta-analyses of catch reconstructions from the Honduran fisheries challenges the long-held belief that industrial fishery is the most important sector, and brings to the fore the critical role of the small-scale fishery sector to both local and national economies. Furthermore, the results in Chapter 2 (published as The hidden value of artisanal fisheries in Honduras, in *Fisheries Management and Ecology,* Canty et al. (2019)), emphasise the important role of small-scale fisheries to the food security of the more than two million people within the coastal communities of Mexico, Belize, Guatemala and Honduras. Whilst individual fishing pressure is diffuse, the combined fishing activities of all small-scale fishers is significant, and growing. There is a critical need to effectively manage these small-scale fisheries, but these fisheries have the greatest potential of being sustainable (Pauly, 2006) and equitable (Beltrán Turriago, 2013). For effective management and to promote sustainability in these fisheries, efforts to collect reliable landed catch data from this sector need to be increased (Pauly & Charles, 2015). Advances in data collection within the small-scale fisheries of the MAR have occurred, collating data pertaining to landed catch in terms of species and volume through mobile applications, such as Ourfish (Canty et al. 2019). However, an important component, identifying fishing location, has proven more difficult due to issues related to privacy, regarding the tracking of people, and the cost of vessel monitoring systems that are satellite- or cellular network based. Knowledge of the distribution of fishing pressure across a seascape is an important component of fisheries management, especially with the increased declaration of territorial user rights for fishing, and marine protected areas as countries aim to increase marine protection targets (O'Leary et al. 2016).

Secrecy surrounding fishing excursions, and favoured fishing grounds, can mean fishers are unwilling to share their fishing location with data collectors. In addition, traditional methods to assess fisher activity, in particular compliance with protected areas, have been shown to have various levels of effectiveness (Dhanjal-Adams et al., 2016). However, knowledge of fishing locations and the fishing pressure at these locations is important for spatial planning, where ecological needs of fisheries and the habitats that support them are balanced with the socio-economic demands of coastal communities. To circumvent privacy issues of tracking people, I tested three tools, in Chapter 3 (published as Evaluating tools for the spatial management of fisheries, in the *Journal of Applied Ecology,* Canty et al. (2018a)), genotyping, otolith microchemistry and morphometrics analyses, which have previously discriminated fish to different stocks and/or fishing grounds, on the yellowtail snapper (*O. chrysurus*). Yellowtail snapper is an important species within the small-scale fisheries of Mexico (Salas, Mexicano-Cítnora, and Cabrera 2006) and Honduras (Box and Canty 2010). Morphometric analyses were identified as the most accurate of the three tools, with an assignment accuracy of ~80% at small spatial scales of 5-60km. Additional benefits of this methodology include cost-effectiveness, and quick turnaround time from data collection through analysis. Whilst refinement of these analyses is required to improve accuracy, the potential of morphometrics analyses as a tool to assist in fisheries management is high. Moreover, a recent study by Nuñez-Vallecillo (2020) identified that morphometric analyses are able to effectively assign lane snapper (*Lutjanus synagris*) and white grunt (*Haemulon plumierii)* to their fishing grounds, and there is potential to expand this type of analysis to more species. Whilst my findings provide useful information for the management of key fisheries within Honduras and the MAR area in general, it is important that management strategies are more inclusive, and ecosystem-based so that sustainable management of the ecosystems that support different fisheries, are implemented (Zhou et al. 2010). Yellowtail snapper move between the habitats, namely coral reefs, mangroves and seagrasses, during different phases of their life and diurnal cycles, similar to many other coral reef fish species such as the lane snapper and white grunt (Nagelkerken et al. 2010; Serafy et al. 2015; Verweij et al. 2006, 2008). Therefore, the health and status of many coral reef fisheries are intricately linked to the health of coral reefs, mangroves and seagrasses, it is therefore critical that the management of fisheries is not separate from the management of the ecosystems that support them (Harvey et al. 2018).

7.1.2 Coral reefs

Overfishing is one of the greatest threats to coral reefs. However, other site-specific stressors such as eutrophication and sedimentation, in addition to global phenomena such as ocean acidification and increasing sea surface temperatures significantly stress coral reef systems (Spalding and Brown 2015). The combination of these stressors has driven the decline in coral cover, and average coral cover in the Caribbean declined from 34.8% in 1970 to 16.3% in 2012 (Jackson et al. 2014). These declines are coupled with increases in macro-algae (Hughes 1994; Hughes et al. 2007) and a reduction in habitat complexity (Alvarez-Filip et al. 2013; Magel et al. 2019), which influence coral reef fish species composition and reduce the capacity of reefs to support fisheries (Wilson et al. 2010). As fish populations decline, the regulatory roles they provide to coral reefs are decreased, which reinforces a further drop in reef health (Edwards et al. 2013; Robinson et al. 2017). Management strategies that promote coral reef health include the implementation of marine protected areas to reduce fishing pressure (Krueck et al. 2017), and ridge to reef management plans which focus on land-based stressors at the watershed level (Carlson, Foo, and Asner 2019). Whilst natural regeneration promotes more complex and resilient systems than active restoration (Crouzeilles et al. 2017), there is a growing realisation that intervention in the form of restoration is required. Ensuring that restored reefs have the capacity to adapt to future environmental conditions is critical for the persistence of reefs, the fisheries they support and the well-being of coastal communities (Hughes et al. 2017), and for this to be achieved there is a need to incorporate genetic diversity into restoration frameworks (Ladd et al. 2018).

Within the MAR and Caribbean two important fast-growing reef building (hermatypic) corals, staghorn coral (*Acropora cervicornis*) and elkhorn coral (*A. palmata*), are the focal species of restoration projects (Boström-Einarsson et al. 2020). The three-dimensional lattice structure they provide is an important habitat for a range of fish species (Johnson et al. 2011), in addition to providing other critical ecosystem services to coastal communities (Costanza et al. 2014). However, during the 1980s the combination of a series of catastrophic hurricanes and the rapid spread of white band disease decimated Acroporid coral populations, reducing them by at least 80% (Gardner et al. 2003), and the overall cover of *Acropora* species has remained low throughout the region (Rodríguez-Martínez et al. 2014). Remnant populations exist throughout the Caribbean, e.g. Belize (Fogarty et al. 2012), Florida (Baums et al. 2006; Hemond and Vollmer 2010), Guadeloupe (Japaud et al. 2015), Honduras (Keck et al. 2005), and Mexico (Porto-Hannes et al. 2015). The problem of sourcing colonies from remnant populations is that genetic diversity may be low, which may limit the ability of colonies to adapt to changing environmental conditions. High levels of clonality have been observed in remnant colonies of *Acropora* in Florida (Baums et al. 2006; Hemond and Vollmer 2010) and Guadeloupe (Japaud et al. 2015). Greater attention needs to be given to genetic diversity when restoring habitats (Granado et al. 2018; Mijangos et al. 2015), especially in those dominated by a single species. Within the restoration process there is the potential to lose or reduce fitness in the restored population, driven by founder effects, genetic swamping and inbreeding or outbreeding depression (Baums 2008). Whilst the genetic difference observed in Chapter 4 (submitted as Genetic structure of a remnant *Acropora cervicornis* population, to *Scientific Reports*), for *A. cervicornis* colonies within the Cordelia Bank site of special importance to wildlife may be subtle, the significantly different and higher than expected genetic structure could be critical for the long-term success of restoration initiatives. Promoting genetic diversity within restored population will ensure that ecological and evolutionary processes are maintained and facilitate adaptation and evolution in a period of environmental change and variability (Ladd et al. 2018; Mcleod et al. 2019).

7.1.3 Mangroves

Over a decade ago, similar to coral reefs (Stone 2007) there was concern that we could face a world without mangroves (Duke et al. 2007). The loss of mangrove ecosystems has significant implications to fisheries (Carrasquilla-Henao and Juanes 2017; Rogers and Mumby 2019), neighbouring marine ecosystems (Guannel et al. 2016), and coastal communities (Blankespoor, Dasgupta, and Lange 2017; del Valle et al. 2020) due to the array of ecosystem services they provide. However, there is some cause for optimism as deforestation rates have slowed and in some instances mangrove cover has increased through restoration initiatives (Friess et al. 2020).

Habitat restoration is becoming an increasingly common component of mangrove management strategies, and the Global Mangrove Alliance aims to increase the global area of mangrove habitat by 20% over current extent by the year 2030 (GMA 2019). Regeneration through secondary succession is preferred, whilst this process may require some facilitation, such as hydrological restructuring (Lewis 2009), recolonization via natural processes provides more complex and resilient systems (Crouzeilles et al. 2017). However, the planting of mangrove propagules and/or seedlings is common place, despite reports of their low success rates (Kodikara et al. 2017; Lee et al. 2019), and loss of genetic diversity (Granado et al. 2018). It is therefore important to work to improve restoration best practices and policies (Lee et al. 2019), importantly there have been increasing requests for the inclusion of genetics within restoration protocols and frameworks (Jalonen et al. 2014; Mijangos et al. 2015; Pacioni et al. 2020). Yet limited fine-scale genetic analyses of mangrove forests have been conducted to date that could inform restoration projects at the required scale. In Chapter 5 (in preparation as Seeing the trees within the forest, a fine-scale genetic analysis of a mangrove forest), I identified high levels of genetic structure between 182 trees within a 400m^2 area of forest at 2m scales at 2 – 8m distances. These data not only provide one of the first detailed genetic analyses of a mangrove forest as such a fine-scale, but also provides critical knowledge to inform mangrove restoration projects, in one of the most widely used genera of mangrove species, *Rhizophora*. My findings highlight greater genetic structure in mangrove forests than previously considered, and suggest that dispersal and subsequent successful recruitment events, from various sources, occur over a range of both temporal and spatial scales. The patchwork of genetic structure observed within the parcel of forest identifies a significant potential source of resilience and adaptation within the ecosystem, which needs to be replicated during restoration initiatives. This is of the utmost importance as mangroves are threatened by a range of climate driven threats, in particular sea-level rise and increased intensity of hurricanes (Gilman et al. 2008).

Mangrove restoration is not the only management tool and should not be used in isolation. It is also important that management strategies are evidence-based with monitoring and evaluation checks in place (Rivas et al. 2020). Within the MAR ~47% of mangroves are within protected areas, yet mangrove cover has declined. In Chapter 6 (published as Dichotomy of mangrove management: A review of research and policy in the Mesoamerican reef region, in *Ocean and Coastal Management*, Canty et al (2018b)), I identified a dichotomy between the focus and needs of managers and researchers, resulting in limited to no evidence-based management strategies being implemented within the ecoregion (Canty et al. 2018b). Whilst stringent national legislation exists within each country, and all four countries have ratified various international agreements which provide protection to mangrove forests, mangroves coverage declined by over 30% between 1990 and 2010. The findings of Canty et al. (2018b) were a critical component in initiating the development of the regional strategy for mangrove management, conservation, restoration and monitoring in the Mesoamerican reef 2020-2025, which was published in early 2020 (Rivas et al. 2020). The strategy was developed through a participatory approach where the Mesoamerican Reef Fund and the Smithsonian Institution convened over 70 people from across the region for a two-and-a-half-day workshop. Participants included community and indigenous people groups, non-governmental organisations, government departments, and academia. The goal is for the strategy to be adopted by the four countries of the MAR, Mexico, Belize, Guatemala and Honduras, as a guiding document for national management plans. A tenet of the mangrove management strategy was understanding the links between mangroves, coral reefs, seagrasses and fisheries, and that mangroves are a key habitat within the larger ecosystem that is the Mesoamerican reef region. This is key for future marine spatial planning efforts, understanding the interconnectivity of the different ecosystems and fisheries, and will promote greater efforts of integrated management plans. Within the MAR this is even more important, with high levels of connectivity between identified between habitats and fisheries throughout the region (Chollett et al. 2017; Truelove et al. 2015), and the use of different habitats throughout different stages of the fish lifecycles (Serafy et al. 2015). Not only building in models of connectivity within marine reserve and other management designs, but monitoring and evaluating the impact of these actions to both ecosystems and fisheries will be essential for resilient and healthy, ecosystems, fisheries and coastal communities of the MAR.

7.2 Thesis conclusions and future direction

In this thesis, I have highlighted the important role of small-scale fisheries to the local and national economies of Mexico, Belize, Guatemala and Honduras. Catch reconstructions from the Honduran fishery identified that whilst individual catches of fishers are small, the combination of all excursions of all these fishers is significantly greater than the industrial fishery, and landed catches have been significantly increasing since the 1970's. I highlight the importance of these fisheries to the economies and food security of coastal communities throughout the MAR. These findings provide critical evidence and justification for the inclusion of small-scale fisheries within national and regional fisheries management plans. To support fisheries management, I tested seafood traceability analyses on the yellowtail snapper (*Ocyurus chrysurus*) an important fishery within the small-scale fisheries of Mexico and Honduras. Morphometric analyses identified subtle differences in fish body shape of yellowtail snapper caught at three fishing grounds across the Honduran north shore, separated by 5-60km. Genetic analyses, using microsatellites, and otolith chemistry analyses were not only less accurate but associated with higher costs and slower processing times. Recently similar analyses were conducted for two other important fisheries of the MAR, lane snapper (*Lutjanus synagris*) and white grunt (*Haemulon plumierii*), demonstrating wider application of morphometric analyses within fisheries management. The critical next-step is moving beyond proof of concept and producing a framework and package that can be implemented within fisheries. I am currently co-leading a collaboration to automate the morphometric analyses and determine, if through artificial intelligence assignment accuracy can be increased. If successful, the aim would be to produce a mobile application for fisheries managers to use in the field.

Reef fisheries cannot be managed in isolation, their dependence on and ecological roles within coral reefs, mangroves and seagrasses is critical for the health and resilience of fish stocks and these ecosystems. However, coral reefs have been in decline for decades, and within the Caribbean populations of corals within the genus *Acropora* have been decimated. I examined the genetic structure of *A. cervicornis*, using microsatellite markers, within a remnant population located on three banks in the Cordelia Bank site of special importance to wildlife, Honduras. I identified low, but significant genetic structure across the three banks and lower than expected clonality across the colonies. These results suggest that recruitment from sexual reproduction has occurred multiple times on all three banks, and has created a small, but important reservoir of genetic diversity. It is important that this area remains protected to maintain this important remnant population. Additionally, if colonies are to be used in restoration projects it will be essential that the observed genetic diversity is maintained in out planted colonies to allow for adaptation and evolution to changing environmental conditions. The aim is to share these results with organizations and practitioners engaged in coral restoration projects to improve best-practices, primarily to ensure genetic diversity is incorporated into restoration frameworks. I conducted a similar fine-scale analysis of a red mangrove (*Rhizophora mangle*) forest, using single nucleotide polymorphism markers. These analyses identified much greater genetic diversity than expected, and spatial structuring was observed at a 2m scale, with significant positive associations observed at 2 – 8m and significant negative associations observed at 10 – 18m. A total of three significantly different genetic clusters of trees were identified within a small forest patch, and the spatial distribution of these clusters relate to the genetic spatial autocorrelation observed. These findings not only identify greater genetic structuring than expected, but also recruitment to the mangrove forest over a range of spatial and temporal scales. The level of genetic structure within the forest has implications for sampling for future population genetic studies, and for restoration initiatives. The next steps will be to complete a large-scale genetic analysis for mangrove forests located throughout the MAR ecoregion, and integrate these results into on-going regional efforts to design a network of marine reserves.

The regional review I conducted identified a disconnection between managers of mangroves and mangrove researchers. To promote greater collaboration and identify pathways for evidence-based management of mangroves I launched the Mesoamerican Mangrove and Seagrass Network in 2018. The network currently has over 100 members, which include managers, researchers and donors from across the region. The review identified stringent laws and regulations specifically protecting mangroves in all four countries, however short falls in management capacity and geopolitical differences have reduced management efficacy and mangrove cover declined by ~30% between 1990 and 2010. These findings provided the foundation for the development and implementation of the regional strategy for mangrove management, conservation, restoration and monitoring in the Mesoamerican reef 2020-2025. Future work will be focused on supporting efforts to achieve the goals set out in the strategy, and work towards the recommendations of: regional mangrove mapping; a standardized regional mangrove monitoring protocol; large-scale genetic connectivity analysis; and creating a repository to provide access to mangrove research to managers.

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8 Appendices

8.1 Appendix 1 – Chapter 2 supplementary material

S1 – In-depth Honduran catch reconstruction methodology

S1.1 The Caribbean Sea (FAO Area 31)

S1.1.1 Reported industrial catch

Industrial fishing in Honduras is limited to Area 31 (Caribbean) with four fleets, licensed to exploit four resource types: Caribbean spiny lobster, queen conch, shrimp, and finfish (primarily grouper and snapper). The industrial sector is diverse, fishing vessel lengths vary from 4 to 78 m (13 to 258 feet), crews range from 6 to 85 people, and the duration of fishing excursions vary from 10 to 90 days, depending on the fishery (USAID, 2012). National industrial fisheries first appeared in Honduras during the late 1950s (FAO, 2002), at which time only limited catch data were reported. Given that industrial catches were always landed at major ports, all catches from 1950 to 1989 reported to FAO were considered industrial catch. In 1990, the governmental body DIGEPESCA was created and began to collate fisheries data; therefore, for the period of 1990-2015 industrial landed catch data was obtained directly from DIGEPESCA records.

S1.1.2. Illegal industrial catch

As the Honduran Grand Banks are situated in the far eastern part of the EEZ, close to the Nicaraguan border, extending northeast to the Jamaican border, the Honduran fleet do enter into Nicaraguan and Jamaican EEZ waters illegally. In order to consider this and still be conservative, we estimated illegal catch as 15% of the total estimated industrial lobster catch, as a constant percentage over time. These data are presented as Honduras fishing in either Jamaican or Nicaraguan water, respectively. Estimations on foreign fishing vessels illegally entering to Honduran EEZ were not included in the analysis.

S1.1.3. Unreported industrial catch

Undeclared discards are part of the industrial unreported catch in Honduras. The major non-selective fishery is bottom-trawl shrimp fishing. Conch are hand-collected and lobster are either hand collected or caught in traps. The capture of finfish is mainly from vertical long lines, where low valued bycatch is usually consumed and accounted for in the ‘subsistence fishery’ category (see below). Thus, the major non-selective industrial fishery component is the bottom-trawl shrimp fishery. To estimate unregulated shrimp discards we followed (Davies et al., 2009) who suggested a bycatch rate of 78%, where no bycatch was landed. This percentage was applied to FAO reported shrimp landings for 1950-2015 to estimate what was taken from the sea to be discarded later. Any bycatch in the industrial finfish fishery was assumed to be either recorded in the official records or used for personal consumption and therefore estimated under 'subsistence'.

S1.1.4. Reported artisanal catch

Artisanal fishing, as defined by the Honduran Fisheries Law of 1959, is "fishing within three nautical miles from the shore using boats with a capacity of 3 tonnes or less and employing basic fishing equipment". Therefore, within Honduras, all small-scale vessels are classified as artisanal. The large extension of the Caribbean coastline provides suitable fishing grounds across the Honduran mainland and island archipelagos, with more than 135 different fishing communities (Stephen Box, personal observation) with over 7,000 registered artisanal fishers included in the DIGEPESCA fisher registration system. The geographical expanse and remoteness of many of these communities has made it difficult to collect catch data from these fisheries, resulting in limited available data.

From 2001, FAO records included some artisanal fishing activity (Diana Vasquez, Centro de Estudios Marinos, personal communication). We assumed that the remainder of FAO catch unaccounted in DIGEPESCA data was artisanal catch for the period of 2001-2015, where FAO landings exceeded DIGEPESCA reports. Since artisanal fishing in this region was not reported until recently, the FAO landings data for the early time periods were assumed to be industrial fisheries. As a conservative estimate, the reporting of artisanal fisheries to the FAO was considered to improve linearly from 0% of catch reported to the FAO in 1989 to the calculated percentage of FAO catch estimated to be artisanal in 2001 (i.e., 74% of reported data).

S1.1.5. Illegal artisanal catch

Transboundary fishing by artisanal fishers is a problem with Honduran boats making excursions into Belizean territorial waters and Guatemalans fishers making excursions into Honduran (and Belizean) waters (Perez, 2009). To incorporate this and remain conservative, we estimated illegal artisanal catch as 15% of the total estimated artisanal catch, as a constant percentage over time. These illegal catches were identified and labeled as Honduras fishing in

Belizean waters. We did not estimate the catches of foreign artisanal fleets fishing illegally in Honduran waters.

S1.1.6. Unreported artisanal catch

Despite artisanal fisheries existing in Honduras since the pre-Columbian period, no data were available for the artisanal fishery for the period 1950-2000. Reporting of artisanal fisheries has occurred since 2001 primarily from the cities of La Ceiba, Puerto Cortex and Tela along the Caribbean coastline. However, no catch data have been collected from many of the smaller fishing communities in between, despite their considerable fishing effort (Stephen Box, unpublished data). In addition, large inconsistencies were found between the FAO dataset of 2011 and other sources of information. For example, differences in reported magnitudes from 4.8 to 10 times, principally for lobster and finfish catch (e.g., FAO, 2002; Heyman and Granados-Dieseldorff, 2012). To be conservative, our estimates of unreported artisanal catch assumed that reported artisanal catch reflected 50% of total catch from artisanal fisheries from 2001-2015, which is a very estimate. Total reconstructed artisanal catch from 2001 to 2015 was used to calculate an average catch rate per artisanal fisher: annual tonnage of the reported artisanal data (2001–2015) divided by the number of fishers for that time period, which led to an overall catch rate (i.e., tonnes of fish per fisher per year). Then from 1950 to 2000, reconstructed artisanal catch per year was obtained by multiplying the catch rate by the number of artisanal fishers estimated for each year (FAO, 2002); see methodology of artisanal fisher's estimation in subsistence section.

S1.1.7. Subsistence fisheries

We estimated subsistence catches for two sources: Fishers from the artisanal sector may set aside a portion of their catch for personal consumption (MacKenzie and Stehlik, 1996); and dedicated subsistence hand-collection of a preferred bivalve, the Caribbean donax (Donax denticulatus) for home consumption. The artisanal fisheries-derived subsistence catch was estimated by multiplying the number of artisanal fishers by an amount of fish per capita for home consumption. FAO (2002) documented at total of 9,132 fishers on the Atlantic coast, which also matched well with grey literature estimates (Box and Canty, 2011). The artisanal fisher population was assumed to change over time as a fixed proportion (0.00177%) of the national population of Honduras from 1950–2015 (World Bank, 2017). The per-fisher quantity of subsistence catch was taken from a study conducted in the neighbouring country of Guatemala (Trujillo et al., 2012), which estimated a take-home subsistence portion of 70 kg·fisher-1·year-1. This estimate is conservative considering that fishers share the catch with their family.

In addition, the common Caribbean donax (Donax denticulatus) is gathered by hand, usually by local women and children (MacKenzie and Stehlik, 1996). The donax catch is intended only for subsistence and not sold at markets (MacKenzie and Stehlik, 1996). As a minimum, we estimated an average of 5 kg of donax per year per artisanal fisher's household. Therefore, we estimated a total subsistence catch of 75 kg·fisher-1·year-1 for the Honduran Caribbean region. This is likely a very conservative estimate.

S1.1.8. Recreational fisheries catch

We categorized recreational fisheries as the capture and non-release of sport fish species (e.g., mahi mahi, Coryphaena hippurus). To estimate catch from this sector, we firstly identified Honduran sport fishing companies using online searches via Google and Trip Advisor with combinations of the following search terms, "sport", "fish*", "recreation*", "trip*", "excursion*", "tourism", "activities", "Honduras", "Bay Islands", "Roatan", "Utila", "Guanaja", "Cayos Cochinos" (*represents derivatives of a search term, e.g., fish, fishing). Secondly, following Belhabib et al., (2016), YouTube videos were identified using names of sport fishing companies collated in the previous search. From each video, we identified and recorded the number of fish caught and their species. The weight of landed catch was sometimes reported by the fisher; where this did not occur, we estimated fish length and subsequently calculated their weight using species-specific parameters to transform length to weight from www.fishbase.org (Froese and Pauly, 2017). The number of annual trips of each company was estimated through tallying the number of reviews and Instagram posts each company received per year, these were cross-referenced to prevent duplication of fishing excursions. The number of reviews ranged from 16-18 for the most popular companies over the last three years, and the number of Instagram posts were around 150. We assumed that recreational tourism fishing to have officially started in 1985, based on information gained from the sport fishing company websites. The number of companies that offered fishing excursions were estimated to have grown linearly from 1 to 32 between 1985 and 2012, by which time all companies had been established. The number of fishing excursions per company was set to vary between 20 and 33 following trends in the number of annual visitors to

Honduras (INE, 2018), as validated by local consultants (Mayra Nuñez Centro de Estudios Marinos, personal communication).

In addition, since 1999 an international annual fishing tournament is held on Roatán, targeting mainly billfishes (Istiophoridae). The amount of fish taken during fishing tournaments was estimated. Lists of the capture, discriminated by participant, in each category, were available for past editions on the tournament's official Facebook page. Total catch was estimated by approximating each species´ weight (available on www.fishbase.org), and considering all the participants and days of tournament. Retained catches decreased after 2009 when the main target species started to be released (i.e., catch and release), but fishers still kept some bycatch species like mahi mahi (Coryphaena hippurus) or wahoo (Acanthocybium solandri). In 2011, captures from tournaments increased as the island of Guanaja started to host an annual sports fishing event.

S2.1 Gulf of Fonseca (FAO Area 77)

S2.1.1 Reported artisanal catch

In the Gulf of Fonseca, an industrial fishery sector as defined by the Honduran Fisheries Law of 1959 is not present; therefore, all data reported by FAO are considered to be from the artisanal fisheries. Any potential Honduran-flagged offshore, industrial tuna catches were nor considered here, as they would occur outside of Honduran waters (Le Manach et al., 2016; Schiller, 2014).

S2.1.2. Illegal artisanal catch

Transboundary fishing activities are known to occur in Pacific waters; fishers from Honduras make fishing excursions into the waters of El Salvador and Nicaragua. We performed a conservative estimation of illegal catches to be a 5% of the total estimated artisanal finfish catch, a constant percentage over time.

S2.1.3 Unreported artisanal catch

Several reports on fishing activities within the Gulf of Fonseca (Box and Bonilla Salgado, 2009; Soto, 2012) presented significantly larger catches than reported in the FAO 2011 dataset. These reports consist of annual assessments in 2004 and 2008. For each major target group, crabs, clams, finfish and shrimp, there were differences between the catches in the assessments and the FAO dataset for the same years. We calculated an unreported catch ratio of the difference between the assessments and the FAO dataset for each of the major target groups and applied this as a fixed ratio of the reported catches through 2015). Although reporting within the artisanal fishery has improved, it remains low and fluctuates year by year. To minimize any bias, we assumed a constant percentage differential between reported and unreported catch throughout the period of 1950-2003. Soto (2012) suggested that there are no significant discards in the shrimp fishery, because the majority of the fish caught as bycatch is retained and consumed. Therefore, any bycatch was assumed to be part of the catch of subsistence fisheries. Furthermore, as artisanal fisheries within this area employ trammel and cast nets rather than trawls (Box and Bonilla Salgado, 2009; Heyman and Granados-Dieseldorff, 2012; MacKenzie and Stehlik, 1996), discarded bycatch should be minimal.

S2.1.4 Subsistence fisheries

Subsistence fisheries catches were calculated following the procedures described for the Caribbean, except that the majority of subsistence catch was based on the incidental fish bycatch from the shrimp fishery (see above). In this case the anchor point for the number of artisanal fishers was 1,600 in 2004 (Soto, 2012).

S2.1.5. Recreational fisheries

We could not find any records of recreational fishing in the Gulf of Fonseca, and local experts had no knowledge of any commercial enterprises engaged in recreational fisheries. We assumed that all landed catch would be consumed and therefore consider any domestic recreational fishing that may occur to actually count as subsistence fishing, whose catch was estimated above.

8.2 Appendix 2 – Published version of Chapter 2

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ORIGINAL ARTICLE

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The hidden value of artisanal fisheries in Honduras

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Abstract

Declining fisheries catches are a global trend, with management failing to keep pace with growth in fishing effort and technological advances. The economic value of Honduras' catches was estimated within the industrial and artisanal sectors. Catches were found to be 2.9 times greater than the official statistics between 1950 and 2015. The merging of industrial and artisanal catch data masked the decline in industrial catches and hid the strong growth of artisanal fisheries. In 1996, annual artisanal fisheries landed catches surpassed the industrial fishery sector, and in 2000, the annual net value of artisanal fisheries eclipsed the value of the industrial fisheries. These data highlight the importance of artisanal fisheries in Honduras and challenge the long-held belief that the industrial sector contributes more to the national economy. The global paucity of fisheries data highlights the need for comprehensive strategies to collect more detailed and accurate fisheries data.

KEYWORDS
artisanal fisheries, catch reconstruction, fisheries data, industrial fisheries, IUU fishing, marine fisheries, small-scale fisheries, subsistence fisheries

1 | INTRODUCTION

The Republic of Honduras is located on the Central America Isthmus, with coastlines on both the Atlantic and Pacific Oceans (Figure 1). In accordance with the United Nations Convention on the Law of the Sea, Honduras claimed its exclusive economic zones (EEZs) in both the Atlantic (within FAO statistical Area 31) and the Pacific (within FAO statistical Area 77). The north shore of Honduras, located within the Caribbean basin of the Atlantic Ocean, is the longer of the two coastlines and is bordered by the EEZs of Guatemala, Belize, Mexico, Cuba, the Cayman Islands, Jamaica and Nicaragua. The Pacific coastline is much smaller and is exclusively within the Gulf of Fonseca, fully enclosed by the EEZs of El Salvador and Nicaragua (Figure 1). The sharing of EEZ borders with numerous countries, particularly within the Honduran Caribbean, has implications for transboundary fish stock management and the potential for cross-border fishing activities (Perez, 2009).

Fishing has been an important economic sector in Honduras for more than 100 years (MacKenzie & Stehlik, 1996), contributing 5% of the country's gross domestic product with an average value of US $385 million per year (Beltrán Turriago, 2011). Fishers employ a diverse range of gears to exploit lagoon and riverine systems, coral reefs, other near-shore habitats (e.g. seagrass beds), extensive offshore banks and pelagic waters (Box & Canty, 2011; Soto, 2012). The main fisheries on the Caribbean coast are for Caribbean spiny lobster, *Panulirus argus* (Latreille), and queen conch, *Lobatus gigas* (L.), while the main fishery on the Pacific coast targets western white shrimp, *Litopenaeus occidentalis* (Streets) (FAO 2002).

Artisanal and subsistence fisheries have been present in Honduras at least since the Mayan era, however, the large expansion of artisanal fisheries across the Caribbean and Pacific coasts is a relatively recent phenomenon, commencing in the 1970s (MacKenzie & Stehlik, 1996). Artisanal fisheries provide an essential source of nutrition and employment to coastal communities, especially in remote coastal areas where there are few other economic alternatives. Due to a lack of processing infrastructure, catches from the Honduran Pacific coast supply only national markets (Box & Bonilla, 2009), while artisanal fisheries on the Caribbean coast supply both national and international markets. In addition, the shallow hydrology precludes the deployment of larger boats within the Gulf of Fonseca, which restricts the Honduran industrial fishery to the Atlantic coast (Soto, 2012).

The Honduran national industrial fishery began in the late 1950s (FAO, 2002). Previously, only foreign industrial fleets, mainly from the United States, were fishing and landing in Honduras. As international fleets began to leave Honduran waters, the national industrial fishing fleet started to develop. An additional trigger was the collapse of the United States industrial conch fishery in 1975, which enabled the Honduran industrial fishery to start supplying the United States market. Currently, 90%–95% of industrial marine catches are exported, primarily to the United States (Espinoza, 2007). Recreational fisheries are practised across the Honduran shore in the Caribbean, but sport fishing operations are primarily located in the Bay Islands, where the majority of international tourism is concentrated, receiving over 700,000 tourists per year (INE, 2018).

Signs of overexploitation have been documented in Honduran fisheries. The conch fishery closed in 2003 due to a trade embargo placed on conch exports by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2003). The Nassau grouper, *Epinephelus striatus* (Bloch), population collapsed in 2004 (Box & Bonilla, 2009). According to Honduran fishers, the decline and collapse of these fisheries was a consequence of irresponsible fishing practices and habitat degradation via destructive fishing gears (Korda, Hills & Gray, 2008), which mirrors trends in Jamaica (Hughes, 1994) and the Caribbean as a whole (Gobert et al., 2005).

Overfishing is a great challenge facing governments and the scientific community (FAO, 2016). As a minimum requirement, effective management requires reliable data, with catch data representing the most fundamental of all fisheries data. Comprehensive and accurate records of fisheries' catches are important to allow monitoring of fisheries' trends over time, with the effect of fisheries' regulations to be observed, and subsequently adjusted if required (Belhabib, Koutob, Sall, Lam & Pauly, 2014). However, while technological advances in fishing vessels and gears are evident, systems to record catch data and monitor fisheries have not kept pace. There is a chronic need for improvements in data collection and the incorporation of these data into fisheries management (Pauly et al., 2002). The status of the world's fisheries may be worse than currently perceived, given that a large fraction of catches has been missing from national fisheries catch estimates in virtually every country of the world (Pauly & Zeller, 2016a,2016b). Crucially, the pattern of missing data changed over time as an inadvertent by-product of well-intentioned efforts to improve data collection systems, resulting in a time series bias now known as "presentist bias" (Zeller & Pauly, 2018). Thus, there is a concerted global effort led by the *Sea Around Us* initiative to reconstruct national, and by extension, regional and global fishing statistics that add comprehensive estimates for all unreported catches to officially reported landing data to derive a better and more comprehensive understanding of fisheries catches over time (Funes et al., 2015; Pauly & Zeller, 2016a,2016b; Zeller, Booth, Davis & Pauly, 2007; Zeller, Harper, Zylich & Pauly, 2015; Zylich et al., 2014).

The starting point for reconstructions is the official reported landing data provided by national agencies to the Food and Agriculture Organization of the United Nations (FAO); these data are subsequently compared with the formal and grey literature, and inferences on additional, previously unreported catches are validated with local experts (Zeller et al., 2016), Funes et al. (2015) and from reconstructed marine fisheries catch data for the Republic of Honduras, by deriving the best time series estimates of unreported catches for 1950–2010, from both the Atlantic and Pacific coastlines to complement reported data. The present study revised, improved and extended the analysis performed in Funes et al. (2015), by updating the time series to 2015, rectifying all estimates of fishing categories, completing the lacking fishing categories and enhancing the sources of data. Once the corrected reconstructed catch was available, the aim was to describe and compare statistically the catch trends over the years, and to evaluate the economies of the fisheries

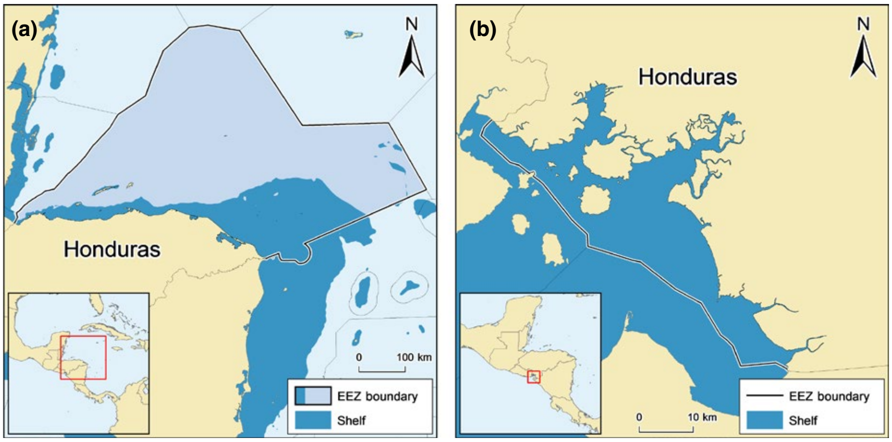


FIGURE 1 Maps of the two parts of the Honduran exclusive economic zone (EEZ). (a): Honduras' EEZ in the Caribbean covers 218,000 km^2, of which 60,300 km2 is shelf, that is, less than 200 m deep. (b): Honduras' EEZ in the Pacific is small (747 km2) and shallow, and consist only of the inner Gulf of Fonseca, shared between El Salvador in the North, Honduras, and Nicaragua in the South

sectors in Honduras and in the context of the Mesoamerican reef countries (Mexico, Guatemala and Belize).

2 | METHODOLOGY

2.1 | Catch reconstructions

Honduran catch reconstructions were conducted using the method of Zeller et al. (2007, 2016), following the principles described in Pauly (1998). Only marine wild capture fisheries were addressed; therefore, aquaculture production and freshwater catches are not included in the estimates, nor are catch records of marine mammal, turtles, worms, seaweed or algae. For a full list of the categories used in this reconstruction, see Supporting Information (Table S1).

Industrial, artisanal, subsistence and recreational fisheries for fishing areas 31 and 77 (Figure 1) were estimated separately. Artisanal fishing was defined by the Honduran Fisheries Law of 1959, as "fishing within three nautical miles from the shore using boats with a capacity of three tonnes or less and employing basic fishing equipment." All commercial fishing activities encompassed by this definition were considered artisanal. Commercial fisheries with vessels of greater capacity and fishing at greater distances were considered industrial. Subsistence fisheries were defined when landed catch was for personal consumption and no commercial transaction is associated with it. Recreational fisheries were defined as sport fishing; whereby, individuals may pay for a fishing excursion, but retained landed catch was not sold.

2.2 | The Caribbean Sea (FAO Area 31)

2.2.1 | Reported industrial catch

Industrial fishing in Honduras is limited to Area 31 (Caribbean) with four fleets licensed to exploit four resource types: Caribbean spiny lobster, queen conch, shrimp and finfish (primarily grouper and snapper). The industrial sector is diverse, fishing vessel lengths vary from 4 to 78 m (13–258 feet), crews range from 6 to 85 people, and the duration of fishing excursions vary from 10 to 90 days, depending on the fishery (CITES, 2003). National industrial fisheries first appeared in Honduras during the late 1950s (FAO, 2002), at which time only limited catch data were reported. Given that industrial catches were always landed at major ports, all catches from 1950 to 1989 reported to FAO were considered industrial. In 1990, the governmental body DIGEPESCA was created and began to collate fisheries data; therefore, for the period of 1990–2015 industrial landed catch data were obtained directly from DIGEPESCA records.

2.2.2 | Illegal industrial catch

Illegal catch is any catch that is acquired or removed from the EEZ of a country without the consent of that country. In instances where these landed catches are processed through Honduran packaging plants, they become included in official data and contribute to the national economy. Here, illegal catches taken by the Honduran fishing fleet from neighbouring EEZs of Nicaragua and Jamaica were estimated. The Honduran Grand Banks are situated in the far eastern part of the EEZ, close to the Nicaraguan border, extending north-east to the Jamaican border, and the Honduran fleet enters into Nicaraguan and Jamaican EEZ waters illegally. To consider this and remain conservative, illegal catch was estimated as 15% of the total estimated industrial lobster catch, as a constant percentage over time. Estimations on foreign fishing vessels illegally entering to Honduran EEZ were not included in the analysis; however, illegal fishing within the Honduran EEZ was assumed to be equivalent to that of the Honduran fleet in other EEZs, and therefore, the illegal capture of the Honduran industrial fleet was included in the estimations.

2.2.3 | Unreported industrial catch

Undeclared discards are part of the industrial unreported catch in Honduras. Discards are absent or minimal in the conch and lobster fisheries, as conch are hand-collected and lobster are either hand-collected or caught in traps. The capture of finfish is mainly from vertical long lines, where low-valued bycatch is usually consumed and accounted for in the subsistence fishery category (see below). The major non-selective industrial fishery component is the bottom-trawl shrimp fishery. Unregulated shrimp discards were estimated following Davies, Cripps, Nickson, and Porter (2009), who suggested a bycatch rate of 78%, where no bycatch was landed. This percentage was applied to FAO reported shrimp landings for 1950–2015 to estimate what was taken from the sea to be discarded later. Any bycatch in the industrial finfish fishery was assumed to be either recorded in the official records or used for personal consumption and therefore estimated under subsistence.

2.2.4 | Reported artisanal catch

The large extent of the Caribbean coastline provides suitable fishing grounds across the Honduran mainland and island archipelagos, with more than 135 different fishing communities (Stephen Box, personal observation) with over 7,000 registered artisanal fishers included in the DIGEPESCA fisher registration system. The geographical dispersion and remoteness of many of these communities have made it difficult to collect catch data from these fisheries, resulting in limited available data.

From 2001, FAO records included some artisanal fishing activity (Diana Vasquez, Centro de Estudios Marinos, personal communication). It was assumed that the remainder of FAO catch unaccounted in DIGEPESCA data was artisanal catch for the period of 2001–2015, where FAO landings exceeded DIGEPESCA reports. Since artisanal fishing in this region was not reported until recently, the FAO landing data for the early time periods were assumed to be industrial fisheries. As a conservative estimate, the reporting of artisanal fisheries to the FAO was considered to improve linearly from 0% of catch reported to the FAO in 1989 to the calculated percentage of FAO catch estimated to be artisanal in 2001 (i.e. 74% of reported data).

2.2.5 | Illegal artisanal catch

Transboundary fishing by artisanal fishers is a problem with Honduran boats making excursions into Belizean territorial waters and Guatemalans fishers making excursions into Honduran (and Belizean) waters (Perez, 2009). To incorporate this and remain conservative, illegal artisanal catch was estimated as 15% of the total estimated artisanal catch, as a constant percentage over time. These illegal catches were identified and labelled as Honduras fishing in Belizean waters. The catches of foreign artisanal fleets fishing illegally in Honduran waters were not estimated. As per the industrial fishery, illegal fishing of others in Honduran waters was assumed to be equivalent to the illegal transboundary fishing activity of the Honduran artisanal fleet and therefore to include illegal landed catch.

2.2.6 | Unreported artisanal catch

Despite artisanal fisheries existing in Honduras since the pre-Columbian period, no data were available for the artisanal fishery for the period 1950–2000. Reporting of artisanal fisheries has occurred since 2001 primarily from the cities of La Ceiba, Puerto Cortex and Tela along the Caribbean coastline. However, no catch data have been collected from many of the smaller fishing communities in more remote location along the Honduran north shore, despite their considerable fishing effort (Stephen Box, unpublished data). In addition, large inconsistencies were found between the FAO data set of 2011 and other sources of information. For example, differences in reported catch vary in magnitudes of 4.8–10 times, principally for lobster and finfish catch (e.g. FAO, 2002; Heyman & Granados-Dieseldorff, 2012). To remain conservative, estimates of unreported artisanal catch assumed that reported artisanal catch reflected 50% of total catch from artisanal fisheries from 2001 to 2015. Total reconstructed artisanal catch from 2001 to 2015 was used to calculate an average catch rate per artisanal fisher: annual tonnage of the reported artisanal data (2001–2015) divided by the number of fishers for that time period, which led to an overall catch rate (i.e. tonnes of fish per fisher per year). In the period of 1950–2000, reconstructed artisanal annual catch was estimated by multiplying the catch rate by the number of artisanal fishers estimated for each year (FAO, 2002); see methodology2 of artisanal fisher's estimation in subsistence section.

2.2.7 | Subsistence fisheries

Fishers from the artisanal sector may set aside a portion of their catch for personal consumption (MacKenzie & Stehlik, 1996); the artisanal fishery-derived subsistence catch was estimated by multiplying the number of artisanal fishers by an amount of fish per capita for home consumption. FAO (2002) documented a total of 9,132 fishers on the Atlantic coast, which also matched well with grey literature estimates (Box & Canty, 2011). The artisanal fisher population was assumed to change over time as a fixed proportion (0.00177%) of the national population of Honduras from 1950 to 2015 (World Bank, 2017). The per-fisher level of subsistence catch was taken from a study conducted in the neighbouring country of Guatemala (Trujillo, Cisneros-Montemayor, Harper, Zylich & Zeller, 2012), which estimated a take-home subsistence portion of 70 kg/fisher/year. This estimate is conservative considering that fishers share the catch with their family.

In addition, the common Caribbean donax, *Donax denticulatus* L., is gathered by hand, usually by local women and children (MacKenzie & Stehlik, 1996). The donax catch is intended only for subsistence and not sold at markets (MacKenzie & Stehlik, 1996). As a minimum, an estimated average of 5 kg of donax per year per artisanal fisher's household was used in our calculations. Therefore, a total subsistence catch of 75 kg/fisher/year was estimated for the Honduran Caribbean region. This is likely a very conservative estimate.

2.2.8 | Recreational fisheries catch

Recreational fisheries were categorised as the capture and non-release of sport fish species (e.g. mahi mahi, *Coryphaena hippurus* (L.)). To estimate catch from this sector, Honduran sport fishing companies using online searches were made via Google and TripAdvisor with combinations of the following search terms, “sport,” “fish*,” “recreation*,” “trip*,” “excursion*,” “tourism,” “activities,” “Honduras,” “Bay Islands,” “Roatan,” “Utila,” “Guanaja,” “Cayos Cochinos” (*represents derivatives of a search term, e.g. fish, fishing). Secondly, following Belhabib et al. (2016), YouTube videos were identified using names of sport fishing companies collated in the previous search. From each video, the number of fish caught and their species were identified and recorded. The weight of landed catch was sometimes reported by the fisher; where this did not occur, fish length and subsequently their weight were estimated using species-specific parameters to transform length to weight from www.fishbase.org (Froese & Pauly, 2018). The number of annual trips of each company was estimated through tallying the number of reviews and Instagram posts each company received per year; these were cross-referenced to prevent duplication of fishing excursions. The number of reviews ranged from 16 to 18 for the most popular companies over the last 3 years, and the number of Instagram posts was around 150. Recreational tourism fishing was assumed to have started officially in 1985, based on information gained from the sport fishing company websites. The number of companies that offered fishing excursions was estimated to have grown linearly from 1 to 32 between 1985 and 2012, by which time all companies had been established. The number of fishing excursions per company was set to vary between 20 and 33 following trends in the number of annual visitors to Honduras (INE, 2018), as validated by local consultants (Mayra Nuñez, Centro de Estudios Marinos, personal communication).

In addition, since 1999 an international annual fishing tournament is held on Roatán, targeting mainly billfishes (Istiophoridae).

The amount of fish taken during fishing tournaments was estimated. Lists of the capture, discriminated by participant, in each category, were available for past editions on the tournament's official Facebook page. Total catch was estimated by approximating each species' weight (available on www.fishbase.org) and considering all the participants and days of tournament. Retained catches decreased after 2009 when the main target species started to be released (i.e. catch and release), but fishers still kept some bycatch species for example mahi mahi or wahoo, *Acanthocybium solandri* (Cuvier),. In 2011, captures from tournaments increased as the island of Guanaja started to host an annual sports fishing event.

2.3 | Gulf of Fonseca (FAO Area 77)

2.3.1 | Reported artisanal catch

An industrial fishery sector as defined by the Honduran Fisheries Law of 1959 is not present in the Gulf of Fonseca; all data reported by FAO are considered to be from the artisanal fisheries. Any Honduran-flagged offshore vessels were not considered in this study, as they fish outside Honduran waters (Le Manach et al., 2016; Schiller, 2014).

2.3.2 | Illegal artisanal catch

Transboundary fishing activities are known to occur in Pacific waters; fishers from Honduras make fishing excursions into the waters of El Salvador and Nicaragua. A conservative estimate of illegal catches was thought to be 5% of the total estimated artisanal finfish catch, a constant percentage over time. Illegal transboundary fishing activity of El Salvadorian and Nicaraguan fishers within Honduran territorial waters was assumed to be equal to the illegal fishing activity of the Honduran artisanal fishers, and all landed catch by the Honduran artisanal fleet was included within current estimates.

2.3.3 | Unreported artisanal catch

Several reports on fishing activities within the Gulf of Fonseca (Box & Bonilla, 2009; Soto, 2012) presented significantly larger catches than reported in the FAO 2011 data set. These reports consist of annual assessments in 2004 and 2008. For each major target group (crabs, clams, finfish and shrimp), there were differences between the catches in the assessments and the FAO data set for the same years. An unreported catch ratio of the difference between the assessments and the FAO data set for each of the major target groups was estimated and applied as a fixed ratio of the reported catches through 2015. Although reporting within the artisanal fishery has improved, it remains low and fluctuates year to year. To minimise any bias, a constant percentage differential between reported and unreported catch was applied throughout the period of 1950–2003.

Soto (2012) suggested that there are no significant discards in the shrimp fishery, because the majority of the fish caught as bycatch is retained and consumed. Therefore, any bycatch was assumed to be part of the catch of subsistence fisheries. Furthermore, as artisanal fisheries within this area employ trammel and cast nets rather than trawls (Box & Bonilla, 2009; Heyman & Granados-Dieseldorff, 2012; MacKenzie & Stehlik, 1996), discarded bycatch is minimal.

2.3.4 | Subsistence fisheries

Subsistence fisheries catches were calculated following the procedures described for the Caribbean, except that the majority of subsistence catch was based on the incidental fish bycatch from the shrimp fishery (see above). In this case, the anchor point for the number of artisanal fishers was 1,600 in 2004 (Soto, 2012).

2.3.5 | Recreational fisheries

No records of recreational fishing in the Gulf of Fonseca could be found, and local experts had no knowledge of any commercial enterprises engaged in recreational fisheries. It was assumed that all landed catch would be consumed and therefore considered any domestic recreational fishing that may occur to count as subsistence fishing, whose catch was estimated above.

2.4 | Fisheries economics

Economic data (i.e. landed value) for the fisheries of Honduras, Mexico, Belize and Guatemala were provided by the *Sea Around Us*. The landed value of the catch is based on the ex-vessel price data which represent the prices in real 2010 US$ paid to fishers at the first point of sale, combined with catch volumes, represent the landed value of the catch (Sumaila, Marsden, Watson & Pauly, 2007; Swartz, Sumaila & Watson, 2013; Tai, Cashion, Lam, Swartz & Sumaila, 2017). The landed value data for the four countries that make up the Mesoamerican reef ecoregion (Honduras, Mexico, Guatemala, and Belize) were examined, and reconstructed landed catch data—discards not included—were downloaded from the *Sea Around Us* data portal (http://www.seaaroundus.org/data/#/search).

2.5 | Statistical analysis

Reported and unreported data from both the Atlantic and Pacific coasts were combined to generate a total Honduran reconstructed catch time series for 1950–2015. Trends of catches tonnages and trends of reconstructed economic values (landed value of catches) over time, from reported and unreported catches of the industrial and artisanal sector, were analysed using segmented linear regressions, in the R package SEGMENTED (Muggeo, 2008), and changes in the slope were evaluated applying Davies tests in the same package. Segmented regression models determine regression breakpoint years that indicate a significant change in trend over time and segmented line slopes. Prior to analysis, all data were evaluated for normality, and all data were identified to be within the boundaries of normal distributions.

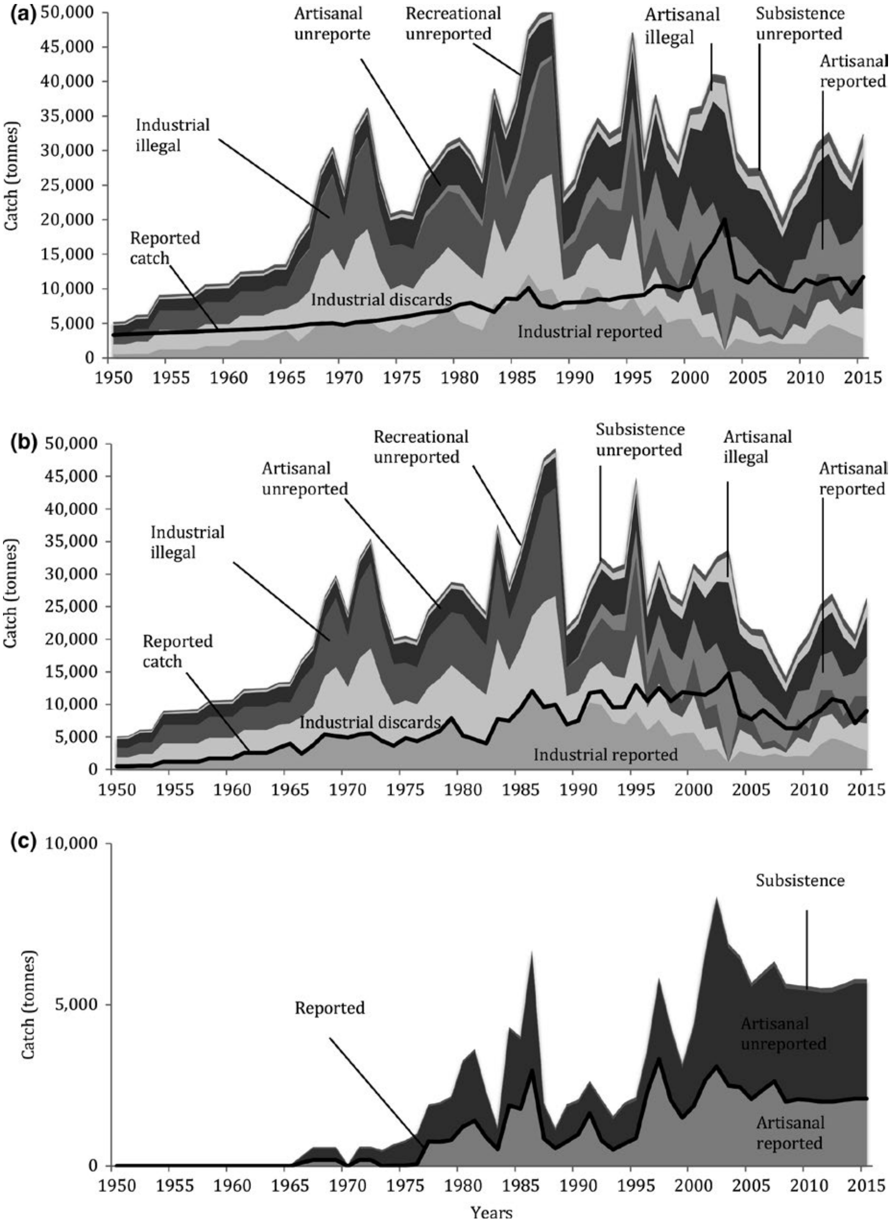


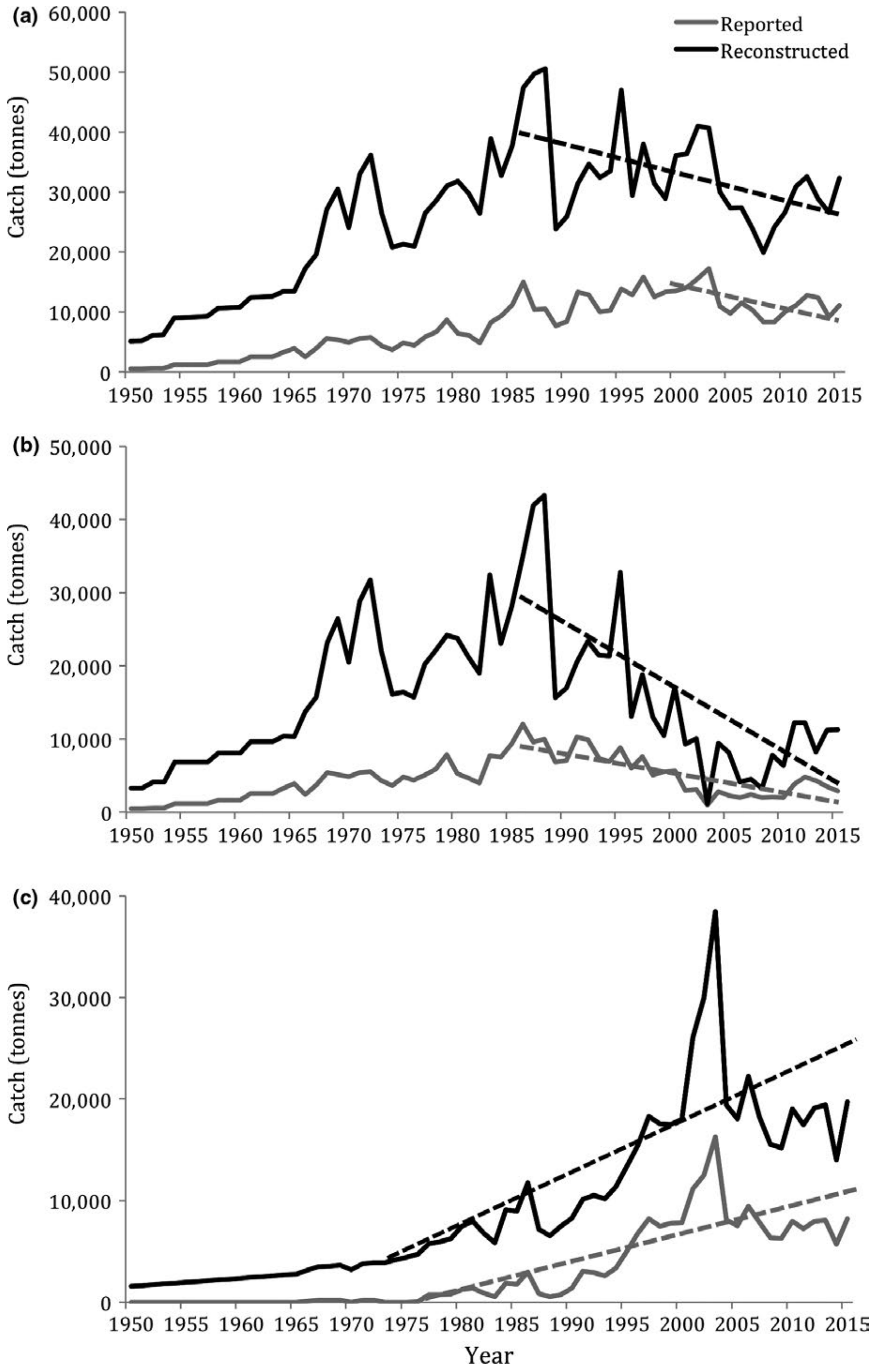
FIGURE 2 Honduran catch reconstructions for the period of 1950-2015. (a) Total combined catch from Areas 31 and 77 (Note: official reported catch black line); (b) catch reconstructions for Area 31; and (c) catch reconstructions for Area 77 (note different *y*-axis scale)

3 | RESULTS

The total reconstructed catches as estimated here for 1950–2015 were 2.9 times greater than the data reported to FAO by Honduras (Figure 2a). Official records reported total landed catches of approximately 500 t in 1950 increasing to 11,079 t by 2015. This compares to the present reconstructions that estimated total catches of around 5,000 t in 1950 and 32,000 t in 2015 (Figure 2a). Catches from the Caribbean Sea in the Atlantic Ocean (FAO Area 31) comprised the greatest contribution to total Honduran catches, with approximately 80% in 2015. For the Caribbean side (FAO Area 31), official catch records reported approximately 500 t in 1950, which increased to just under 9,000 t in 2015, while the catch reconstruction estimated 5,000 t in 1950, which increased to over 26,000 t in 2015 (Figure 2b). Catches from the Pacific Ocean (FAO Area 77) have increased in importance: in 1950, they accounted for less than 0.01% of the total catch, while by 2015 they comprised over 20% of the total reconstructed catch. No official records were identified for this area in 1950, while the reconstruction suggested catches of 23 t in 1950 (Figure 2c). By 2015, official records reported catches of 2,000 t, while this reconstruction estimated catches of nearly 6,000 t (Figure 2c).

Differences in trends between reported and reconstructed catch time series were observed (Figure 3). Reported total catches suggested a continuous period of growth from 1950 to 2000, after which catches began to decline (Figure 3a, Table 1). These reconstruction estimates followed a similar trend, but the period of growth is shorter, 1950–1986, after which time catches declined (Figure 3a, Table 1). In the industrial fishery, reported and reconstructed estimates followed the same trend; a period of growth from 1950 to 1986 was observed, followed by a significant decline (Figure 3b, Table 1). However, reconstruction estimates suggested a

FIGURE 3 Reported catches (grey) and total reconstructed catch estimates (black) for total catches of (a) all Honduran fisheries, (b) industrial fisheries and (c) artisanal fisheries (note different *y*-axis scale). The regression trend lines (dashed lines) represent periods of catch decline or increase (identified as a breakpoint by segmented regression analyses)



much stronger decline in industrial catches (which include discards) after 1986 (Figure 3b, Table 1). While unreported industrial landings drove much of this difference, unreported discards from this sector also contributed (Figure 2a). Reconstructed and reported estimates for the artisanal fisheries followed matching trends, with a period of relatively gradual growth followed by a period of more rapid growth, starting in the early and late 1970s, respectively (Figure 3c, Table 1). The growth of artisanal fisheries is associated with an increased contribution of this sector to total landed catches of the country, and by 2015, artisanal catches accounted for approximately 61% (nearly 20,000 t) of the total catch (Figure 2a).

Historically, the industrial fishery was of greatest value; however, as catches declined in this fishery and increased in the artisanal fishery, the artisanal fishery increased in value and surpassed the landed value of the industrial fishery in 2000. The industrial fishery peaked in landed value in 1987, at US$ 59 million, and declined to just under US$ 13 million by 2015 (Figure 4a). The Caribbean (Area 31) artisanal fisheries from the same period showed an increasing value in the fishery since 1950; in 1996, a significant increase in the value of the fishery was observed with a peak value of US$ 35 million in 2003 (Figure 4a). The pattern of artisanal fisheries being of greater economic value was found in all four countries of the Mesoamerican

TABLE 1 Results of segmented regressions and Davies tests for total, industrial and artisanal reconstructed and reported catches of Honduras for the time period 1950–2015, and for reconstructed economic landed value (2010 US$) of the industrial and artisanal fisheries

		Segmented regressions			
Catch sector	**Landed catch time series**	**Breakpoint (year)**	**Line**	**Slope (t./year)**	**Davies test**
Total	Reconstructed	–	1	951.8	–
		1986	2	−407.8	0.0001
	Reported	–	1	284.5	–
		2000	2	−276.4	0.0001
Industrial	Reconstructed	–	1	706.3	–
		1986	2	−909.2	0.0001
	Reported	–	1	226.6	–
		1986	2	−261.9	0.0001
Artisanal	Reconstructed	–	1	105.4	–
		1972	2	456.5	0.04
	Reported	–	1	4.9	–
		1979	2	261.8	0.0002

		Segmented regression			
Catch sector	**Landed value time series**	**Breakpoint (year)**	**Line**	**Slope (US$million/year)**	**Davies test**
Industrial	Reconstructed	–	1	1.2	–
		1986	2	−2.4	0.0001
Artisanal	Reconstructed	–	1	0.2	–
		1996	2	0.8	0.0001

reef region (Figure 4). In Mexico and Belize, artisanal fisheries have been of greater value since 1950, but this gap has only increased over time (Figure 4b,c). In Guatemala, as in Honduras, artisanal fisheries became more valuable around 2001 (Figure 4d).

4 | DISCUSSION

The reconstructed catches for the Honduran fisheries in the Atlantic (FAO Area 31) and Pacific (FAO Area 77) EEZs were 2.9 times greater than the catches (landings only) reported by FAO on behalf of Honduras. The reconstruction illustrated that contrary to the official reported data, which implied a period of continuous growth from 1950 to 2000, total reconstructed catches suggested that the Honduran catches have actually been in decline since 1986. This decline, driven by strongly declining industrial catches, was masked by significant increases in artisanal catches starting in the early 1970s. The growth in artisanal catches meant that by 1996, catches of the artisanal sector exceeded the catches of the industrial fishery and by 2015 accounted for approximately 61% of the total reconstructed catches. Associated with the change in the dominance of landed catch from the industrial to the artisanal sector is a distinct shift in economic importance since 2000, with the artisanal fishery worth more annually than the industrial fishery. There is lag of approximately 4 years between landed catch and the economic value of the artisanal fishery surpassing the industrial fishery. This is due to the high-value species associated with the industrial fishery, for example spiny lobster; in contrast to the lower priced finfish, which contribute a greater proportion of artisanal fishery catches. A similar trend has been observed in Guatemala, while artisanal fisheries have been more economically valuable than industrial catches in Mexico and Belize since 1950. These economic data highlight the importance of artisanal fisheries within the Mesoamerican reef ecoregion, which supports over 2 million coastal people (Kramer & Kramer, 2002), and highlight the need for focused management within this important fishing sector.

The shift in sector emphasis from industrial to artisanal fisheries has important implications for fisheries management, as artisanal fisheries have a greater potential for sustainable use of coastal resources (Pauly, 2006), and to ensure the resilience of coastal communities through food security (Golden et al., 2016) and employment (Beltrán Turriago, 2013). These findings highlight the critical importance of disaggregating data to fisheries sectors to identify important trends and patterns within a country's fishery (Pauly & Zeller, 2016a) and for investing in data collection systems for artisanal fisheries (Pauly & Charles, 2015). The majority of artisanal fisheries in Honduras are within the informal sector and therefore no official records of catches or the associated value exist, which proliferates the underestimation of their importance to coastal communities and their economies.

The reported data for Honduras suggested mistakenly that the country's fisheries were growing until 2000, whereas the

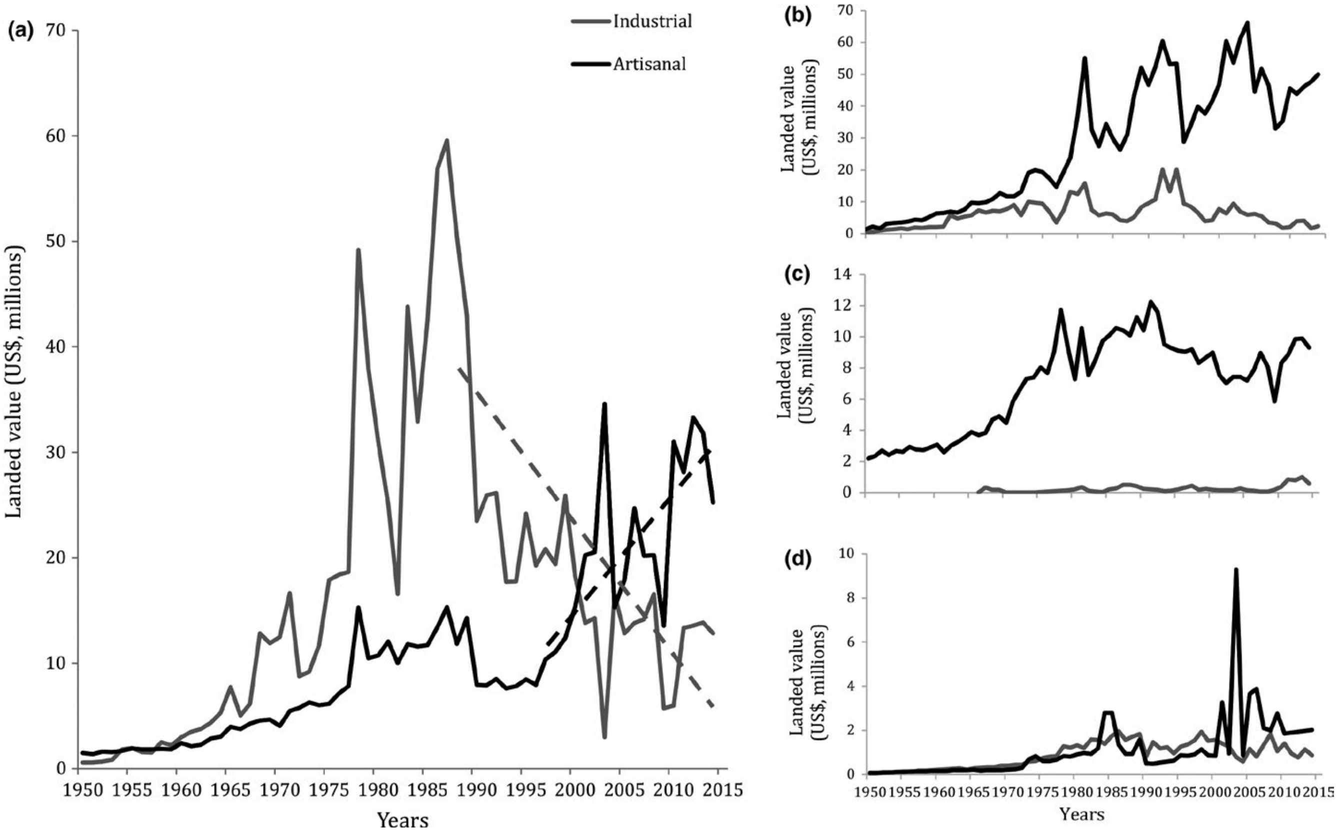


FIGURE 4 Mesoamerican reef ecoregion fishery valuations, based on reconstructed landed data (discards are not included) from the Caribbean Sea fisheries of (a) Honduras, (b) Mexico, (c) Belize and (d) Guatemala (note different *y*-axis scale). Landed catch values are of reconstructed catches, and data for all countries were downloaded from the Sea Around Us online database. The regression trend lines (dashed lines) represent periods of catch decline or increase (identified as a breakpoint by segmented regression analyses) in the Honduran fishery

reconstruction illustrated that the growth period ended much earlier, in 1986, followed by a much stronger decline in catches. The disparity in trends between these two data sets has important implications for fisheries management and data collection from all fisheries sectors. The results highlight that the aggregation of data from different fisheries sectors can mask important changes within a country's fishery (Pauly & Charles, 2015). By disaggregating the industrial and artisanal sectors, it was possible to show how the industrial fisheries have been in decline since 1986, while catches from artisanal fisheries, from both the Atlantic and Pacific Oceans, have increased. The combined catches from the Atlantic and Pacific are greater than the industrial fishery landings. Although a lack of consistent fishing effort data prevented determination of whether the decline in industrial catches was related to a shift in fishing effort from the industrial sector to the artisanal sector, it is likely that the artisanal fishery has undergone independent growth in parallel, rather than in response to a decline in the industrial fleet. This has been mirrored in the economic growth in the artisanal sector and provides further evidence for the need of comprehensive management of artisanal fisheries to maintain food security and livelihoods in coastal communities.

The general results of this catch reconstruction for Honduras are comparable to other reconstructions for Central American countries, with reconstructed data being higher than reported data, 1.4 times for Panama (Harper, Guzman, Zylich & Zeller, 2014), 2.6 times for Costa Rica (Trujillo et al., 2012), 3.4 times for Nicaragua (Haas, Harper, Zylich & Zeller, 2015) and 3.5 times for Belize (Zeller, Graham & Harper, 2011), and about 1.5 globally (Pauly & Zeller, 2016a,2016b). Additionally, artisanal fisheries are of greatest economic importance in the Caribbean fisheries of the four countries of the Mesoamerican reef ecoregion, Mexico, Belize, Guatemala and Honduras. Interannual variability on the reported and reconstructed catches trend is commonly found in all catch reconstruction analysis (e.g. Trujillo et al., 2012; Harper et al., 2014; Haas et al., 2015). This could be a phenomenon based on the natural species fluctuations or a result of changing fishing pressure due to externalities such as fuel prices.

While the estimates of catches improved in terms of tonnages, the taxonomic resolution of these reconstructions is low, and for effective management, the collection of data with greater taxonomic resolution is required. Greater investment needs to be made in collecting such improved data, which should also include fishing effort data across all fisheries sectors. There have been important advances to address the complex task of collecting fisheries data from widely dispersed artisanal fisheries, which are characterised by geographical remoteness, the diversity of supply-chain participants (commercial fish buyers, markets and restaurants) and fishing gears used. Specifically, in Honduras and Belize a novel freeware application, *OurFish* (https://ourfish.org/), is being implemented that records transactions between fishers and fish buyers, including restaurants, using widely available and extensively used cell phone and Wi-fi technology. This application is connected to national fisher licensing databases, which links each transaction to individual fishers, thus allowing for fisheries data at the individual, community, region and national level to be collated and used for management. This initiative has been a collaborative effort between multiple institutions, including government departments, non-government organisations and local communities. The system supports the aim to provide managers with up-to-date, comprehensive fisheries data on an ongoing basis, which can be used to develop local, regional and national fisheries management plans, and directly include and link principle stakeholders (i.e. local artisanal fishers and fish buyers) within the data collection and data use process. With the advent of these digital platforms that can be used directly by fishing communities, the onus is now on those involved in fisheries management and governance to help scale-up the adoption of these systems to transform fisheries data collection to support data for decision making around the status and use of marine fisheries. Finally, these fisheries management and governance participants also need to ensure that these new data are seamlessly incorporated in all national and international (i.e. FAO) data reporting schemes.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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8.3 Appendix 3 – Chapter 3 supplementary material

S2. In-depth methodologies of genetic and otolith laboratory analyses.

S2.1 Genetic analysis

Microsatellite fragment analysis was performed at the University of Manchester DNA Sequencing Facility with an ABI 3730xl automatic DNA sequencer (Applied Biosystems). GeneMapper® v3.7 software package (Applied Biosystems) was used for scoring microsatellite alleles, and the binning of alleles was conducted in the R-package MsatAllele version 1.02 (Alberto 2009). No duplicate genotypes were identified when checked with R-package Allelematch (Galpern et al. 2012). All microsatellite loci were analyzed with MICRO-CHECKER to assess levels of null alleles and to detect potential scoring errors causing the dropout of large alleles or stutter (van Oosterhout et al. 2004). We tested all combinations of loci for linkage disequilibrium (LD) with the R-package Genepop (Raymond and Rousset 1995; Rousset 2008) but no evidence of LD was found.

S2.2 Otolith elemental analysis

Only adults (≥250mm FL) were used in the otolith elemental analyses. Juveniles were not used, we considered individuals of <250mm FL to not have recruited permanently to adult populations (Verweij et al. 2008). If an individual has not fully recruited to a habitat the otoliths would not have accumulated sufficient signatures from the habitat (fishing ground). Instead the element signature of their nursery area would be a confounding factor in the analysis (Gao et al. 2005; Gerard & Muhling 2010). Yellowtail snapper, although semi-pelagic, are likely to have high site fidelity, with an estimated home range of 1.5km2, and conduct limited daily movements within their home range (Farmer & Ault 2011). Otolith signatures would therefore be indicative of the fishing ground. Both otoliths were removed from the cranium of individuals, they were subsequently cleaned with distilled water before being dried and stored prior to sectioning. Where possible the left otolith was used, right otoliths were used in the case of damage to the left otolith. No significant differences have been found between the elemental signatures of left and right otoliths (Campana 1999), therefore signatures from left and right otoliths are comparable. Due to breakages during sectioning and the cost associated with laser ablation a total of 71 individual otoliths were analyzed.

Otoliths were sent to the British Antarctic Survey for sectioning prior to elemental analysis at the British Geological Society. A total of fifteen elements, strontium, manganese, barium, lithium, boron, sodium, magnesium, potassium, copper, tin, lead, aluminium, iron, zinc and rubidium, were measured with 42Ca used as the internal standard to correct for ablation volume differences. Measured concentrations were subsequently converted to element:Ca ratios. National Institute of Standards and Technology (NIST) 610 glass reference material was used to standardize the otolith data using preferred reference values from the Geological and Environmental Reference Materials database (Jochum et al. 2005). NIST 610 was analysed before and after each analytical run (c. 1 hour) and the sample data normalised to this set of analyses. A UP193FX laser ablation system was used to analyse the sectioned otoliths, which includes a 193nm excimer laser system with a 4ns pulse width and typical fluence of 3J.cm-2. A single ablation chamber contained 10 otoliths mounted on a slide along with the glass reference materials. Helium was used (0.8 L.min-1) as a carrier gas in the ablation chamber and then mixed with an argon gas stream supplied by a Cetac Aridus 2 desolvating nebulizer aspirating air, partway between the ablation cell and the plasma of the mass spectrometer. Before analysis the Agilent 7500 ICP-MS instrument was tuned using a multi-element solution for optimum sensitivity balanced against minimal oxide and doubly charged species; the octopole reaction cell using c.1.5 mL.min-1 He gas flow further reduced polyatomic gas interferences. Laser ablation was conducted from the centre to the edge of the otolith at intervals of 150 microns, a minimum of 5 and maximum of 15 ablations were taken per otolith. The elemental signatures of the outer two ablations, which we consider to be the most recent accretions by the adult fish, produce a mean elemental ratio which comprised the signature for each otolith.

8.4 Appendix 4 – Published version of Chapter 3

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RESEARCH ARTICLE

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Evaluating tools for the spatial management of fisheries

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Abstract

1. The ability to define the spatial dynamics of fish stocks is critical to fisheries management. Combating illegal, unreported and unregulated fishing and the regulation of area-based management through physical patrols and port side controls are growing areas of management attention. Augmenting the existing approaches to fisheries management with forensic techniques has the potential to increase compliance and enforcement success rates.
2. We tested the accuracy of three techniques (genotyping, otolith microchemistry and morphometrics) that can be used to identify geographic origin. We used fish caught from three fishing grounds, separated by a minimum of 5 km and a maximum of 60 km, to test the accuracy of these approaches at relatively small spatial scales.
3. Using nearest-neighbour analyses, morphometric analysis was the most accurate (79.5%) in assigning individual fish to their fishing ground of origin. Neither otolith microchemistry (54.0%) or genetic analyses (52.4%) had sufficient accuracy at the spatial scales we examined.
4. *Synthesis and applications*. The combination of accuracy and minimal resource requirements make morphometric analysis a promising tool for assessing compliance with area-based fishing restrictions at the scale of kilometres. Furthermore, this approach has promising application, in small-scale fisheries through to community-based management approaches where technical and financial resources are limited.

KEYWORDS

fisheries tools, fishing restrictions, genetics, morphometrics, *Ocyurus chrysurus*, otoliths, small-scale fisheries, spatial management

1 | INTRODUCTION

Fisheries management aims to manage exploited fish populations, based on estimating maximum sustainable yield or maximum economic yield, and setting catch limits around these targets to maximize catches and profits (Christensen, 2010). The financial investment and technical expertise required to conduct fish stock assessments is significant as are the resources required to implement harvest control rules and effectively limit total allowable catch. Therefore, the majority of the world's fish stocks remain unassessed and largely unmanaged. To address declines in fish stocks, managers have a suite of input and output controls over fishing activities, including limiting entry, empirical harvest control rules and area-based management approaches, such as marine protected areas (MPA's), no-take zones (NTZ's) and territorial user rights fisheries (TURFs; Selig et al., 2017). MPA's and NTZ's aim to reduce or eliminate fishing pressure across defined areas, which allow fish populations to increase and then potentially spill-over into surrounding waters to replenish the exploited areas and/or populations (Gaines, White, Carr, & Palumbi, 2010). TURF's link area-based management to explicit access rights of a geographically defined fishing area or areas to which an individual fisher or fishing community have been granted exclusive access (Nguyen, Quynh, Schilizzi, Hailu, & Iftekhar, 2017). A combination of increased compliance and effective enforcement of regulations is required to effectively manage MPA's, NTZ's and TURF's and combat illegal, unreported and unregulated (IUU) fishing. Current top-down enforcement strategies focus on physical patrols, onboard monitoring and port side measures. However, these can be prohibitively expensive to conduct routinely (Arias, Pressley, Jones, Alvarez-Romero, & Cinner, 2014; Dhanjal-Adams, Mustin, Possingham, & Fuller, 2016). Additionally, fishers have been observed to alter their behaviour when they know patrols are in operation or when enforcement vessels come into view, resulting in diminishing returns of physical patrols (Dhanjal-Adams et al., 2016). Shortfalls in enforcement personnel and financial stability have been identified as primary factors that undermine the effectiveness of area-based management (Gill et al., 2017). Alternative cost-effective tools are required to help improve management efficacy. We evaluated the potential of three approaches currently used to identify the geographic origin of individual fish; microsatellite genetic analysis, otolith elemental analysis, and morphometric analysis, all of which have successfully been used to delineate fish stocks (Cadrin, 2000). The ability to assign individual fish to their fishing ground of origin using forensic methods could provide evidence to either confirm compliance or identify fishing infractions, e.g. fishing within an NTZ or in an area outside a fisher's designated fishing area, providing an additional tool to fisheries managers to verify origin or identify illegal fishing activity. Additionally, the ability to independently verify the origin of landed catch is key for fisheries management. Fishing grounds are often shared among multiple communities, each of which have individual names for their fishing ground (personal observations), therefore local and regional management plans may underestimate fishing pressure at fishing grounds. Here we examine three methods for identifying origin and compared them in terms of accuracy, cost, time versus technical difficulty and applicability at small spatial scales—kilometres to tens of kilometres.

1.1 | Genetic analysis

Previous studies have used this approach at large spatial scales (10s–100s kilometres). However, many reserves and community-based management approaches often established under a TURF system, and managed access initiatives operate at smaller scales (smaller than 10s km). Many of these fisheries are also relatively low value and any management operates under severe resource constraints. Genetics analysis uses the variation of allele frequencies within and among sample groups to identify stocks or populations. Microsatellites (simple sequence repeats) produce comparable estimates of population structure to other molecular markers (Nybom, 2004; Powell et al., 1996). Microsatellites offer some specific advantages over other markers, which include the selective neutrality of loci (Meloni, Albanese, Ravassard, Treilhou, & Mallet, 1998), and very high levels of allelic polymorphism (Bhargava & Fuentes, 2010). High levels of allelic polymorphism is useful when assessing species that exhibit very low levels of variation (Bhargava & Fuentes, 2010), and thus may be more indicative when sampling at fine spatial scales (less than 100 km). Microsatellite markers have important applications in fisheries management and conservation strategies (Abdul-Muneer, 2014) and have successfully been used to discriminate fish stocks at spatial scales varying from 100s to 1,000s km (e.g. Gold, Saillant, Ebelt, & Lem, 2009; Saillant, Renshaw, Cummings, & Gold, 2012).

1.2 | Microchemistry

Otoliths provide an archive of environmental conditions of fish habitats through elemental deposits. Otoliths are acellular and metabolically inert; elements constantly accrete onto the growing (outer) surface from surrounding waters throughout the life cycle of the fish, and dietary derived inorganic elements are minimal (Hoff & Fuiman, 1995). The accreted elements provide a permanent record of the environment which they inhabit (Campana & Neilson, 1985), and can be used to identify and classify individuals to specific stocks or populations. Otolith microchemistry can be analysed through laser ablation inductively coupled plasma mass spectrometry, which is costly and time-consuming. Otolith element signatures have successfully distinguished fish stocks across different geographies and spatial scales of 10s–1,000s km (e.g. Bickford & Hannigan, 2005; Sohn, Kang, & Kim, 2005; Wells, Rooker, & Prince, 2010).

1.3 | Morphometrics

Morphometric analysis uses a series of standard anatomical features to create a truss network, which provides a representation of an individual fish's body shape using interlandmark distances (Strauss & Bookstein, 1982). Several environmental variables can influence fish morphology, including diet (Wimberger, 1992), water temperature (Lõhmus, Sundström, Björklund, & Devlin, 2010), predation pressure (Scharnweber et al., 2013), habitat structure (Willis, Winemiller, & Lopez-Fernandez, 2005), depth (Mwanja et al., 2011) and water currents (Franssen, Stewart, & Schaefer, 2013). These environmental differences can vary geographically. Morphometric analyses have been used successfully to discriminate fish populations at spatial scales of 100s–1,000s km (e.g. Turan, 2004; Vasconcellos, Vianna, Paiva, Schama, & Sole-Cava, 2008).

Here, we compared the accuracy of genetic, otolith and morphometric analyses at assigning individual fish to three fishing grounds separated by 5–60 km, using the yellowtail snapper (*Ocyurus chrysurus*) as a model species. Yellowtail snapper is an important fishery within the Wider Caribbean especially for small-scale fisheries

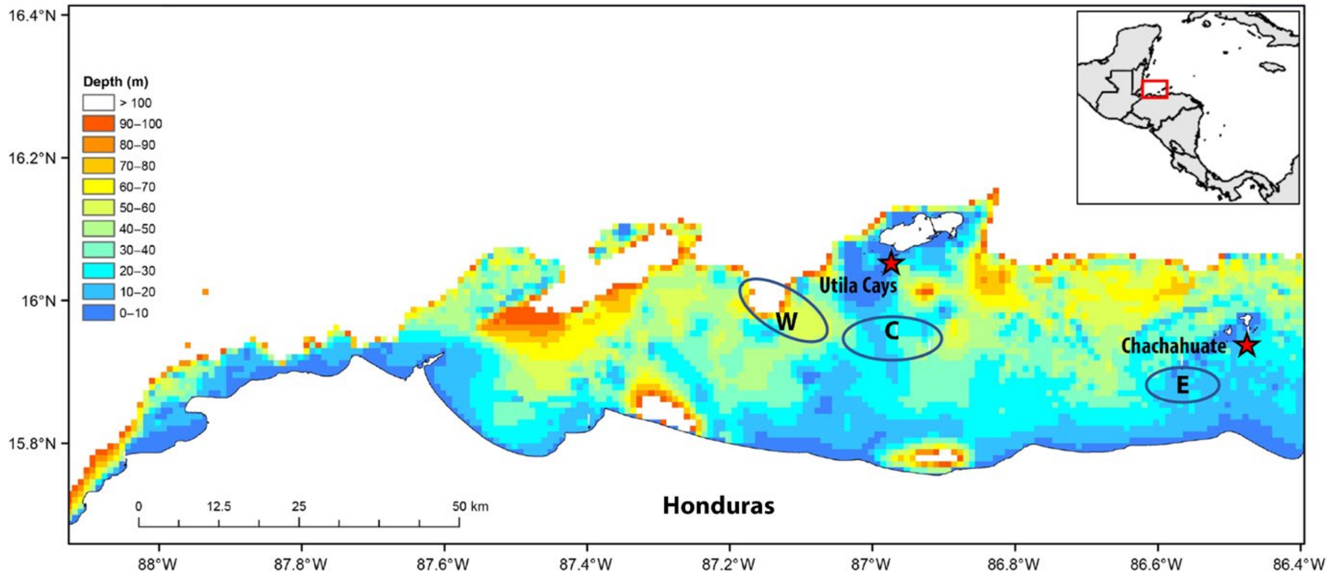

FIGURE 1 Map of the Honduran north shore, highlighting the fishing communities of the Utila Cays and Chachahuate, Cayos Cochinos, and the eastern (E), central (C) and western (W) fishing grounds. Colour is the depth profile produced from an interpolation of Gebco data (Bathymetric map created by Iliana Chollett). Inset map is of Central America, highlighting area of interest in this study

(Claro, Sadovy de Mitcheson, Lindeman, & Garcia-Cagide, 2009). Our model fishery was the Honduran small-scale fishery, where yellowtail snapper contributes substantially to the total catch of local fishing communities (Box & Canty, 2010).

2 | MATERIALS AND METHODS

Our study was based on samples from three distinct fishing grounds, separated by 5–60 km, and fished by communities based on the Utila Cays (N16.06°; W086.96°) and Chachahuate (N15.96°; W086.47°), Honduras (Figure 1). A total of 149 individuals, 93 adults (≥250 mm fork length [FL]) and 56 juveniles (150–249 mm FL) from the fishery, caught by local fishers were collected (Summary statistics in Figure 2). Sampling was conducted from August 2011 to March 2012, and fish were caught using hook and line and the fishing ground georeferenced. For complete descriptions of methodologies of genetic and otolith analyses see Appendix S1.

2.1 | Fishing grounds

The eastern fishing ground is part of the Chachahuate small-scale fishery, located within the Cayos Cochinos archipelago, and the central and western fishing grounds are part of the Utila Cays small-scale fishery (Figure 1). Each of the fishing grounds are associated with different bathymetries, and terrestrial and oceanic inputs (Table 1). We assume these will have a differential effect on otolith element signatures and morphometrics of fish found within each of the fishing grounds. Despite the close proximity of two of the fishing grounds (5 km), we assume that deep water (60–70 m) separating the shallow banks would preclude the mixing of individuals across the different fishing grounds, due to the association of yellowtail snapper with reef habitats.

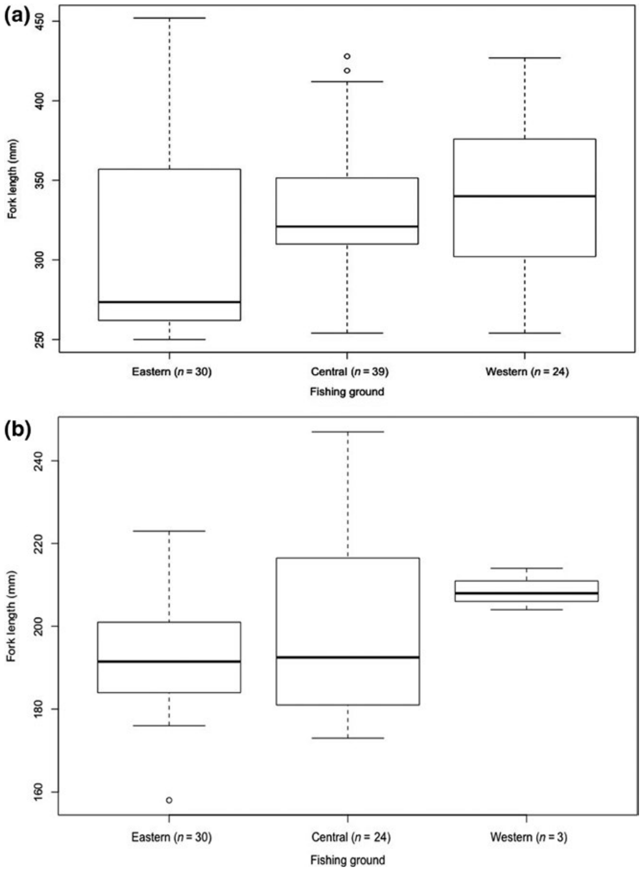

FIGURE 2 Summary statistics of adult (a) and juvenile (b) yellowtail snapper used in the testing of genetic, otolith microchemistry and morphometric analyses

TABLE 1 Abiotic characteristics of the three fishing grounds within the Honduran small-scale fishery

	Fishing grounds		
	Eastern	Central	Western
Depth range (m)	1–30	10–60	60–100
Depth profile[a]	Shallow	Medium	Deep
Distance to mainland (km)	12.7	19.7	28.6
Terrestrial input[a]	High	Medium	Low
Distance to continental shelf drop-off (km)	15.1	16.0	0.0
Oceanic input[a]	Medium	Medium	High

[a]Relative scales in respect to characteristics of the three fishing grounds.

2.2 | Genetic analysis

All 149 fish were used in the genetic analyses. A 1 cm^2 caudal fin clip was taken from each individual and stored in alcohol at −20°C prior to DNA extraction, which was conducted using a Qiagen DNeasy Blood and Tissue Kit. We used 15 previously described microsatellite markers; seven for yellowtail snapper (*och2*, *och4*, *och6*, *och9*, *och10*, *och13*, *och14*), five for lane snapper (*lsy2*, *lsy5*, *lsy7*, *lsy11*, *lsy13*) and three for mutton snapper (*lan3*, *lan5*, *lan11*), all of which have been validated as polymorphic and easy to score for yellowtail snapper (Renshaw, Karlsson, & Gold, 2007), we used the scored genotypes for statistical analyses.

2.3 | Otolith elemental analysis

Only adults (≥250 mm FL) were used in the otolith elemental analyses. Only 71 individual otoliths were analysed due to breakages during sectioning and the cost associated with laser ablation. Otoliths were sent to the British Antarctic Survey for sectioning prior to elemental analysis at the British Geological Society. A total of 15 elements: strontium, manganese, barium, lithium, boron, sodium, magnesium, potassium, copper, tin, lead, aluminium, iron, zinc and rubidium, were measured, with ^{42}Ca used as the internal standard to correct for ablation volume differences. The elemental signatures of the outer two ablations, which we consider to be the most recent accretions by the adult fish, produce a mean elemental ratio which comprised the signature for each otolith.

2.4 | Morphometric analysis

Only adults were used in the morphometric analyses ($n = 93$). Juveniles were not included in the morphometric analysis due to allometric growth differences (Huxley, 1932). Additionally, individuals that have not fully recruited to the fishing ground would not have been subjected to the environmental conditions that influence fish morphology, and therefore may not have a true signal for the ground.

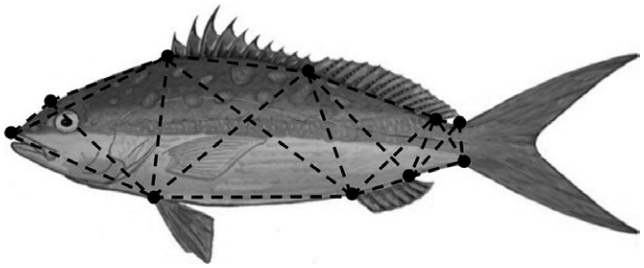

FIGURE 3 Ten morphometric truss points overlaid on a yellowtail snapper used for the canonical correspondence analysis (adapted from Strauss & Bookstein, 1982; portrait of yellowtail snapper by Javier Maradiaga)

Ten truss points, which provided a truss network with 21 discrete measurements, were used in the morphometric analysis (Strauss & Bookstein, 1982; Figure 3). Measurements were taken with callipers of 1.0 mm precision, using methods adapted from Vasconcellos et al. (2008). Each measurement was transformed to a proportion of the total length of the individual to remove bias of size differences, making interlandmark measurements directly comparable among individuals.

2.5 | Statistical analysis

We conducted pairwise permutational analyses of variance (PERMANOVA) tests between the fishing grounds using the ADONIS function in the R-package VEGAN, using 999 permutations. The PERMANOVA test does not assume that the data are normally distributed. We conducted nearest neighbour analyses, a nonparametric test, on microsatellite genotypes, otolith elemental signatures and morphometric truss ratios, using the R-package kknn. Data were normalized along a scale of 0–1, where 0 is the minimum value and 1 the maximum value of a variable, to reduce bias associated with large numbers. Original *K* values were assigned based on the square root of the number of observations. However, once the model was run an optimal *K* value was provided by the model, this value was subsequently selected for each permutation of the model (Table 2). Each model was trained using 10% of the associated dataset, which was randomly selected for each of the 100 iterations of the model, from which we calculated a mean assignment accuracy for each of the tools.

Sample sizes were relatively small, particularly for otolith analyses ($n = 71$). However, our sample sizes are comparable with those for discrete sampling sites in similar studies that used microsatellite genetic analyses (e.g. Davies, Gosling, Was, Brophy, & Tysklind, 2011) and otolith analyses (e.g. Carlson, Fincel, & Graeb, 2016). Our sample size conformed to minimum samples sizes recommended for morphometric analyses (Cardini, Seetah, & Barker, 2015; Kocovsky, Adams, & Bronte, 2009). We therefore consider our sample sizes sufficient to provide robust statistical analyses.

2.6 | Tool comparisons

We tabulated the different steps required to get from initial sampling to data interpretation for each of the tools we tested. We

TABLE 2 Management tool nearest neighbour analysis parameters and assignment accuracies to their correct fishing ground

Management tool	N	Initial K	Optimal K	Assignment accuracy		
				Minimum	Maximum	Mean[a]
Microsatellite genotypes	149	11	7	26.7%	80.0%	52.4%
Otolith chemical signatures	71	8	5	12.5%	87.5%	54.0%
Morphometric truss ratios	93	9	8	50.0%	100.0%	79.5%

[a] Mean is calculated from 100 permutations.

constructed a relative scale for the expertise, a time requirement and a cost per sample to conduct each of the analyses, based on obtaining initial samples (i.e. genetic material, otoliths, and truss measurements) through to data interpretation (usable data outputs). We assumed that fishers would provide access to fish for genetic and morphometric measurements free of charge, while due to the otolith extraction process the purchase of individual fish is required for otolith analyses. For each of the analyses we reviewed the costs associated for each analysis that are required to fulfil each procedural step. However, we did not include the costs of basic equipment (e.g. thermocycler, mass spectrometer, calipers), nor did we include estimates of labour costs.

3 | RESULTS

Of the three techniques morphometric analysis was the most accurate. Pairwise PERMANOVA analyses of morphometric truss ratios identified highly significant differences between all pairs of fishing grounds (eastern and central, $F = 10.29$, $p = 0.001$; eastern and western, $F = 6.63$, $p = 0.001$; central and western, $F = 9.37$, $p = 0.001$). Significant differences of genotypes were observed between all three fishing grounds (eastern and central, $F = 4.06$, $p = 0.014$; eastern and western, $F = 5.46$, $p = 0.009$; central and western, $F = 5.31$, $p = 0.004$). With otolith microchemistry, significant differences were only observed between central and western fishing grounds ($F = 5.67$, $p = 0.011$), and no significant differences were observed between central and eastern ($F = 1.17$, $p = 0.31$) or eastern and western fishing grounds ($F = 1.58$, $p = 0.183$; Table 3).

Nearest neighbour assignment accuracy was greatest for morphometric truss ratios, with a mean accuracy of 79.5%. The mean assignment accuracies for otolith element signatures and microsatellite genotypes were 54.0% and 52.4%, respectively (Table 2).

Morphometric truss ratio analysis requires a lower level of technical expertise, has the fastest turnaround time from data collection to interpretation, and the lowest cost per sample. Microsatellite genotyping and otolith chemical signature analyses require high levels of technical expertise and an average turnaround time of 2 months from data collection to data interpretation. Of these two laboratory analyses-based approaches microsatellite genotyping was cheaper than otolith chemical signature analysis (Table 4).

TABLE 3 Fishing ground pairwise PERMANOVA analyses of microsatellite alleles, otolith chemistry signatures and morphometric truss ratios

	F-static	*p*
Microsatellite genotypes (*n* = 149)		
Eastern–Central	4.06	**0.016**
Eastern–Western	5.46	**0.009**
Central–Western	5.31	**0.004**
Otolith chemical signatures (*n* = 71)		
Eastern–Central	1.58	0.183
Eastern–Western	1.17	0.310
Central–Western	5.67	**0.011**
Morphometric truss ratios (*n* = 93)		
Eastern–Central	10.29	**0.001**
Eastern–Western	6.63	**0.001**
Central–Western	9.37	**0.001**

Significant results are highlighted in bold.

4 | DISCUSSION

We found that measuring the truss points of a fish and using those to provide a morphometric profile provided the highest accuracy of assigning individual fish to their fishing ground of origin (79.5%), at spatial scales of 5–60 km compared with laboratory-based microchemistry or genetic approaches. Importantly, measuring fish post capture has low cost other than labour, with no specialized equipment or installations required. Results are available within a day, requiring a medium level of technical expertise and analyses. The low cost and high accuracy of morphometric analyses make it an appropriate method for use by fisheries managers, and also accessible to management groups focused on low value, or community-based fisheries. In addition to minimal equipment requirements, data analyses are simple and the short turnaround time from sampling to results, make morphometric nearest neighbour analyses a powerful tool and relatively easy to adopt. Forensic methods can augment physical patrols, with sampling possible at fish landing sites or at sea. To improve the accuracy of the tool a greater number of individuals should be used to provide the baseline morphometric signature of each fishing ground. Based on the current accuracy level, morphometric analysis is best paired with physical patrols, the tool can

TABLE 4 Processes required for each of the three analyses tested, including level of expertise and time required to conduct each analysis and a typical cost per sample

Processes	Microsatellite genotyping	Otolith chemical signatures	Morphometric truss ratios
1	Tissue collection	Otolith removal	Fish measurements
2	DNA extraction	Sectioning and mounting	Data analysis
3	PCR reactions	Laser ablation	Data interpretation
4	Sequencing	Data analysis	
5	Data analysis	Data interpretation	
6	Data interpretation		
Technical expertise and specialized equipment	High	High	Medium
Time requirement	2 months	2 months	Hours
Typical cost per sample[a]	US$ 20	US$ 35	US$ 0

[a] Costs were based on processing costs only, i.e. reagents and costs of running specific equipment. The purchase of any specialized equipment and/or labour was not included in the cost estimate.

be used to support in situ observations of fishing infractions. While tested on the yellowtail snapper, there is the potential for morphometric analyses to be appropriate for other fisheries, for example groupers (Serranidae), snappers (Lutjanidae), grunts (Haemulidae) and spiny lobsters (Palinuridae). However, applicability of this methodology to species within these families requires explicit testing. An important caveat is morphometric analyses is not a "one size fits all" management tool. It may not be a useful tool for fish species with large home ranges, low residency rates or in regions with homogeneous environmental conditions. However, the potential for morphometric analyses to be a useful management for species with high residency times and in areas where the spatial unit of management is tens of kilometres.

Otolith element signatures and microsatellite genotypes assignment accuracies were low (54.0% and 52.4% respectively). Significant genetic differences were observed between the three grounds. However, these differences were not sufficient to accurately assign individuals to their fishing ground of origin. Significant differences in otolith element signatures were only observed between central and west fishing grounds. Fishing ground assignment accuracy for otolith measures were slightly greater than for the genetic analyses. However, the range of assignment accuracy was highly variable. We therefore do not consider otolith element signatures and microsatellite genotypes suitable tools to assist in fisheries management for this species at these spatial scales. Assignment accuracy could be improved by the analysis of additional elements for otolith element signatures, testing genomic analyses (single-nucleotide polymorphisms), and increasing sample size. Additionally, pairwise analyses of genetic, otolith and morphometric analyses could have increased assignment accuracy. However, the high costs of laboratory-based tools and the slow turnaround time from sample collection to final analysis reduces the utility of both otolith and genetic analyses for fisheries managers with limited resources and therefore the adoption of the management tool. Nevertheless, both genetic and otolith analyses have important roles in fisheries management (e.g. Ferguson, Ward, & Gillanders, 2011; Truelove et al., 2017). None of the tools examined in this study are stand-alone tools, they constitute options that need to be incorporated where appropriate into fisheries management and monitoring strategies.

Our findings suggest the presence of three distinct body shapes of yellowtail snapper, each distinct to one of the three fishing grounds and detectable over small spatial scales (5–60 km). Our results do not, however, show where the boundaries between these differences occur or explain causation. Vasconcellos et al. (2008) had similar findings within the yellowtail snapper fisheries of Brazil, but at larger scales. In their study, morphometric analyses differentiated yellowtail snapper among four areas separated by hundreds of kilometres where genetic analyses lacked discriminatory power. We hypothesize that the environmental conditions at each of the three fishing grounds in our study influenced the body shape of individuals which provides additional evidence of a limited home range of yellowtail snapper (Farmer & Ault, 2011). Medina, Brêthes, and Sévigny (2008) identified morphometric differences in the African hind (*Cephalopholis taeniops*) that were directly correlated with geographical distance of sampling sites and depth. Bathymetry of each of our sampling sites suggest a range of depth gradients, thus depth could be an environmental driver of morphology within the Honduran yellowtail snapper fishery. Local hydrology may also be a driver of morphometric differences. For example, differences have been observed in the northern pike (*Esox lucius*) as a result of flow variations in different streams (Senay, Harvey-Lavoie, Macnaughton, Bourque, & Boisclair, 2017). There are likely to be differences in local hydrological conditions at each of the fishing grounds in this study based on their proximity to the continental shelf and Honduran mainland where riverine inputs will impact hydrological patterns, salinity and sediment load. Local hydrology and bathymetry influence water temperature, which is another known driver of body shape (Lõhmus et al., 2010). Additional research is required to untangle which environmental factor or factors are driving the morphology of yellowtail snapper in the Honduran fishery, and to identify the extent of similar morphology on a continuum.

5 | CONCLUSIONS

Accurate and robust tools to support evidence-based management are critical to achieving sustainable fisheries. Expensive and highly technical management tools are constrained in their applicability through financial and technical limitations. Morphometric analyses offer a cost-effective and accurate tool to assist in site based management approaches, with the potential application to fisher compliance of NTZs and/or TURFs. Importantly, it would be possible to automate this approach using off the shelf digital technology and a digital image of the sampled fish. Incorporating these data into user-friendly systems with outputs that are easily interpreted by mangers, fishers and other stakeholders can increase the availability of data for decision-making.

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AUTHORS' CONTRIBUTIONS

S.W.J.C. conducted research design, fieldwork, statistical analyses and provided the main input into the writing of the manuscript; N.K.T. conducted genetic analyses through allele scoring, wrote relevant methods section and provided editorial input; R.F.P. assisted with genetic and statistical analyses, and provided editorial input; S.C. and M.A.S.H. conducted the laser ablation of otoliths, wrote the relevant methods section and provided editorial input; S.J.B. conducted research design and provided editorial input. All authors have given their approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.1n51337 (Canty et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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8.5 Appendix 5 – Published version of Chapter 4

Chapter 34 was published in Scientific Reports. A copy of the printed article is below.

scientific reports

OPEN

Genetic structure of a remnant *Acropora cervicornis* population

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Amongst the global decline of coral reefs, hope spots such as Cordelia Bank in Honduras, have been identified. This site contains dense, remnant thickets of the endangered species *Acropora cervicornis*, which local managers and conservation organizations view as a potential source population for coral restoration projects. The aim of this study was to determine the genetic diversity of colonies across three banks within the protected area. We identified low genetic diversity ($F_{ST} = 0.02$) across the three banks, and genetic similarity of colonies ranged from 91.3 to 95.8% between the banks. Clonality rates were approximately 30% across the three banks, however, each genotype identified was unique to each bank. Despite the low genetic diversity, subtle genetic differences within and among banks were demonstrated, and these dense thickets were shown not to be comprised of a single or a few genotypes. The presence of multiple genotypes suggests *A. cervicornis* colonies from these banks could be used to maintain and enhance genetic diversity in restoration projects. Management of hope spots, such as Cordelia Bank, and the incorporation of genetic information into restoration projects to ensure genetic diversity within out-planted populations, will be critical in the ongoing challenge of conserving and preserving coral reefs.

Coral reefs are under severe threat from global climate change. Particular issues include increases in sea surface temperature[1,2], ocean acidification[3], and localized stressors such as overfishing[4] and eutrophication[5]. Coral reefs are reaching a tipping point, with phase shifts from coral to algal dominance becoming increasingly prevalent[6,7], and potentially irreversible. As the biological and physical structure of coral reefs change, ecosystem service provision and the resilience of these systems to future stresses is reduced[8]. The loss of ecosystem services is of concern for coastal populations who rely on them, both directly, e.g., for fisheries[9], and indirectly, e.g., for storm protection[10]. To abate phase shifts and conserve coral reef biodiversity, urgent management is required at both global and local scales.

Within the Caribbean, average coral cover declined from 34.8% in 1970 to 16.3% in 2012[11]. Of significance during this period was the loss of approximately 80% of Caribbean Acroporid corals, which was triggered by an outbreak of white band disease in combination with multiple climatic events, including hurricanes[12]. During the intervening decades, there has been little to no recovery of these populations, and both *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral) have been listed as critically endangered by the International Union for Conservation of Nature[13,14]. However, remnant Acroporid populations have been documented throughout the Caribbean, e.g. in Mexico and Belize[15], Honduras[16], Guadeloupe[17], U.S. Virgin Islands, St. Vincent and the Grenadines, Bonaire and Curacao[18].

Low genetic diversity and high clonal frequency can be common within Acroporid populations[17]. Asexual or clonal reproduction strategies are associated with maintaining and preserving existing genetic diversity during periods of population decline and poor recruitment from sexual reproduction, a particular concern in fragmented and remnant populations[19]. Critically, remnant populations have the potential to become sexually extinct after prolonged periods of clonal growth, if recruitment of sexually reproduced individuals from other populations is low[20]. Which may be attributed to the Allee effect, as fertilization success in broadcast spawning corals, such as Acroporids, is density dependent[21]. Caribbean Acroporid populations are generally considered to be dominated by clones, and thus non-sexual reproduction, however, there are exceptions to this; high levels of genetic diversity have been observed in populations of *A. palmata* in Mexico, Belize[15], and the Eastern Caribbean[22], and *A. cervicornis* populations along the Florida Reef Tract[23]. Higher levels of genetic diversity suggest a greater prevalence of sexual reproduction, and within the Eastern Caribbean this has been considered to be related to habitat characteristics[22]. Sexual reproduction has the potential to promote genetic diversity and, therefore, the ability to respond to environmental change within a species, increasing resilience in the face of

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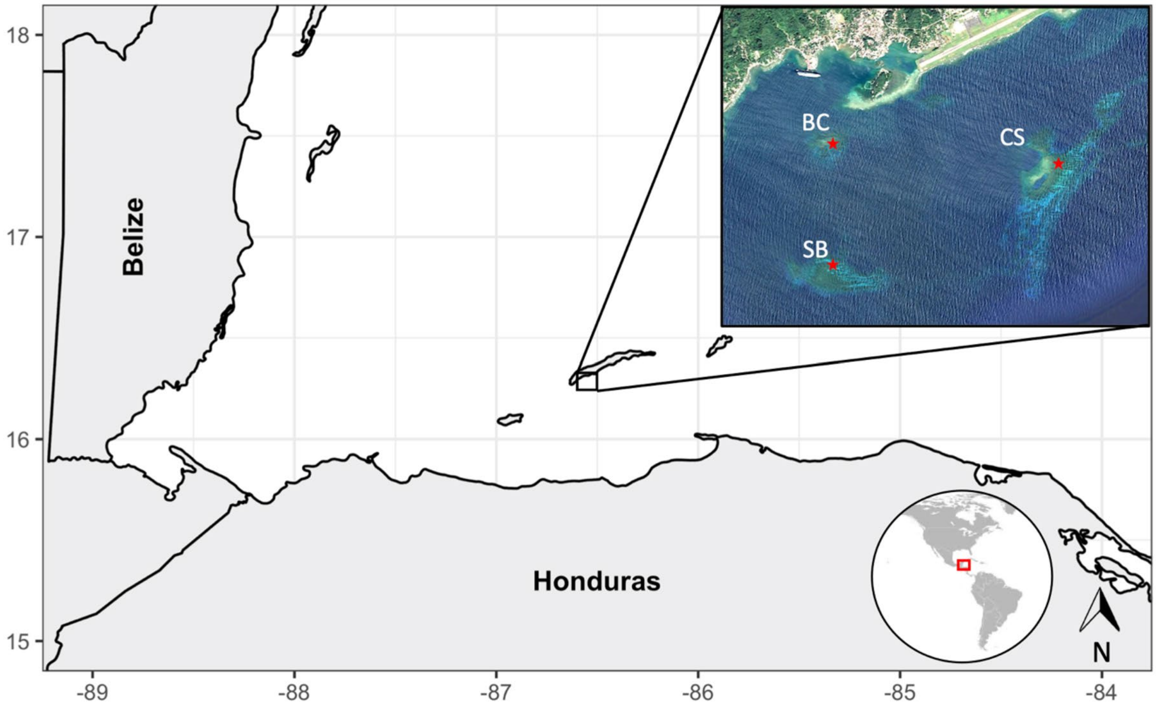


Figure 1. Map of the Honduran north shore, highlighting the location of Cordelia Bank Site of Special Importance to Wildlife, and the three banks with dense thickets of *Acropora cervicornis*, BC—Big Cay, CS—Cordelia Shoal, SB—Smith Bank, approximate sampling locations are indicated by red stars. Maps were created with R Studio version 1.2.1335[37] using satellite images provided by Google Maps.

environmental stresses[24], and may enhance species diversity at the community level[25]. Further, areas with high genetic diversity have been associated with higher coral cover[26]. Within *A. cervicornis* clumping of ramets, or clonal genotypes, has been observed across the reef scape[22,27]. This clumping suggests low genetic diversity at the micro-scale and increased genetic diversity at the macro-scale, therefore greater allelic diversity is observed in larger populations.

Whilst the presence of remnant populations of threatened species is a cause for hope, there is a realization that coral reefs are unlikely to return to past configurations in terms of community assemblage. Therefore, the challenge for both the scientific and management communities is to maintain ecosystem function in these critical systems[28]. There is concern that recovery by natural processes may not be sufficient, e.g., if coral settlement is inhibited by algae[29], interventions such as anthropogenic restoration may also be required[30]. In light of this, initiatives are focusing on remnant populations as potential seed populations[31], at least at the local scale.

Remnant populations of *A. palmata* and *A. cervicornis* have been observed in Honduras[16], and Guadeloupe[17] and corals from these populations have the potential to seed the recovery of Caribbean Acroporid populations[31]. The Cordelia Bank Site of Special Importance to Wildlife is one such area. The reef system, located in the Honduran Caribbean, was identified to contain extensive *A. cervicornis* colonies[16] (Fig. 1). Due to the prevalence of colonies, the area is being considered as the potential source of colonies for use in local restoration projects. Knowledge of the genetic composition of colonies prior to restoration is essential[32–34], but to date, no genetic studies have been conducted on the colonies within Cordelia Bank Site of Special Importance to Wildlife. It is not known if a single, or multiple genotypes are found within these populations. We used microsatellite markers to assess the genetic diversity of individual sexually mature colonies of *A. cervicornis* across three banks within Cordelia Bank Site of Special Importance to Wildlife. Our aim was to provide a genetic baseline of colonies within the protected area prior to the implementation of restoration projects that plan to use these colonies as a source population.

Materials and methods

Study site and sample collection.

Cordelia Bank (N 16.30°; W 086.52°) was officially declared a Site of Special Importance for Wildlife in 2012, by the Honduran government[35]. The area consists of four offshore banks, Cordelia Shoal, Smith Bank, Big Cay and Little Cay, located approximately one mile south-west of the island of Roatan, Bay Islands, Honduras (Fig. 1). The area was given protective status due to the abundance of *A. cervicornis*, with colonies estimated to extend over an area of 63,440m^2, across three primary banks[36].

Sampling was conducted in April 2014 on three of the four banks: Big Cay; Cordelia Shoal and Smith Bank, based on the presence of high densities of *A. cervicornis,* as identified by Riegl et al.[36]. Sampling was not undertaken on Little Cay due to weather constraints. In-water observations were first conducted to confirm the suitability of sampling areas and ensure that the selected locations had close to 100% *A. cervicornis* coral cover. For each bank, 100 5 m × 5 m sampling cells were initially established across a 50 m × 50 m grid. Due to inclement

	N	N_g	N_g/N	C_g	C	Colonies per ramet			Percentage clones (%)
						Maximum	Minimum	Mean	
Big Cay	50	42	0.84	7	15	3	2	2.1	30.0
Cordelia Shoal	57	44	0.77	4	17	10	2	4.3	29.8
Smith Bank	98	75	0.77	10	33	8	2	3.3	33.7
Combined	205	161	0.79	21	65	10	2	3.1	31.7

Table 1. Description of ramet and clonal diversity of *Acropora cervicornis* within the Cordelia Bank Site of Special Importance to Wildlife. N, is the total number of colonies sampled; N_g, is the number of unique genotypes identified; N_g/N is the genotype to colony ratio; C_g is the number of ramets identified; C is the total number of colonies identified as clones. No significant difference in the number of clones per bank (chi-squared = 4.125 p = 0.127), the number clonal genets per bank (chi-squared = 1.348 p = 0.510), or the mean ramets per genotype per bank (chi-squared = 0.392 p = 0.822) were observed.

weather and the risk of causing damage to the reef, the sampling grid was modified on the shallowest banks: Big Cay to 50 m x 25 m and on Cordelia Shoal to 50 m × 30 m. This provided a combined area of 5250m^2, representing over 8% of the total estimated cover of *A. cervicornis* cover across the three banks.

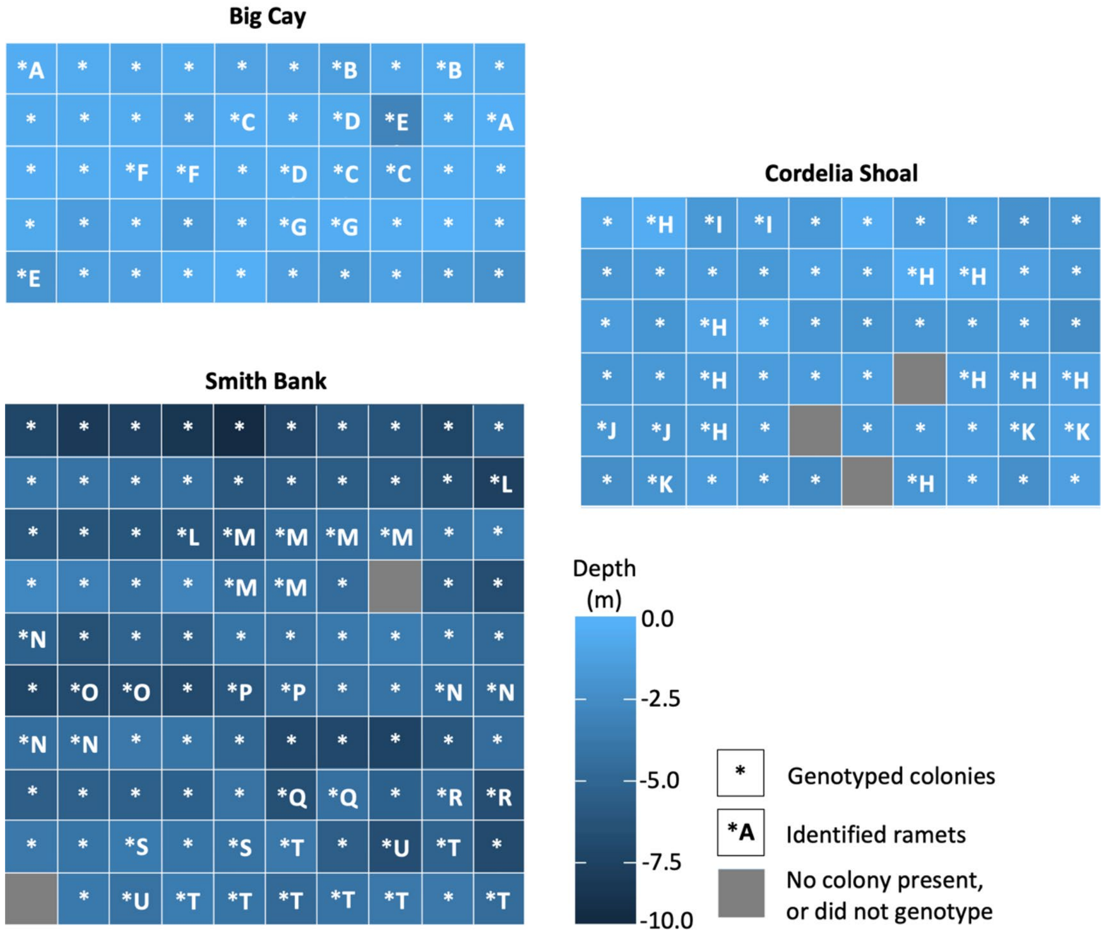
The sampling grid was laid out on the reef using four 50 m measuring tapes, to demark the sampling area. Three additional measuring tapes were used to make horizontal internal lines at 5 m intervals, to create two adjacent rows. Flagging tape placed at 5 m intervals along the measuring tapes was used to demark individual sampling cells of 5 m x 5 m. Once sampling was completed for these two rows, measuring tapes were moved further up the reef to create two subsequent rows and repeated until the sampling was complete. Sampling started at the deepest part of the reef, working up to the shallows.

Corals were sampled by taking a small cutting, 2–3 cm long, from the branch of a single *A. cervicornis* colony within each of the sampling cells. Cuttings were placed into individually labelled bags containing seawater, taken ashore and then transferred to 100% ethanol and frozen for storage prior to genetic analyses. Sampled colonies were chosen if: (1) they were the dominant colony within the grid that had a basal attachment, and had not been sampled in a previous grid; and (2) they had a minimum branch length of 17 cm, to ensure they were sexually mature[38]. If the dominant colony had been sampled previously, the next largest colony in the grid was sampled instead. Sampling only mature colonies was a specific strategy to detect the full genetic composition of the potential reproductive stock of *A. cervicornis* within the protected area. Each sample was geo-referenced, with GPS coordinates recorded by a snorkeler at the surface, and depth recorded to 0.1 m accuracy using a Matrix dive computer (Mares™, Rapallo, Italy). A total of 205 samples were collected and successfully genotyped from across three offshore banks, Big Cay n = 50, Cordelia Shoal n = 57, Smith bank n = 98 (Table 1).

Genotyping. Fragments of approximately 1 cm length of coral were used for DNA extraction. These were crushed using a 0.5″ chisel and transferred to a microcentrifuge tube, to which Qiagen DNeasy Blood and Tissue ATL buffer and Proteinase K were added. Samples were then placed in an Eppendorf thermomixer (Hamburg, Germany) at 56 °C and 600 rpm for 4 h. Once digestion was completed, DNA extractions followed the Qiagen DNeasy Blood and Tissue protocol. DNA concentration was calculated using a BioTek Epoch Microplate Spectrophotometer (Winooski Vermont, United States), and where necessary, DNA was concentrated to ensure that 20 ng of DNA was used in each subsequent amplification reaction.

Individual *A. cervicornis* colonies were genotyped using fourteen polymorphic microsatellite loci: 0166, 0181, 0182, 0192 & 0207[39] and 0513, 0585, 1195, 1490, 2637, 5047, 6212, 9253 & 0007[40]. Polymerase chain reactions were carried out on BIO-RAD T100™ Thermal Cyclers (Hercules California, United States), with an initial denaturation step at 95 °C for 5 min followed by 35 cycles of 95 °C for 20 s, 51–55 °C for 20 s, 72 °C for 30 s, and a final extension of 30 min at 72 °C, with the exception of 0007. This marker required an initial denaturation step at 95 °C for 5 min followed by 31 cycles of 95 °C for 15 s, 55 °C for 15 s, 72 °C for 30 s, and a final extension of 30 min at 72 °C. Genotyping was performed using an ABI 3730xl automatic DNA analyzer (Applied Biosystems, Waltham, Massachusetts, United States). An internal size standard (GeneScan 500-LiIZ, Applied Biosystems) was used for accurate sizing. Electropherograms were analyzed using GeneMapper v.5.0 and alleles were subsequently binned with the R-package Msatallele version 1.02[41]. Genotyped colonies with more than 20% missing data (missing data from three or more loci) were removed from subsequent analyses. The locus 0192 did not genotype evenly across samples and therefore was removed from the analysis. All of the laboratory and computer work was conducted in and with the support of the Laboratories of Analytical Biology facilities of the Smithsonian's National Museum of Natural History (Washington, D.C., United States).

Data analysis. Clones were identified as genetically identical to another individual, and these individuals were then assigned to a ramet, using a two-step process. Firstly in GenoDive[42], a distance matrix was calculated using a stepwise mutation model, where missing data was not counted, the threshold was set at zero, and clonal structure was tested using a stepwise mutation model of the corrected Nei's diversity index statistic with the randomize alleles over individual colonies of all three banks, using 999 permutations. These outputs were cross-checked in GenAlEx 6.5[43], which allows for the inclusion of colonies with missing data, using the matching function where all data is considered as a single population and alleles are codominant. Through this step, an additional three colonies were identified as clones and assigned to corresponding ramets. Where clones were



Big Cay

*A	*	*	*	*	*	*B	*	*B	*
*	*	*	*	*C	*	*D	*E	*	*A
*	*	*F	*F	*	*D	*C	*C	*	*
*	*	*	*	*	*G	*G	*	*	*
*E	*	*	*	*	*	*	*	*	*

Cordelia Shoal

*	*H	*I	*I	*	*	*	*	*	*
*	*	*	*	*	*	*H	*H	*	*
*	*	*H	*	*	*	*	*	*	*
*	*	*H	*	*	*	▨	*H	*H	*H
*J	*J	*H	*	▨	*	*	*	*K	*K
*	*K	*	*	*	▨	*H	*	*	*

Smith Bank

*	*	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	*	*L
*	*	*	*L	*M	*M	*M	*M	*	*
*	*	*	*	*M	*M	*	▨	*	*
*N	*	*	*	*	*	*	*	*	*
*	*O	*O	*	*P	*P	*	*	*N	*N
*N	*N	*	*	*	*	*	*	*	*
*	*	*	*	*	*Q	*Q	*	*R	*R
*	*	*S	*	*S	*T	*	*U	*T	*
▨	*	*U	*T	*T	*T	*T	*T	*	*T

Figure 2. Depth profiles of sampled *Acropora cervicornis* colonies and location of clones within the three banks of Cordelia Bank Site of Special Importance to Wildlife, each letter represents a unique ramet (clonal genotype).

corroborated, a single representative of the ramet was used in further analysis. Summary data of each locus (number of alleles, expected and observed heterozygosity) were calculated for each population, and pairwise F_{ST} and Nei unbiased genetic identity tests were conducted in GenAlEx 6.5[43].

Population structure of *A. cervicornis* colonies was analyzed using the software *STRUCTURE*[44], using an admixture model with allele correlation. The Burn-in period length was set at 100,000, and the number of Markov chain Monte Carlo replications after Burn-in was set at 100,000. We ran the model with K values of 1 through 10, and with 10 permutations for each K value. To identify the optimal K, the model outputs were analyzed in STRUCTURE HARVESTER[45], with the highest delta K value used to identify the optimal K value. Mantel tests were conducted to test for correlations between genetic distance and geographic distance, and genetic distance and depth, and a partial Mantel test to test for partial correlations among all three, these analyses were conducted using the *vegan* package[46]. Additional Chi-squared analyses of clonal diversity across the three banks were conducted in R Studio version 1.2.1335[37].

Results

Clonal genetic analysis.

A total of 65 clones, belonging to 21 ramets, were identified across the three banks, and were unique to individual banks (Fig. 2, Table 1). Approximately one third (31.7%) of all colonies sampled were identified as a clone. Ranging from 29.8% to 33.7% across the three banks, no significant differences in the occurrence of colonies identified as clones were observed (chi-squared, $p = 0.846$). Across all alleles, the number of ramets varied among banks, as did the mean number of colonies per ramet, and neither was significant (chi-squared, $p = 0.654$, chi-squared, $p = 0.132$ respectively), nor was there an interaction between the number of ramets and the number of colonies per ramet, per bank (chi-squared, $p = 0.654$) (Table 1).

Genetic structure.

Genetic diversity across the Cordelia Bank Site of Special Importance to Wildlife was low ($F_{ST} = 0.020$), varying from $F_{ST} = -0.032$ to 0.102 across the individual banks (Table 2). Pairwise F_{ST} analyses suggested low genetic differentiation among the colonies sampled across the three banks, with values ranging from 0.014 to 0.025. Nei's unbiased genetic identity analyses corroborate these findings, indicating limited genetic differentiation among the three banks, ranging from 0.913 to 0.958, with greatest similarities observed between Big Cay and Smith Bank (Table 3). A weak significant relationship was observed between genetic dis-

	Big Cay		Cordelia Shoal		Smith Bank		All sites	
	N_a	F_{ST}	N_a	F_{ST}	N_a	F_{ST}	N_a	F_{ST}
0166	7	−0.086	6	0.017	7	0.021	9	0.024
0181	8	−0.081	12	0.026	12	0.064	13	0.015
0182	10	−0.124	11	0.006	14	0.031	16	0.013
0207	8	−0.094	7	−0.060	8	0.014	9	0.034
0513	6	−0.088	8	0.009	8	−0.190	10	0.009
0585	7	0.020	7	0.146	4	−0.013	7	0.004
1195	4	0.071	5	0.242	6	0.372	6	0.021
1490	5	0.220	3	0.634	5	0.404	6	0.065
2637	7	0.012	6	−0.178	10	0.030	10	0.005
5047	7	−0.159	7	0.293	7	−0.068	9	0.023
6212	12	−0.026	10	0.120	13	0.122	15	0.006
9253	2	−0.024	3	−0.018	4	−0.030	6	0.047
0007	10	−0.060	12	0.093	12	0.063	13	0.017
Overall		−0.032		0.102		0.063		0.020

Table 2. Genetic diversity at 13 microsatellite loci for *Acropora cervicornis* for the three sample sites of Cordelia Bank Site of Special Importance to Wildlife. Only one representative of each clonal genotype is included in the analysis. N_a, number of alleles; F_{ST}, Fixation coefficient.

	Big Cay	Cordelia Shoal	Smith Bank
Pairwise F_{ST}			
Big Cay	–		
Cordelia Shoal	0.025	–	
Smith Bank	0.014	0.017	–
Nei unbiased genetic identity			
Big Cay	–		
Cordelia Shoal	0.913	–	
Smith Bank	0.958	0.939	–

Table 3. Pairwise F_{ST} and Nei unbiased genetic identity values of *Acropora cervicornis* colonies from three banks within the Cordelia Bank site of special importance to wildlife.

tance and geographic distance (Mantel test, $r = 0.108$, $p = 0.002$), no relationship was observed between genetic distance and depth (Mantel test, $r = -0.038$, $p = 0.909$) or between genetic distance and a combination of geographic distance and depth (Partial mantel, $r = -0.089$, $p = 0.993$). Population structure analyses highlight the similarities in the genetic structure of *A. cervicornis* colonies within and across the sampling locations, with individual colonies having both K clusters well represented and no individual colony fully assigned to either cluster (Fig. 3a). However, subtle differences in cluster allocation were observed at the bank level. Greater proportions of cluster 2, 56% and 55%, were presented in colonies on Big Cay (Fig. 3b), and Smith Bank (Fig. 3c), respectively. Whereas colonies on Cordelia Shoal (~51%) have a slightly greater proportion of cluster 1 (Fig. 3d).

Discussion

The extensive thickets of *Acropora cervicornis* colonies within the Cordelia Bank Site of Special Importance to Wildlife are comprised of numerous genetically distinct colonies, however genetic diversity within and among the three banks was low. Clones were observed in each of the three banks, with mean clonality across the three banks at 31.7%. However, genotypes were unique to individual banks suggesting spatial structuring between the banks, which has been observed in other populations[22,27]. The high number of unique genotypes which was observed (mean $N_g/N = 0.79$) differs from how *Acropora* reefs are generally considered and what has been observed in other populations, e.g. Florida ($N_g/N = 0.33$), Belize ($N_g/N = 0.39$)[47] and Guadeloupe ($N_g/N = 0.01$)[17]. The systematic sampling methodology used in this study, which ensured that multiple sexually mature colonies were sampled, can maximize the genetic diversity observed. This may have contributed to the lower prevalence of clonality than that observed in other studies. However, similar to this study, high frequencies of unique genotypes and low clonality have been observed in *A. cervicornis* populations, e.g., the Bahamas ($N_g/N = 0.64$), Turks and Caicos ($N_g/N = 0.65$), and Panama ($N_g/N = 0.66$). The high frequency of distinct, but similar, genotypes within and across the three banks of Cordelia Bank Site of Special Importance to Wildlife provide a small, but potentially significant, reservoir of genetic diversity. Whilst genetic diversity may be low within, and across *A. cervicornis* populations, significant, but weak, genetic differences driven by geographic distance were observed.

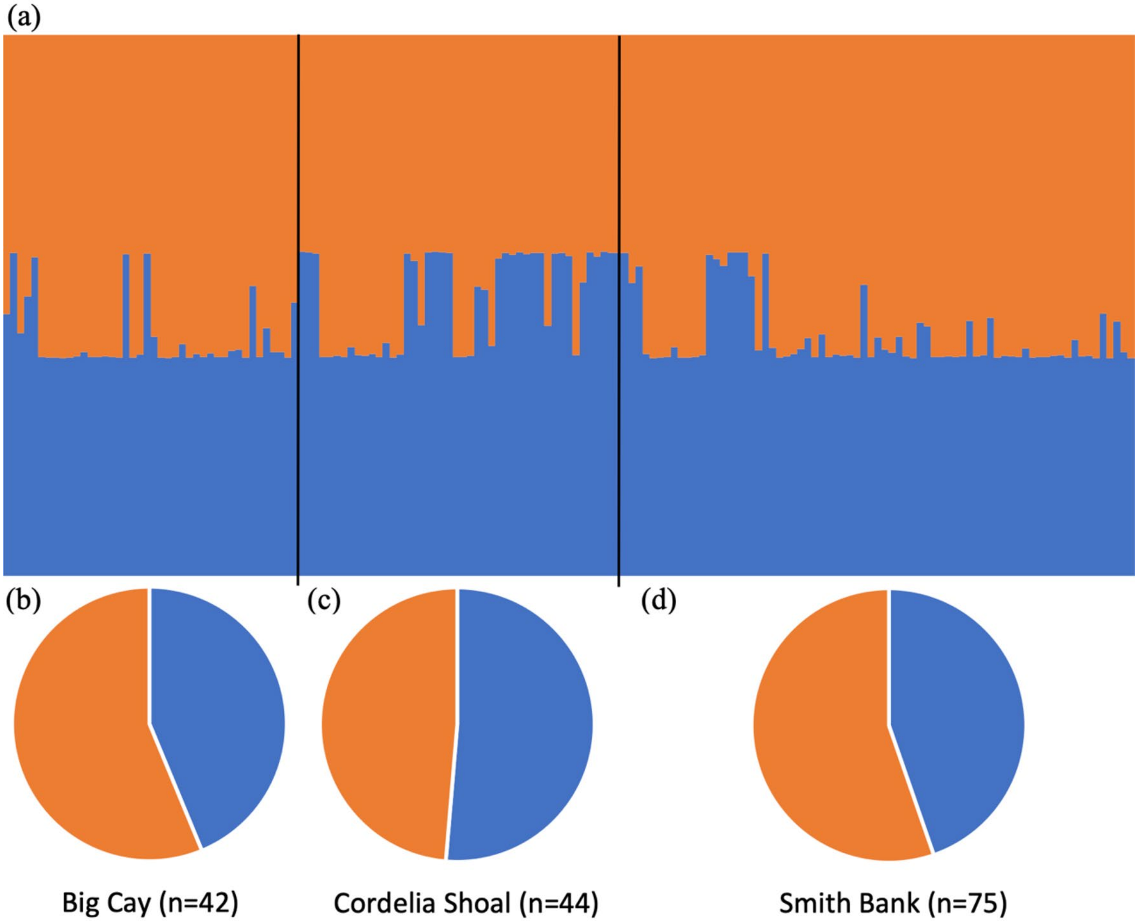


Figure 3. STRUCTURE outputs for all genotypes (K = 2), mean of 10 permutations, for each colony within each of the banks (**a**); and the mean cluster classifications of all colonies within Big Cay (**b**); Cordelia Shoal (**c**); and Smith Bank (**d**). Blue—Cluster 1; and Orange—Cluster 2.

This research did not address the drivers of genetic differentiation, and therefore we can only postulate that the genetic differentiation observed is a result of natural selection or a founder effect. These subtle genetic differentiations could be key in allowing individual colonies to adapt to future stressors, and therefore it is critical that this diversity is protected and conserved, this will become more important if these reefs, and others, are not restored through sexual recruitment.

Maintaining this genetic diversity will be crucial if sexual reproduction events are triggered in the future; such events provide the opportunity to increase genetic diversity within populations[48]. Spawning activity within Acroporid populations has been observed in the Florida Keys, Panama and Belize, July through October[49], and spawning in Belizean *A. palmata* has been observed most years from 2010–2019 (Personal communication, M. Scott Jones, Smithsonian Marine Station). Monitoring for spawning activity of *A. cervicornis* in Cordelia Bank Site of Special Importance to Wildlife was last conducted during the full moons of June, July and August 2013. No spawning was observed in *A. cervicornis* colonies during this period, however, spawning of *Orbicella annularis* and *O. faveolata* was observed during the August full moon (Personal observations, SWJC). Spawning in multiple *A. palmata* colonies in Tela Bay, Honduras, was observed during the same August 2013 full moon (Personal communications, Andrea Rivera, Universidad Nacional Autónoma de México). These observations suggest that environmental cues to trigger spawning are present in the region. Whilst the potential for natural recovery exists, even where spawning has regularly been observed, the overall cover of Acroporids has remained low[50]. It is therefore likely that further intervention is required to assist in the recovery of Caribbean Acroporid populations.

Restoration is becoming an increasingly popular tool for conservation and management of marine habitats[51,52] and within the Caribbean over 150 projects in more than 20 countries have been implemented[53]. Coral gardening, a preferred technique in the Caribbean, inherently limits genetic diversity as the technique focuses on the growing and out-planting of clones[54]. Despite genetics being an important factor that complements traditional restoration ecology methodologies[55], and ensures ecological and evolutionary processes are incorporated into the restoration process[56]. Genetic diversity provides colonies with the potential to respond to changing environmental conditions, and where no genetic variation exists, responses are limited to phenotypic plasticity to deal with these stressors. During restoration there is the potential for the loss or reduction of fitness in the restored population, driven by founder effects, genetic swamping and inbreeding or outbreeding depression[32]. Greater attention needs to be given to genetic diversity when restoring systems[57], especially when projects are dominated by a single species, such as coral gardening of *A. cervicornis*, the genetic diversity represents the primary biodiversity of the habitat. Genetic composition of out-planted colonies is one of many important criteria that should be considered within a best practices approach to restoration[58].

Understanding the drivers of existing genetic structure and environmental conditions will be important in the successful management and conservation of these populations, and of restoration projects that use colonies from these populations. If a restoration project using colonies from Cordelia Bank Site of Special Importance to Wildlife is to be implemented, then the genetic diversity across the banks observed in this study should be considered. Selectivity of colonies during the restoration process can ensure representation of a range of genotypes maximizing the potential for evolutionary adaptation of corals within a restored area. There is an important caveat that underlies this potential and the future of the corals within Cordelia Bank, the Caribbean, and globally. Understanding and reversing the ultimate localized drivers of reef decline (e.g., overfishing and eutrophication) must be part of comprehensive local and regional management strategies. The coral populations of the Mesoamerican barrier reef system, which encompasses Cordelia Bank, are under pressure from ocean acidification, hurricanes, pollution and fishing, and at high risk from mass bleaching over the next decades, and the ecosystem has been categorized as critically endangered by the IUCN[59]. In the specific case of Cordelia Bank, fishing and recreational activities have been excluded from highly sensitive areas, however, urban runoff and untreated effluents from Coxen Hole, and the proximity of two major cruise ship docks and an international airport, represent potential major threats[60]. If coral reefs are to have sufficient resilience to climate change and continue to provide critical ecosystem services to the coastal communities that depend on these resources, the drivers of their decline must be reduced. Whilst management cannot prevent the damaging effects of major disturbances, it can provide protection to reefs that have the greatest potential to be resilient and contribute to recovery through natural processes[61]. Natural regeneration promotes more complex and resilient systems than active restoration[62], therefore restoration should be considered as one of a multitude of management tools in the conservation of coral reefs.

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Author contributions

S.W.J.C. and R.F.P. conceived the study. S.W.J.C. conducted the fieldwork, laboratory analyses and genotyping. G.F. produced the bioinformatics pipeline. S.W.J.C. and G.F. conducted the statistical analysis. S.W.J.C. produced the first draft. S.W.J.C., J.K.R., R.F.P. and G.F. contributed to writing and editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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8.6 Appendix 6 – Chapter 6 supplementary material

A. Full list of publications identified related to mangroves from the Mesoamerican Reef Ecoregion

Acosta, C. A., & Butler, M. J. (1997). Role of mangrove habitat as a nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. Mar. Freshwater Res., 48, 721–727.

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B. List of threats provided by Ramsar to stakeholders of prospective Ramsar sites.

Factors adversely affecting the sites ecological character		*Description*
Human settlements (non- agricultural)		**Human settlements or other non-agricultural land uses with a substantial footprint**
	Housing & urban areas	Human cities, towns, & settlements including non-housing development typically integrated with housing *Urban areas, suburbs, villages, vacation homes, shopping areas, offices, schools, hospitals*
	Commercial & industrial areas	Factories & other commercial centers *Manufacturing plants, shopping centers, office parks, military bases, power plants, train & ship yards, airports*
	Tourism & recreation areas	Tourism & recreation sites with a substantial footprint *Ski areas, golf courses, beach resorts, cricket fields, county parks, campgrounds*
	Unspecified development	
Agriculture & aquaculture		**Threats from farming & ranching as a result of agricultural expansion & intensification, including silviculture, mariculture, & aquaculture**
	Annual & perennial non- timber crops	Crops planted for food, fodder, fiber, fuel, or other uses *Farms, household swidden plots, plantations, orchards, vineyards, mixed agroforestry systems*
	Wood & pulp plantations	Stands of trees planted for timber or fiber outside of natural forests, often with non-native species, *Teak or eucalyptus plantations, silviculture, christmas tree farms*
	Livestock farming & ranching	Domestic terrestrial animals raised in one location on farmed or nonlocal resources (farming); also domestic or semi-domesticated animals allowed to roam in the wild & supported by natural habitats (ranching) *Cattle feed lots, dairy farms, cattle ranching, chicken or duck farms, goat, camel, or yak herding*
	Marine & freshwater aquaculture	Aquatic animals raised in one location on farmed or nonlocal resources; also hatchery fish allowed to roam in the wild *Shrimp or fin fish aquaculture, fish ponds on farms, hatchery salmon, seeded shellfish beds, artificial algal beds*

	Non specified	
Energy production & mining		**Threats from production of non-biological resources**
	Oil & gas drilling	Exploring for, developing, & producing petroleum & other liquid hydrocarbons *Oil wells, deep sea natural gas drilling*
	Mining & quarrying	Exploring for, developing, & producing minerals & rocks *Coal mines, alluvial gold panning, gold mines, rock quarries, coral mining, deep sea nodules, guano harvesting*
	Renewable energy	Exploring, developing, & producing renewable energy *Geothermal power production, solar farms, wind farms (including birds flying into wind turbines), tidal farms*
	Unspecified	
Transportation & service corridors		**Threats from long, narrow transport corridors & the vehicles that use them including associated wildlife mortality**
	Roads & railroads	Surface transport on roadways & dedicated tracks *Highways, secondary roads, logging roads, bridges & causeways, road kill, fencing associated with roads, railroads*
	Utility & service lines (e.g., pipelines)	Transport of energy & resources *Electrical & phone wires, aqueducts, oil & gas pipelines, electrocution of wildlife*
	Shipping lanes	Transport on & in freshwater & ocean waterways *Dredging, canals, shipping lanes, ships running into whales, wakes from cargo ships*
	Aircraft flight paths	Air & space transport *Flight paths, jets impacting birds*
	Unspecified	
Biological resource use		**Threats from consumptive use of "wild" biological resources including deliberate & unintentional harvesting effects; also persecution or control of specific species**
	Hunting & collecting terrestrial animals	Killing or trapping terrestrial wild animals or animal products for commercial, recreation, subsistence, research or cultural purposes, or for control/persecution reasons; includes accidental mortality/bycatch *Bush meat hunting, trophy hunting, fur trapping, insect collecting, honey or bird nest hunting, predator control, pest control, persecution*
	Gathering terrestrial plants	Harvesting plants, fungi, & other non-timber/non-animal products for commercial, recreation, subsistence, research or cultural purposes, or for control reasons

		Wild mushrooms, forage for stall fed animals, orchids, rattan, control of host plants to combat timber diseases
	Logging & wood harvesting	Harvesting trees & other woody vegetation for timber, fiber, or fuel *Clear cutting of hardwoods, selective commercial logging of ironwood, pulp operations, fuel wood collection, charcoal production*
	Fishing & harvesting aquatic resources	Harvesting aquatic wild animals or plants for commercial, recreation, subsistence, research, or cultural purposes, or for control/persecution reasons; includes accidental mortality/bycatch *Trawling, blast fishing, spear fishing, shellfish harvesting, whaling, seal hunting, turtle egg collection, live coral collection, seaweed collection*
	Unspecified	
Human intrusions & disturbance		**Threats from human activities that alter, destroy & disturb habitats & species associated with non- consumptive uses of biological resources**
	Recreational & tourism activities	People spending time in nature or traveling in vehicles outside of established transport corridors, usually for recreational reasons *Off-road vehicles, motorboats, jet-skis, snowmobiles, ultralight planes, dive boats, whale watching, mountain bikes, hikers, birdwatchers, skiers, pets in rec areas, temporary campsites, caving, rock-climbing*
	(Para)military activities	Actions by formal or paramilitary forces without a permanent footprint *Armed conflict, mine fields, tanks & other military vehicles, training exercises & ranges, defoliation, munitions testing*
	Unspecified/others	People spending time in or travelling in natural environments for reasons other than recreation or military activities *Law enforcement, drug smugglers, illegal immigrants, species research, vandalism*
Natural system modifications		**Threats from actions that convert or degrade habitat in service of "managing" natural or semi-natural systems, often to improve human welfare**
	Fire & fire suppression	Suppression or increase in fire frequency and/or intensity outside of its natural range of variation *Fire suppression to protect homes, inappropriate fire management, escaped agricultural fires, arson, campfires, fires for hunting*
	Dams & water management/use	Changing water flow patterns from their natural range of variation either deliberately or as a result of other activities

		Dam construction, dam operations, sediment control, change in salt regime, wetland filling for mosquito control, levees & dikes, surface water diversion, groundwater pumping, channelization, artificial lakes
	Unspecified/others	Other actions that convert or degrade habitat in service of "managing" natural systems to improve human welfare *Land reclamation projects, abandonment of managed lands, rip-rap along shoreline, mowing grass, tree thinning in parks, beach construction, removal of snags from streams*
Invasive & other problematic species & genes		**Threats from non-native & native plants, animals, pathogens/microbes, or genetic materials that have or are predicted to have harmful effects on biodiversity following their introduction, spread and/or increase in abundance**
	Invasive non-native/alien species	Harmful plants, animals, pathogens & other microbes not originally found within the ecosystem(s) in question & directly or indirectly introduced & spread into it by human activities *Feral cattle, household pets, zebra mussels, Dutch elm disease or chestnut blight, Miconia tree, introduction of species for biocontrol, Chytrid fungus affecting amphibians outside of Africa*
	Problematic native species	Harmful plants, animals, or pathogens & other microbes that are originally found within the ecosystem(s) in question, but have become "out of balance" or "released" directly or indirectly due to human activities *Overabundant native deer, overabundant algae due to loss of native grazing fish, native plants that hybridize with other plants, plague affecting rodents*
	Introduced genetic material	Human-altered or transported organisms or genes *Pesticide resistant crops, hatchery salmon, restoration projects using nonlocal seed stock, genetically modified insects for biocontrol, genetically modified trees, genetically modified salmon*
	Unspecified	
Pollution		**Threats from introduction of exotic and/or excess materials or energy from point & nonpoint sources**
	Household sewage, urban waste water	Water-borne sewage & nonpoint runoff from housing & urban areas that include nutrients, toxic chemicals and/or sediments *Discharge from municipal waste treatment plants, leaking septic systems, untreated*

		sewage, outhouses, oil or sediment from roads, fertilizers & pesticides from lawns & golf-courses, road salt
	Industrial & military effluents	Water-borne pollutants from industrial & military sources including mining, energy production, & other resource extraction industries that include nutrients, toxic chemicals and/or sediments *Toxic chemicals from factories, illegal dumping of chemicals, mine tailings, arsenic from gold mining, leakage from fuel tanks, PCBs in river sediments*
	Agricultural & forestry effluents	Water-borne pollutants from agricultural, silvicultural, & aquaculture systems that include nutrients, toxic chemicals and/or sediments including the effects of these pollutants on the site where they are applied *Nutrient loading from fertilizer runoff, herbicide runoff, manure from feedlots, nutrients from aquaculture, soil erosion*
	Garbage & solid waste	Rubbish & other solid materials including those that entangle wildlife *Municipal waste, litter from cars, flotsam & jetsam from recreational boats, waste that entangles wildlife, construction debris*
	Air-borne pollutants	Atmospheric pollutants from point & nonpoint sources *Acid rain, smog from vehicle emissions, excess nitrogen deposition, radioactive fallout, wind dispersion of pollutants or sediments, smoke from forest fires or wood stoves*
	Excess heat, sound, light	Inputs of heat, sound, or light that disturb wildlife or ecosystems *Noise from highways or airplanes, sonar from submarines that disturbs whales, heated water from power plants, lamps attracting insects, beach lights disorienting turtles, atmospheric radiation from ozone holes*
	Unspecified	
Geological events		
	Volcanoes	Volcanic events *Eruptions, emissions of volcanic gasses*
	Earthquakes/tsunamis	Earthquakes & associated events *Earthquakes, tsunamis*
	Avalanches/landslides	Avalanches or landslides *Avalanches, landslides, mudslides*
	Unspecified	
Climate change & severe weather		**Long-term climatic changes that may be linked to global warming & other severe climatic or weather events outside the natural range of variation that could wipe out a vulnerable species or habitat**

	Habitat shifting & alteration	Major changes in habitat composition & location *Sea-level rise, desertification, tundra thawing, coral bleaching*
	Droughts	Periods in which rainfall falls below the normal range of variation *Severe lack of rain, loss of surface water sources*
	Temperature extremes	Periods in which temperatures exceed or go below the normal range of variation *Heat waves, cold spells, oceanic temperature changes, disappearance of glaciers/sea ice*
	Storms & flooding	Extreme precipitation and/or wind events or major shifts in seasonality of storms *Thunderstorms, tropical storms, hurricanes, cyclones, tornados, hailstorms, ice storms or blizzards, dust storms, erosion of beaches during storms*
	Unspecified	

8.7 Appendix 7 – Published version of Chapter 6

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Dichotomy of mangrove management: A review of research and policy in the Mesoamerican reef region

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ABSTRACT

Mangroves are declining globally at faster rates than tropical forests and coral reefs, with primary threats including, aquaculture, agriculture and climate change. Mangroves provide ecosystem services to coastal communities of Mexico, Belize, Guatemala and Honduras, which comprise the Mesoamerican Reef (MAR) ecoregion. Over the past two decades mangroves within the MAR have declined. Current estimates of mangrove cover in the region suggest that mangroves cover 239,176 ha of the MAR, equivalent to 1.7% of the world's mangroves. Concerted efforts to manage, conserve and protect mangrove forest are apparent in all four countries. Comprehensive laws that prohibit the cutting and clearing of mangroves have been implemented in Mexico, Guatemala and Honduras. Belize has a permitting system to regulate mangrove alterations. In addition, a total of seven international and regional agreements have been ratified. Across the ecoregion, forty-three protected areas have been designated that contain mangroves, providing protection to 111,396 ha of mangroves (47% of the total). However, our findings suggest a lack of transparency in the governance framework, a disconnect between management and research, and geopolitical differences have all played a role in reducing management efficacy. A key finding of our study reveals a distinct division in the perceived major threats to mangroves between Ramsar site managers and researchers. Ramsar site managers identify anthropogenic disturbances as key threats, while in contrast, the bulk of research focuses on natural disturbances. To promote the inclusion of evidence-based research within mangrove management plans, greater efforts to connect these important stakeholders are required.

1. Introduction

Mangroves are a diverse group of halophytic plant species, which form highly productive forests in the area between mean sea level and the highest spring tide mark along tropical and sub-tropical coastlines and estuaries (Tomlinson, 1994). Once perceived as mosquito infested wastelands, mangroves have now been recognized as highly productive and ecologically important ecosystems. Providing ecosystem services to marine and terrestrial environments, and human societies (Gilman et al., 2008; Nagelkerken et al., 2008), which are valued at US $9900–35,900 ha^{-1}yr^{-1} (Costanza et al., 1997; Sathirithai and Barbier, 2001; Barbier, Hacker, Kennedy, Kock, Stier, 2011). Some of the most important mangrove ecosystem services include: coastline protection (in particular storm, hurricane and tsunami protection); waste water treatment; production of extractable materials; and provision of cultural sites (Rönnbäck et al., 2007; Warren-Rhodes et al., 2011). Despite the known value of these forests, mangroves are highly threatened. Deforestation estimates suggest mangrove cover has declined by 30–86% since the mid 1990's (Duke et al., 2007), and mangroves continue to decline globally at unprecedented rates (FAO, 2007). Globally the main threats to mangrove forests include: coastal development; logging for timber and fuel; aquaculture; salt extraction; and agriculture (Valiela et al., 2001; Alongi, 2002; Rönnbäck et al., 2007). The additional threats of climate change, e.g. sea-level rise, are also of concern (Schaeffer-Novelli et al., 2016; Short et al., 2016). Understanding if or how mangroves can adapt to such changes is of particular relevance to already threatened ecosystems, e.g. in the Caribbean (Godoy and De Lacerda, 2015; Sasmito et al., 2016).

The majority (over 70%) of mangroves are located within developing countries (Giri et al., 2011), where limited resources and capacity can inhibit effective management. At the international level, a number of treaties and conventions afford some protection to mangroves (Macintosh and Ashton, 2002), for example: the Ramsar Convention (1974); the Cartagena Convention (1983); and the International Tropical Timber Agreement (2011). However, few of these treaties provide any effective legal protection and none of them address the

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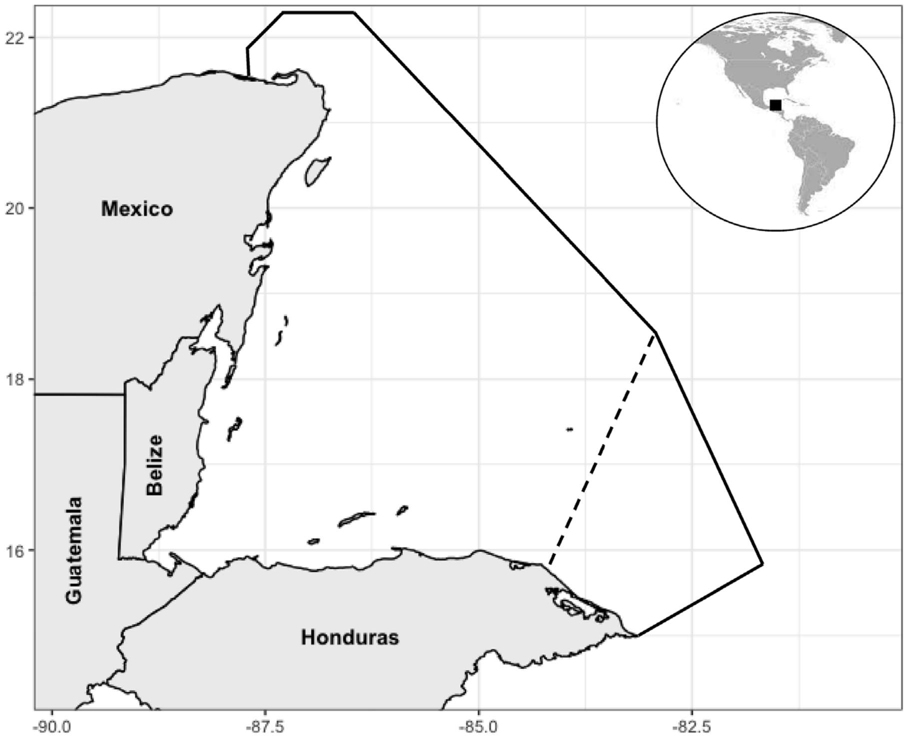

Fig. 1. Map of the Mesoamerican Reef Eco-region. Solid line highlights the area included within the study, the official boundary of the MAR (dotted line) does not include the eastern north shore of Honduras.

conservation, preservation, or management of a particular mangrove species (Polidoro et al., 2010). National legislation pertaining to mangrove management in the 1960's was primarily focused on mangrove exploitation (Carter et al., 2015). However, over the past five decades management has progressed which has led to the integration of mangroves into coastal zone management plans (Carter et al., 2015).

Common tools for the preservation and management of mangrove and other marine ecosystems include: marine protected areas (MPA's); nature reserves; wilderness areas; national monuments and national parks. Since 1974, increasing protection has been provided through Ramsar site designation. To date, 281 Ramsar sites (12.5% of all Ramsar sites) are intertidal forested wetlands, which includes mangrove forests (www.ramsar.org). Although increased recognition of mangroves in management plans is encouraging, the majority of plans associated with MPA's and Ramsar sites are based on generalized characteristics and threats, with limited reference to prior scientific research. In fact, there appears to be no effective mechanism for creating links between management activities for, and scientific research on, mangroves, thus research is rarely incorporated into management plans. Similar observations have been made in the management of coral reef ecosystems, where a mere 14% of information cited in management plans for the reefs of Australia, Kenya and Belize was primary research (Cvitanovic et al., 2014). In this case, research was deemed to be inaccessible to managers due to, long publication times, subscription only access to research and poor articulation of management implications of the research (Cvitanovic et al., 2014). Yet, for effective management to take place, evidence based decision-making is critical (Christensen et al., 1996; Ruckelshaus et al., 2008).

In this article we use the Mesoamerican reef (MAR) ecoregion as a case study, to examine the current status of mangroves, the legislation implemented to protect, manage and conserve mangroves, and review peer-reviewed scientific outputs from the region. The aim of this paper is to understand the current management paradigms within the MAR and identify threats to mangroves within the region. We compare the foci of management strategies and research programs in order to determine where overlap occurs and where there are gaps in the knowledge base.

2. Methods

2.1. Study area

We have chosen to focus on the Mesoamerican Reef (MAR) ecoregion because the majority of mangrove research is concentrated in South-East Asia, where larger and more diverse stands of mangroves are located (Saenger, 2002). Much less is known about these ecosystems in Latin America and the Caribbean (but see, Ellison and Farnsworth, 1997; Núñez-Farfán et al., 2002; Ellison, 2004). The MAR ecoregion extends over 1000 km from the Yucatan peninsula, Mexico (21.56°N; 087.09°W) to the east coast of Honduras (14.97°N; 083.16°W), encompassing the Caribbean coastlines, open-ocean, networks of cays, and offshore banks of Mexico, Belize, Guatemala and Honduras (Kramer and Kramer, 2002) (Fig. 1). It is home to the largest barrier reef in the western hemisphere and supports the livelihoods of approximately two million people (Kramer and Kramer, 2002), of particular importance are the fishing (Box and Canty, 2010) and tourism industries (Doiron and Weissenberger, 2014). Considerable attention has been given to coral reefs in the region, however seagrass and mangrove ecosystems have often been overlooked. In this review we consider the entire Honduran north shore as part of the MAR ecoregion, due to potentially high levels of connectivity between the Honduran east coast and the MAR (Butler et al., 2011; Truelove et al., 2015; Chollett et al., 2017). The boundaries of the ecoregion were originally defined by the presence of several physiogeographic boundaries, these include the Gulf of Mexico, strong oceanic currents between the Yucatan peninsular, Mexico and south west Cuba, the shallow waters of the Nicaraguan rise, Honduras, in addition to a number of terrestrial environmental variables, e.g. rainfall. The ecoregion was officially declared in 1997 as part of the Tulum agreement, where all four counties came together recognizing the importance of the region and the need to jointly manage a shared marine resource (Kramer and Kramer, 2002).

2.2. Mangrove cover estimations

First, we estimated mangrove forest cover for each country across the region. The three true mangrove species: *Rhizophora mangle; Avicennia germinans* and *Laguncularia racemosa* are considered as part of the mangrove forest system in all four countries. However, the mangrove associate *Conocarpus erectus* (Buttonwood mangrove) is only defined as part of the mangrove forest in Guatemala and Honduras. Regardless of a country's definition of the mangrove complex, mangrove cover estimates herein include all four species. Country specific estimates of mangrove cover were taken from the most recent estimates available (Mexico (Rodríguez-Zúñiga et al., 2013), imagery from 2010; Belize (Cherrington et al., 2010), imagery from 2010; Guatemala (MARN, 2013), imagery from 2010; and Honduras (Carrasco and Caviedes, 2014), imagery from 2008 to 2010).

2.3. Mangrove management plans

To ascertain the level of management and protection directly focused on mangroves in each country, we first reviewed national environmental legislation, using Google searches and accessing management plans. We subsequently identified which international and regional conventions and agreements relating to mangroves each country has signed or ratified. Within the Caribbean, protected areas that contain mangroves include Ramsar sites and Marine Protected Areas (MPAs). Ramsar sites that contain mangroves were identified through the American Ramsar Secretariat (Pers. Comms.) and the Ramsar website (www.ramsar.org). The Healthy Reefs for Healthy People Initiative (HRI; www.healthyreefs.org) provides the names of all of the MPAs within the MAR, which have marine territory, and provides the associated management plan. If a managment plan was not available on the HRI website a wider web search was conducted, if after the search we did not identify a management plan we assumed that one did not exist or is not publicly available. Web searches (in English and Spanish), were used to identify management plans for each of the named protected areas. Management plans for protected areas, where available, were downloaded and searched using the keywords mangroves (mangr*) in English, and manglar (mangl*) in Spanish to find explicit references to the management of mangroves. It must be noted that the most recent management plans were used in this review and that management plans within the region are generally designed for a five-year period. In many cases the management period had expired, but we assume that current management strategies are based on the most recent plans.

2.4. Scientific literature review

To determine the focus of scientific research on mangroves in the MAR, peer-reviewed scientific publications were searched for using the Boolean search methodology. Multiple combinations of the following keywords (and their equivalents in Spanish) were used in the search: 'Mangrove'; '*Rhizophora*'; '*Avicennia*'; '*Laguncularia*'; '*Conocarpus*'; 'Mesoamerica'; 'MBRS'; 'MAR'; 'Caribbean'; 'Mexico'; 'Belize'; 'Guatemala'; and 'Honduras'. Only articles published from 1997 to date were used, as this date coincides with the declaration of the MAR as an ecoregion by all four countries, and therefore to the direct management of the ecoregion. Books or book sections were not used, as we could not be sure of the peer-review process, and reviews were not included. Methodologies of articles were examined to ensure that research occurred in at least one of the four MAR countries and within the boundaries of the MAR ecoregion, as we delimited it. A total of 81 peer-reviewed publications (see supplementary materials for a full list of publications) were identified and the research undertaken in each country was tallied. Where research occurred in multiple countries in a single paper, each country received a tally.

2.5. Identification of threats

A fine scale analysis of articles that were identified to focus on threats to mangroves was conducted to categorize the type of threat. Eight different threats were identified, a total of 29 times, and each threat was categorized as either natural or anthropogenic disturbances. *Natural disturbances* were: hurricanes; sea-level change; light gaps; seismic activity; tsunamis; and subsidence. *Anthropogenic disturbances* were: commercial development and deforestation. Threats identified were tallied and a proportion of each threat category was calculated based on the total number of threats identified.

A list of threats to Ramsar sites was obtained from the American Ramsar Secretariat. The threats were identified by future managers of Ramsar sites from a list of 51 options supplied by Ramsar (see supplementary materials for the full list of threats and their definitions) during the Ramsar site application process. The list of threats provided was pre-defined, and as a result not all threats reported may be relevant to the protected area, e.g. in Guatemala 'agriculture and aquaculture' was a reported threat. However, aquaculture is currently not present in the Guatemalan Caribbean, in contrast agriculture is present and is considered a threat to mangroves.

Thirty-seven different threats were identified by Ramsar managers, across the four countries, a total of 236 times, with a maximum of twenty-two at a single site. We categorized threats as either natural disturbances or anthropogenic disturbances. *Natural disturbances* were: storms and flooding; fire and fire suppression; problematic native species; invasive and other problematic species and genes; climate change and severe weather; and invasive non-native/alien species. *Anthropogenic disturbances* were: biological resource use; human settlements (non-agricultural); tourism and recreation areas; housing and urban areas; fishing and harvesting aquatic resources; natural system modifications; agriculture and aquaculture; pollution; logging and wood harvesting; human intrusions and disturbances; hunting and collecting terrestrial animals; vegetation clearance/land conversion; recreational and tourism activities; gathering terrestrial plants; transportation and service corridors; water regulation; household sewage; livestock farming and ranching; urban waste water; agriculture and forestry effluents; drainage; dams and water management/use; energy production and mining; unspecified development; wood and pulp plantations; mining and quarrying; industrial and military effluents; water abstraction; garbage and solid waste; shipping lanes; and airborne pollutants. Individual threats that were reported were tallied as either natural or anthropogenic disturbances, a proportion of each threat category was calculated from the combined number of threats identified.

3. Results

3.1. Mangrove cover

Mangrove cover in the MAR is estimated at 239,176 ha, cover has declined across the region since the 1990's, where mangroves covered approximately 350,000 ha (Fig. 2), a loss of over 110,000 ha in a twenty-year period. Proportional cover of mangroves in the MAR region varies considerably between and within the four countries. The majority of mangrove cover within the MAR is located along the Yucatan Peninsula, Campeche and Quintana Roo regions of Mexico (53.5%; 128,049 ha; Fig. 2), however Mexico has significantly greater mangrove cover in the Gulf of Mexico and on the Pacific coastlines. Belize is the only country to have its entire coastline in the MAR, and approximately one third of mangrove cover of the MAR is found in Belize (31.2%; 74,684 ha; Fig. 2). Only a small fraction of the total mangrove cover of the region is located in Guatemala (0.5%; 1170 ha; Fig. 2), the majority of Guatemalan mangroves are located on the Pacific coast. Despite the

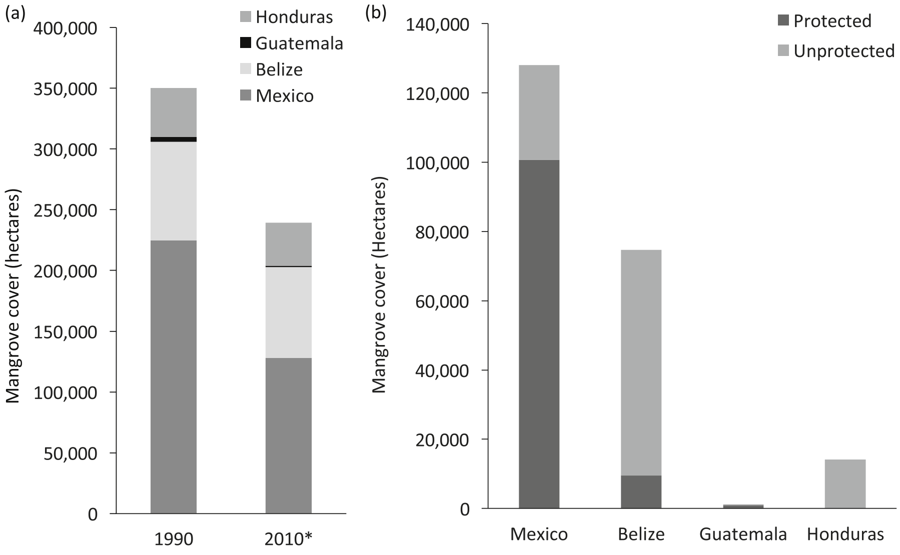

Fig. 2. Mangrove cover within the MAR region. (a) Historical (Kramer and Kramer, 2002) and recent estimations of mangrove cover. (b) Total mangrove cover in each of the four MAR countries, with hectares of protected and unprotected mangrove highlighted. (Mexico (Rodríguez-Zúñiga et al., 2013); Belize (Cherrington et al., 2010); Guatemala (MARN, 2013); Honduras (Carrasco and Caviedes, 2014). *Some data from Honduras is from 2008.

size of its coastline, mangrove cover in Honduras is a small proportion of the MAR total (14.7%; 35,273 ha; Fig. 2). Mangrove cover in Honduras is almost equally divided between the Caribbean and Pacific coasts.

3.2. Legislation and management

Comprehensive legislation exists within the region to protect mangroves. In Mexico, Guatemala and Honduras, mangroves are property of the state and stringent laws exist which prohibit the removal and cutting of mangroves and prevent changes in land use (Table 1). In contrast, the majority of Belizean mangroves are privately owned and only 30% are state owned. However, national legislation in Belize is applicable to all mangroves regardless of ownership. Within Belize, the cutting and clearance of mangroves is controlled by a permitting system, however the dredging and landfill of mangroves is only permitted under exceptional circumstances.

At the international level, the four countries of the MAR have ratified a total of seven international conventions and agreements to promote the management and sustainable use of marine and wetland resources (Table 1). The most important of these for mangroves is the Ramsar (wetlands) convention. Geopolitical differences influence regional cooperation, e.g. Mexico, a North American country, is excluded from Central American agreements, and Belize with a British rather than Spanish colonial heritage exhibits preferences with Caribbean Community agreements. All four countries are parties of the two main international conventions that are relevant to environmental protection: the Cartagena convention and Ramsar convention (Table 1). Honduras is the only country not to have ratified the Cartagena convention, but is a signatory to the convention. Additionally, all four countries ratified the Tulum declaration and the subsequent Mesoamerican barrier reef system project (www.mbrs.doe.gov.bz).

We identified a total of 43 protected areas in the MAR which have mangroves within their boundaries (Table 2), and estimate that just under half (46.6%; 111,396 ha) of the mangroves in the MAR are within the boundaries of a protected area (Fig. 2). Over two thirds (31) of the protected areas have management plans (Table 2), although implementation of these plans may vary. The majority of management plans had no specific management strategies for mangroves, other than a reference to the national legislation, in the few instances where strategies were stated they were related to mangrove restoration, e.g. Shipstern Conservation and Management Area, Belize.

In Mexico, mangroves are the responsibility of the Department of Ecology and Environment, and the Institute for Flora, Fauna and Culture within the Secretariat of the Environment and Natural Resources. In addition, the National Commission for Natural Protected Areas (CONANP) assumes responsibility for mangroves when they are located within a protected area. CONANP may co-manage protected areas with a local non-governmental organization (NGO). We identified 13 protected areas that contain mangroves in Mexico, these areas provide protection to approximately 80% (100,764 ha) of Mexican mangroves forests in the MAR (Table 2; Fig. 2).

In Belize, the Forestry Department within the Ministry of Agriculture and Fisheries is responsible for managing Belizean mangroves. The Coastal Zone Management Authority and Institute and Fisheries Department may also assume a management role. NGO's co-manage a number of protected areas in Belize and therefore assume a direct role in the management of mangroves. Private protected areas are increasingly popular, and these areas are coordinated by the Belize Association of Private Protected Areas. We were not able to identify any private protected areas that provided protection to mangroves. Only a small proportion (12.9%) of the total mangrove cover of Belize is located within the 15 protected areas (Table 2; Fig. 2).

Mangroves in Guatemala are the responsibility of the National Forest Institute within the Ministry of the Environment and Natural Resources. The National Council for Protected Areas (CONAP) has a role in mangrove management when mangroves are located in protected areas (Table 1). Protected areas are co-managed by CONAP and local NGO's and these organizations assume the day to day responsibilities of the protected areas. The majority of mangroves within Guatemala (88.2%) are located within the two protected areas (Table 2; Fig. 2).

The responsibility of mangroves in Honduras resides with the Department of Fisheries under the Secretariat of Energy, Natural Resources, Natural Environment and Mines, and local municipal environmental units have a role in mangrove management within their jurisdiction. Within protected areas, mangroves receive additional management from the Conservation and Forest Development, Protection and Wildlife Institute and local NGO's. The NGO's assume the day-to-day responsibilities of the protected areas. A total of 13 protected areas have been declared that have mangroves within their boundaries, however limited mangrove cover data is available, which precludes an accurate estimation of mangrove coverage within Honduran protected areas (Table 2).

3.3. Threats to mangroves

A total of 81 peer-reviewed articles focusing on mangroves were

Table 1
Legislation, agreements and protection of mangroves in the Mesoamerican reef region.

Mangrove Legislation		**Mexico**	**Belize**	**Guatemala**	**Honduras**
Legislation		General Wildlife Act 2000, Article 60.	Forestry Act 1989, Article 52. Forests Act Chapter 213, revised in 2003	Forestry Act 1996, Article 35.	Fisheries Act 1959, Article 52.
		It is prohibited to remove, transplant, prune or conduct any work or activity that may affect the integrality of the hydrological flow of mangroves.	Dredging and landfill is strictly prohibited unless there is significant benefit to the general population. Three types of permits can be issued for the alteration of mangroves, depending on the area of mangrove to be altered. Permits can be denied.	Change of land use of mangrove ecosystems is prohibited. By-law Resolution No. 01.25.98, Article 15 allows family consumption to a maximum of $5\,m^3\,yr^{-1}$	The removal and cutting of mangroves is prohibited.
State ownership of mangroves		100%	30%	100%	100%
Government Agencies					
Government hierarchy for the management of mangroves	*Ministry*	Secretariat of the Environment and Natural Resources	Ministry of Agriculture and Fisheries	Ministry of the Environment and Natural Resources	Secretariat of Energy, Natural Resources, Natural Environment and Mines
	Department	Department of Ecology and Environment; Institute for Flora, Fauna and Culture	Department of Forestry	National Forest Institute	Fisheries department
	External departments		Coastal Zone Management Authority and Institute; Department of Fisheries	National Council for Protected Areas	Institute for Conservation and Forest Development, Protected Areas and Wildlife
	Other Agencies	National Commission for Protected Natural Areas		National Council for Protected Areas	Local Municipal Environment Units
	Non-government organizations	e.g. Comunidad y Biodiversidad Asociacion Civil; Amigos de Sian Ka'an	e.g. Belize Association of Private Protected Areas; Toledo Institute for Development Environment	e.g. Fundación para el Ecodesarrollo y la Conservación	e.g. Bay Island Conservation Association; Roatan Marine Park
International and Regional Agreements					
Cartagena Convention (*Signatory only)		1985	1999	1989	1983*
Wetlands Convention (Ramsar)		1986	1998	1990	1993
Tulum Agreement		1995	1995	1995	1995
Mesoamerican Barrier Reef System Project		1997	1997	1997	1997
Central American Policy for the Conservation and Rational Use of Wetlands		N/A	2002	2002	2002
Ramsar Regional Initiative for the Integral Management and Wise use of Mangroves and Coral Reefs		2009	–	2009	2009
Ramsar Caribbean Wetlands Initiative		–	2009	–	–

Table 2
Protected areas of the Mesoamerican Reef ecoregion with mangroves within their borders.

	MPA/NP	Ramsar site	Management plan	Reference
Mexico (n = 13)				
Área de Protección de Fauna y Flora Yum Balam	X	X	Y	(CONANP, 2013)
Parque Nacional Isla Contoy	X	X	Y	(SEMARNAT & CONANP, 2015b)
Manglares de Nichupte		X	Y	(SEMARNAT & CONANP, 2014)
Parque Nacional Arrecifes de Puerto Morelos	X	X	Y	(SEMARNAP, 2000a)
Manglares y humedales del norte de la isla Cozumel		X	Y	(SEMARNAT, 2014)
Parque Marino Nacional Arrecifes de Cozumel	X	X	Y	(SEMARNAP, 1998a)
Playa Tortuguera X'Cacel-X'Cacelito		X	–	
Reserva de la Biósfera de Sian Ka'an	X	X	Y	(SEMARNAT & CONANP, 2015a)
Reserva de la Biósfera Banco Chinchorro	X	X	Y	(SEMARNAP, 2000b)
Parque Nacional Arrecifes de Xcalak	X	X	Y	(CONANP, 2004)
Parque Marino Nacional Punta Occidental Isla Mujeres, Punta Cancun y Punta Nizuc	X		Y	(SEMARNAP, 1998b)
Área Marina y Costera Protegida Actam Chuleb	X		–	
Zona Sujeta de Conservación Ecologica Santuario Manati Bahia Chetumal	X		–	
Total:	*10*	*10*	*10*	
Belize (n = 14)				
Bacalar Chico National Park and Marine Reserve	X		Y	(BFD, 2004)
Laughing Bird Caye National Park	X		Y	(BFoD, 2010)
Payne's Creek National Park	X		–	
Sarstoon-Temash National Park	X	X	Y	
Shipstern Conservation & Management Area	X		Y	(PACT, 2016)
Corozal Bay Wildlife Sanctuary	X		–	
Swallow Caye Wildlife Sanctuary	X		–	
Half Moon Caye Natural Monument	X		Y	(BAS, 2007)
Caye Caulker Marine Reserve	X		Y	(BCZMIA & BFD, 2004)
Gladden Spit and Silk Cayes Marine Reserve	X		Y	(BFD, 2010a)
Glover's Reef Marine Reserve	X		Y	(BFD, 2007)
Hol Chan Marine Reserve	X		Y	(BFD, 2002)
Port Honduras Marine Reserve	X		Y	(BFD, 2012a)
Sapodilla Cayes Marine Reserve	X		Y	(BFD, 2010b)
South Water Caye Marine Reserve	X		Y	(BFD, 2009)
Turneffe Atoll Marine Reserve	X		Y	(BFD, 2012b)
Total:	*15*	*1*	*12*	
Guatemala (n = 2)				
Reserva de usos multiples rio Sartsun	X	X	Y	(CONAP, 2009)
Punta de Manabique	X	X	Y	(CONAP, 2011)
Total:	*2*	*2*	*2*	
Honduras (n = 13)				
Parque Nacional Sistema de Humidales de Cuyamel – Omoa	X	X	–	
Parque Nacional Jeannette Kawas	X	X	Y	(ICF, 2012a)
Refugia de Vida Silvestre Punto Izopo	X	X	Y	(ICF, 2012b)
Sistema Humedales Laguna de Zambuco		X	–	
Refugio de Vida Silvestre Cuero y Salado (Barras de Cuero y Salado)	X	X	Y	(ICF, 2011)
Parque Nacional de las islas de la Bahia	X		Y	(IHT y ICF, 2015)
Zona de Proteccion Especial Marina Turtle Harbour – Rock Harboury el Sistema de Humedales de la Isla de Utila	X	X	Y	(IHT y ICF, 2012)
Zona de Protección Especial Marina Sandy Bay West End	X		–	
Parque Nacional Port Royal	X		–	
Monumento Natural Marino Archipielago Cayos Cochinos	X		Y	(CMCC, 2009)
Refugio de Vida Silvestre Laguna de Guaimoreto	X		–	
Reserva de la Biósfera del Rio Platano	X		Y	(ICF, 2013)
Laguna de Bacalar		X	–	
Total:	*11*	*7*	*7*	
Grand totals **43**	**38**	**18**	**31**	

identified within the MAR region. The majority of the research was conducted in Belize (68.2%), the remaining studies were conducted in Mexico (22.0%) and Honduras (9.8%). No peer-reviewed primary mangrove research identified from Guatemala. Of the 81 peer-reviewed articles identified, 15 of these address threats to mangroves (Ellison and Farnsworth, 1997; Feller et al., 1999; Cahoon et al., 2003; Piou et al., 2006; Mckee, Cahoon and Feller, 2007; McKee, Rooth and Feller, 2007; Taylor et al., 2007; Vaneslow et al., 2007; Granek and Ruttenberg, 2007; Carrillo-Bastos et al., 2008; Islebe et al., 2009; Macintyre et al., 2009; Mckee and Vervaeke, 2009; Hirales-Cota et al., 2010; McCloskey and Liu, 2013), a total of 8 different threats were classified. A total of 37 different threats, were identified from the 20 Ramsar sites, the majority of which were anthropogenic (90.7%), e.g. 'logging', 'aquaculture and coastal development' (Fig. 3). The majority of peer-reviewed mangrove research from the MAR region has focused on natural disturbances (71.4%) of mangrove systems (Fig. 3). These trends are not just a regional trend, but hold for each of the individual countries, where researchers and managers foci are on natural and anthropogenic disturbances, respectively (Fig. 3). Primary research interests include hurricanes and sea -level change, and Ramsar managers across the region are concerned with deforestation, agriculture, and development.

4. Discussion

Despite the stringent national legislation and international agreements which provide protection to mangrove forests, and the additional protection provided by the 43 protected areas (which contain mangroves), mangrove cover in the MAR declined by over 110,000 ha from 1990 to 2010, with an estimated current cover of 239,176 ha, equivalent to 1.7% of the world's mangroves (Giri et al., 2011). The greatest

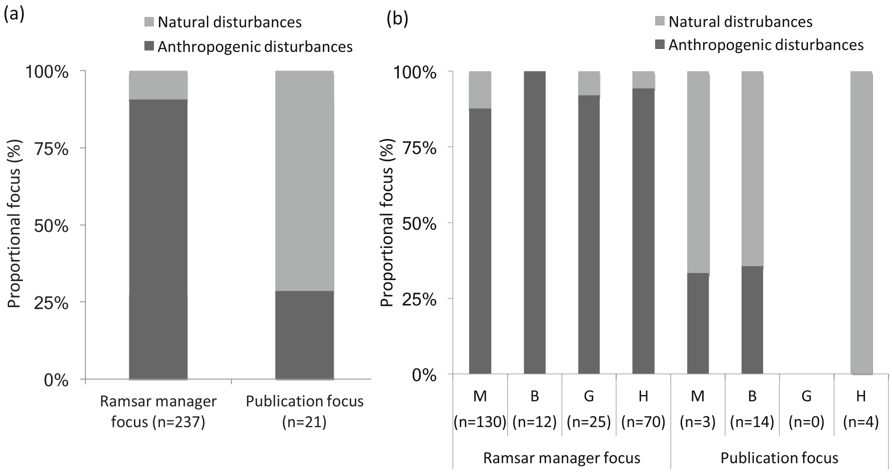

Fig. 3. Threats to mangroves of the MAR as identified by Ramsar managers and within peer-reviewed publications (a) throughout the MAR; and (b) individual countries: M – Mexico; B – Belize; G – Guatemala; and H - Honduras.

losses were observed in Mexico and Honduras. The decline in mangrove cover suggests a problem with enforcement. We suggest a lack of resources for enforcement, transparency within the governance framework, and lack of political will as potential reasons for the failure in the enforcement of mangrove legislation. The number of organizations responsible for the management and protection of mangroves in each country varies and causes confusion, with the exact role of each party unclear. Each country has a specific government department responsible for mangrove protection, with additional oversight from external agencies and non-government organizations (NGO's) when mangroves are located in protected areas. It must be noted that such discrepancies are not unique to mangrove systems or to this region (Rife et al., 2013). Limited national budgets of the four countries reduce governmental institutional capacity, which has resulted in civil society in the form of NGO's filling the void in the management of protected areas. NGO's assume an important role as co-managers of protected areas, fulfilling the day-to-day management duties. However, a lack of authoritative power and a lack of human capacity to physically patrol often large and remote areas, inhibits the ability of NGO's to enforce environmental legislation (Cudney-Bueno et al., 2009; Rife et al., 2013). In essence many of the protected areas in each of the four countries could be considered “paper parks”, as they provide no greater protection or management to mangroves than national legislation (Rife et al., 2013). It is important not to be too critical of these institutions, however, all of which are operating on limited resources. The focus should be on how to support and build capacity of these organizations to allow them to improve mangroves and natural resource management efficacy.

Geopolitical interests of the different countries have reduced collaborative efforts of mangrove protection. Despite the four countries sharing an ecoregion, significant geopolitical divisions exist. This is exemplified by Belize ratifying a separate Ramsar initiative to the other three countries. The paradox is that despite having the same or very similar objectives, the four countries are not working together to achieve these goals. A lack of collaboration and harmonization in how management strategies are developed and implemented can reduce mangrove protection, especially in forests that straddle international borders (McCallum et al., 2015). Belize is the only country where all of mangroves are within the boundaries of the MAR. In contrast Mexico and Guatemala have significantly greater mangrove cover on other coastlines, and a little more than half of the mangrove cover of Honduras is concentrated within the Gulf of Fonseca, on the Pacific coast. Threats to mangroves may vary significantly on the different coasts, and therefore influence how national mangrove legislation is developed, and how governments prioritize limited management resources. Regardless, greater collaborative efforts, such as the Mesoamerican Barrier Reef System Project, need to be established to promote the protection of marine resources, and facilitate transboundary initiatives that recognize that ecological populations do not align with geopolitical boundaries. There is a high probability that mangrove forests within the region are connected as recent studies have shown high levels of ecological connectivity in the MAR region for lobster, fish and corals (Butler et al., 2011; Truelove et al., 2015; Chollett et al., 2017).

Evidence based decision-making has been well documented as an important component of resource management (Christensen et al., 1996; Ruckelshaus et al., 2008). However, in the papers we reviewed there appears to be no discernible link between researcher recommendations and resource manager decision-making or actions. Concluding statements within articles may make some reference to conservation or management, but usually included no advice on how to apply research findings directly to management. Additionally, our study identified a disconnection between Ramsar site managers and the scientific community. Managers were primarily focused on localized anthropogenic threats (e.g. Macintyre et al. (2009)), while researchers focused on natural disturbances, such as hurricane events (Vaneslow et al., 2007) and the impact of sea-level change (Mckee, Cahoon and Feller, 2007). Both anthropogenic and natural threats have either had, or have, the potential to negatively affect mangrove cover, but the different foci of researchers and managers is likely to hinder progress in mitigating threats from either source.

It is crucial that researchers and managers increase their communication and work together to understand the full complexity of the threats to mangrove forests. Combining these different priorities could bring important benefits. For example, the identification of areas of mangrove forests resilient to climate change can focus management efforts and create local priority conservation zones where anthropogenic disturbances should be minimized. Both groups are focusing on important issues, however the assumed lack of dialogue between stakeholders precludes the integration of science into mangrove management plans. Cvitanovic et al. (2014) have reported similar disconnects in the management of coral dominant marine protected areas. They proposed knowledge brokers, boundary organizations, knowledge co-production and management-orientated summaries in research articles as potential solutions to provide managers access to scientific outputs. The HRI program has put some of these in place within the MAR primarily focused on coral reefs, but these could be adapted to facilitate greater communications between managers to promote science lead mangrove management. In addition, discussion forums exist, such as the mangrove list (majordomo@essun1.murdoch.edu.au). List serves provide a forum where individuals can pose questions to experts in an array of different fields and can provide useful dialogue between practitioners and researchers.

These potential solutions provide important links between peer-reviewed conservation science and conservation managers, but the dichotomy of researcher and manager foci must also be addressed. Combining current research interests of natural disturbances with local management concerns of anthropogenic stresses, in particular the understanding of local drivers of deforestation, is critical. However, if institutional capacity is lacking, then the implementation of management strategies will always be problematic. Building capacity within and among government departments and NGO's to ensure the effective enforcement of legislation and promote links with the scientific community to facilitate science-based decision-making is vital for the management of mangroves in the MAR, and elsewhere. It is important that managers have access to and make use of current research, especially when developing management plans (Adeel and Pomeroy, 2002; Iftekhar and Islam, 2004; Schmitt and Duke, 2015). There is also an onus on researchers to increase the availability of their research to management authorities, not just government agencies, potentially through regional online archives or data repositories. Additionally, researchers should engage managers prior to conducting their research to foster a dialogue that can promote mangrove management and conservation efforts. Promoting public awareness to garner political will is also important, and a greater understanding of the ecosystem services provided by mangroves to local communities and their inclusion in management has the potential to increase the protection and conservation of mangroves (Shunula, 2002; Sudtongkong and Webb, 2008; Datta et al., 2012).

We propose the following recommendations to promote management of mangroves within the region:

(1) Coordinated and detailed mapping projects in Belize and Honduras to provide more recent estimates of mangrove cover that can be used to set baselines from which management actions can be monitored and assessed;
(2) The implementation of a systematic, harmonized, mangrove monitoring protocol throughout the region that will facilitate comparisons of mangrove forest status;
(3) A program of work to increase understanding of the connectivity of mangrove populations throughout and beyond the MAR ecoregion, which can then be used to identify areas where greater collaborations are needed;
(4) The creation of a repository of scientific literature of the region to which researchers can submit their research, making it available for practitioners in the region and providing another step towards an increased dialogue between managers and the scientific community.

Our proposals require coordination and management of resources and information across the MAR. The HRI program already brings together stakeholders from across the region, but at present is heavily coral reef focused. Mangrove coverage was a key indicator within the original HRI guide (McField and Kramer, 2007), and therefore could become part of the biennially produced report card, which provides stakeholders an update on the status of marine resources. Our suggestion is that the network of contacts and collaborations within this program could be used to facilitate more coordinated monitoring and assessment of mangroves and seagrass ecosystems in the region.

5. Conclusion

The stringent national legislation and international agreements which should provide protection to mangrove forests within the MAR are ineffective. A number of local anthropogenic stressors threaten mangrove forests, and despite comprehensive legislation, mangrove cover has declined in all four countries. Capacity building of government and non-government institutions is required, as a lack of capacity has reduced environmental regulation enforcement. Local anthropogenic stressors are of greatest concern to managers of protected areas, whilst scientific research is focused on natural disturbances, primarily climate change. These different focuses can be advantageous if they can be linked effectively. For example, the identification of climate change resilient mangrove forests can channel mangrove management efforts to maximize effectiveness of limited resources. Greater understanding of drivers of local anthropogenic threats to mangroves is required to provide managers with the necessary tools to reduce these threats and promote mangrove forests and the ecosystem services they provide. To promote successful management, we suggest the reinforcement of institutional capacity, enhance links between government departments and civil society and increase science-based decision-making within protected areas management plans.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2018.02.011.

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