Linking human impacts to recent declines in coral reef fish communities in the Bay Islands

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ABSTRACT

The Bay Islands of Honduras are home to hundreds of species of fishes, and vast areas of coral reefs, seagrass, and mangroves. While protection for the area was nationally established in 2003 and in 2010; numerous anthropogenic impacts persist (e.g., fishing, coastal development, land-based pollution, and tourism) and a decline of -44 to -56% of reef fish biomass was reported by the Healthy Reefs Initiative (HRI) in 2020. Underwater visual surveys on SCUBA (n = 4,101) were used to assess reef fish biomass and community composition in shallow coral reefs (0 – 30 m), across 83 sites in the Bay Islands from 2006 to 2021. Anthropogenic impact (fisheries, coastal development, changing population and demographic, land-based pollution, tourism, and climate change) were assessed. Both the rates of declines in reef fish biomass and intensity of anthropogenic impacts differed across the four subregions of Cayos Cochinos, Guanaja, Roatan, and Utila. Our results highlight declines in total and herbivorous reef fish biomass, as well as low quantities of commercially valuable reef fish (e.g., snappers and groupers). Fish assemblages in the Bay Islands are dominated by herbivorous fishes, and contributions from targeted fish species is very low (<5%). To mitigate further losses of reef fish biomass and address ongoing human impacts, four recommendations are provided including: i) begin government-led enforcement; ii) implement size and catch restrictions and record-keeping; iii) reduce sedimentation and land-based pollution; and iv) increase capacity for local organizations. Amplified initiatives to reduce human impacts that are degrading coral reef fish communities are integral to allow the recovery of fish populations and to sustain communities in the Bay Islands for years to come.

Keywords: biomass decline, marine management, community structure, Meso-American reef, reef fishes, Western Caribbean

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"There's no other place anywhere near this place just like this place, so this must be the place"
– Utila proverb

ABBREVIATIONS

AGRRA = Atlantic Gulf Rapid Reef Assessment

BICA = Bay Islands Conservation Association

BINMP = Bay Islands National Marine Park

CIP = coastal Indigenous people(s)

DIGEPESCA = Department of Fisheries in Honduras

HCRF = Honduran Coral Reef Fund

HRI = Healthy Reefs for Healthy People Initiative

ICF = Institute of Forestry and Conservation in Honduras

IHT = Institute of Tourism in Honduras

MAR = Meso-American barrier reef

MPA = marine protected area

RMP = Roatan Marine Park

SBMR = Sandy Bay Marine Reserve

SIDS = small island developing state

SST = sea surface temperature

TL = total length

W = weight

UVS = underwater visual survey

1. INTRODUCTION

1.1 Global threats to coral reef fishes

Globally, coral reefs and their species assemblages are under threat from numerous anthropogenic and climatic stressors. Coral reef ecosystems are the most structurally complex marine environment and provide a disproportionately large contribution to biodiversity and ecosystem services for their given space occupied in the global ocean (Pandolfi et al. 2003). Millions of people, including coastal and island communities and Indigenous peoples, rely on coral reefs for food provision (e.g., fisheries), livelihoods (e.g., tourism), and for regulative processes (e.g., storm protection) (Woodhead et al. 2019; Eddy et al. 2021; Sala et al. 2021). Reefs provide critical livelihoods for millions of people (Kittinger et al. 2015), and support one-quarter of the world's small-scale fishers (Darling and D'agata 2017). Despite the bounty of benefits derived from these vulnerable ecosystems, most reefs are loosing the capability of continuing to provide essential services because of overfishing, climate change, habitat destruction, and pollution (Eddy et al. 2021). These stressors have intensified in the recent Anthropocene, a period where humans are the major drivers of environmental change and where ecosystems reflect socio-economic and cultural influences as opposed to being shaped by biophysical characteristics that once governed their state (Woodhead et al. 2019; Williams et al. 2019). As humans have the greatest influence on these vulnerable marine ecosystems, decision-makers must consider the delicate balance of protecting coral reefs and continuing to extract resources for social and economic purposes (Teh et al. 2013), as well as aim to strengthen governance to ensure sustainable livelihoods in coastal and island societies (Darling and D'agata 2017).

Humans have removed, altered, and destroyed many natural habitats (Halpern et al. 2008; Mora, 2008), accelerated loss of populations and species (Worm et al. 2006; Ward-Paige et al. 2010), decreased abundance and diversity (Pandolfi et al. 2003), and caused widespread changes in reef ecosystems over the past two centuries (Hughes et al. 2003). On reefs around the world, people have caused pervasive ecosystem effects by severely reducing fish biomass, altering sedimentation and nutrient inputs, re-structuring microbial communities, promoting disease-causing bacteria and viruses via the addition of plastic waste with unique biotopes, and influencing species biogeography with the introduction of invasive species (Williams et al. 2019). Anthropogenic activities at a global scale have increased the intensity and frequency of some stressors, such as marine heatwaves, ocean acidification, and physical damage from storms (Woodhead et al. 2019). The scale of impacts from major anthropogenic drivers has grown exponentially with growing human populations, increased globalization, and improved storage and transport systems (Hughes et al. 2003). The multiple human impacts on reef ecosystems are inherently linked to underlying social, economic, and cultural drivers (Williams et al. 2019), and the demand on reef resources is a result of the needs of coastal communities and the desires of the global population.

Although the footprint of human impacts on coral reef ecosystems is well documented world-wide (Williams et al. 2019), the severe degredation which threatenes the livelihood, security, and well-being of millions continues to persist and is projected to continue (Kittinger et al. 2015; Eddy et al. 2021). For over a century, humans have regarded coral reefs as extraordinary natural structures containing a wealth of resources, which require specific bio-physical conditions to thrive (Saville-Kent 1900; Davis 1928). Despite this early understanding of the vulnerability of these ecosystems, and projections of massive global loss nearly twenty years ago (-60% by year 2030) (Hughes et al. 2003), these severe and persistent pertubations continue to undermine the natural resilience of coral reef ecosystems to adapt in the face of increasing change and to continue providing socio-economic and cultural services (Kittinger et al. 2015). This threat is perhaps most prevelant in terms of the loss of reef fishes.

While evidence of human activities is present within coral reef ecosystems at all trophic levels (Williams et al. 2019), the measure of fish biomass is commonly used to determine the status of reefs (Barnes et al. 2019). Overfishing was the first major anthropogenic impact on coral reefs and it continues to precede all other stressors including pollution and climate change (Jackson et al. 2001) because it dramatically reduces fish biomass, particularly of herbivores and top predators (Williams et al. 2019). Reefs that were surveyed decades ago were already severely degraded with early declines being attributed to over-fishing (Pandolfi et al. 2003) and across many coasts, large fauna are essentially absent (Jackson et al. 2001; Ward-Paige et al. 2010). Historically, humans have rapidly depleted coastal resources in sequence, beginning with larger, high value species followed by smaller, less valuable ones (Lotze et al. 2006; Pandolfi et al. 2003). The loss of reef fish biomass threats the entire ecosystem, as fishes drive critical processes linked to ecosystem stability, structure, function, and benthic state (Barnes et al. 2019). Reefs become more vulnerable to other types of stressors (e.g., nutrient pollution, disease, storms) (Jackson et al. 2001), which in turn compromise their capacity to continue to provide for coastal communities (e.g., food security, income, storm protection) (Teh et al. 2013; Eddy et al. 2021). Thus, the millions of people in reef-dependent communities are stuck in a catch-22; regions that are highly reliant on reef fishes are where humans exert the greatest pressures, and where a greater risk for loss of critical functioning and provision of services exists.

Globally, one third of coral reefs are highly threatened by overfishing and an estimated 5.2 to 6.8 million fishers target reef fishes for subsistence, local income, and export (Teh et al. 2013). Coral reef fisheries only account for 2% – 5% of global fish catch (Newton et al. 2007); yet nearly 90% of the studies of these fisheries cited overfishing as a concern (Johnson et al. 2013; Nash and Graham 2016). Notwithstanding the small-scale and artisanal nature of coral reef fisheries, they are the primary cause of the decline of reef fishes (Johnson et al. 2013). In 2002, the global catches of coral reef fishes peaked and have since been in decline despite increasing fishing effort (Eddy et al. 2021) and total landings of coral reef fisheries are 64% higher than sustainable levels (Newton et al. 2007). The demand for reef fish (and other reef resources) extends far beyond the tropics (Hughes et al. 2003), and all coral reef fisheries are subject to the tragedy of the commons (Barnes et al. 2019). Mitigating further losses of coral reef fishes requires the restoration of reef ecosystems, and supporting sustainable livelihoods and governance in coastal and island societies (Darling and D'agata 2017).

1.2 MPAs as potential solutions

In order to mitigate the negative impacts of human activities on ocean ecosystems, marine protected areas (MPAs) have increasingly become the primary conservation tool for conserving the ecological integrity and naturalness of critical areas. Nations and international organizations alike have established targets to increase the number and the size of MPAs world-wide (e.g., Convention on Biological Diversity; 30% by 2030) (Edgar et al. 2014). First designed to protect biodiversity of highly productive areas, MPAs are increasingly used to manage fish populations (Aronson and Precht 2006; Cholett et al. 2016) and may be the best management tool for coral reef conservation (Hughes et al. 2003). In some cases, MPAs have increased the diversity, density, biomass and average body size of targeted fish and provided other fisheries benefits such as export of larvae and spillover of adults outside the boundaries of the reserve (Cholett et al. 2016). Hypothetically, networks of MPAs can concurrently support conservation (e.g., increase biodiversity) and fisheries (e.g., increase yield and profits) (Gaines et al. 2010). MPAs can also support the reef ecosystem as a whole; for example, protection enables increases in herbivorous fish populations which increases herbivory action on reefs, reducing algal cover allowing the recovery of coral colonies (Aronson and Precht 2006). However, the success stories of fish recovery, biomass spillover, and increased fisheries profits are few and far between for the numerous MPAs that exist at the global level (Edgar et al. 2014).

The effectiveness of MPAs has been in question since their wide-spread emergence in the late 1990s with the term "paper parks" – where legislation provides a false sense of protection (Wright et al. 2020). The reasons behind MPA ineffectiveness range from shortfalls in staff and financial resources (Gill et al. 2017), lack of governance and enforcement (Wright et al. 2020), regulations that allow continued harvesting or illegal harvesting (Edgar et al. 2014), or are simply too small and newly established to have a significant impact (Mumby et al. 2006). As such, many MPAs fail to achieve their conservation goals (Wright et al. 2020) and management performance of existing MPAs is considered low (Dalton et al. 2012), which inhibits further implementation of MPAs because socio-economic and ecological benefits are under debate (Edgar et al. 2014). The trade-off between short-term economic loss and long-term benefits (both socio-economic and ecological) can cause conflict resulting in a zero-sum game (Cholett et al. 2016; Sala et al. 2021). However, with evolving management and novel approaches such as integration of socio-cultural drivers into coral reef ecology (Williams et al. 2019), MPAs could produce the anticipated benefits for biodiversity, food, and climate. (Sala et al. 2021).

1.3 Case study: Bay Islands of Honduras

The Bay Islands archipelago contains vast areas of coral reef, seagrasses, and mangrove forests which form the southernmost area of the Meso-American Barrier Reef (MAR) (Harborne et al. 2001). The region is known for the variety of marine animals that inhabit them, such as endangered species like hawksbill turtles (*Eretmochelys imbricata*) and the Nassau grouper (*Ephinephelus striatus)*, exploited species such as the spiny lobster (*Panuulirus argus*) and queen conch *(Lobatus gigas)*, and charismatic megafauna like the whale shark (*Rhincodon typus)* (Charteris, 2017). Most of the region is protected by the Bay Islands National Marine Park (BINMP), an MPA covering 6,770km^2 of coastal and marine space established by the Honduran

Government in 2010 (Zepeda, 2018). In addition, a smaller section of the Bay Islands is protected by a smaller MPA, the Cayos Cochinos National Monument reserve, which was established in 1991 (Bown et al. 2013). Both MPAs fulfill three of the five key features suggested by Edgar et al. (2014) to exponentially increase effectiveness; old (>10 years), large (>100km^2), and isolated, but they are not fully no-take nor heavily enforced. The region is an ideal candidate to examine ongoing human impacts within established marine parks because it is a hotspot for divers, cruise-ship tourists, sport-fishers and beach goers (Doiron and Weissenberger 2014) and multiple human pressures occur within its boundaries (e.g., nutrient pollution, overfishing, and habitat destruction) (HRI, 2020). A variety of marine management issues exist in the park including lack of sanitation infrastructure and untreated wastewater, unplanned coastal development with large hotels, non-sustainable tourism, and recent declines in reef fish biomass (HRI, 2020).

Continued environmental degradation (e.g. coastal development) and pressures from extractive activities (e.g., fishing) are hypothesized to contribute to the ongoing loss of reef fish biomass across the Bay Islands. Over the last few years, the region has faced unprecedented pressures and commercially valuable stocks such as lobster and conch have decreased significantly (Zepeda, 2018). The national legislation of the Bay Islands National Marine Park (Republic of Honduras, 2010), the Cayos Cochinos National Monument Reserve (Republic of Honduras, 2003), and their associated regulations have done little to combat the increased modernization of fishing gear and boats, and open access fisheries regulations (Zepeda, 2018). According to a monitoring report by the Healthy Reefs Initiative (HRI), herbivorous fish biomass declined by 56% (from 4474 to 1981g/100m^2), and commercially valuable fish biomass declined by 44% (from 675 to 383g/100m^2) in Honduras (HRI, 2020). Moreover, fishing pressure and illegal fishing has increased, even within the no-take zones (HRI, 2020) and the region faces new threats from climatic stressors, such as increased reef disease (RMP, 2021). These severe declines in reef fish biomass threaten the livelihoods and well-being of island communities within the Bay Islands who rely on coral reef fisheries and coastal tourism (e.g., artisanal fishers, boat tour operators). In this paper, the linkages between continuing and intensifying anthropogenic and climatic impacts and the decline of reef fishes within the Bay Islands are examined.

1.4 Research aims and objectives

As anthropogenic pressures and climatic stressors continue within the Bay Islands despite regulatory legislation, I hypothesize that humans have drastically altered reef fish communities in recent years by lowering the amount of biomass on the reef. The coastal ecosystems upon which many islanders rely on for food, their livelihoods and well-being, and regulative processes, are under threat. The overall aim of this research is to highlight the magnitude of human pressures persisting in the region, and to understand the consequences for coral reef fish communities. My objectives are to: 1) quantify fish biomass declines and changes in fish community structure, 2) quantify human impacts based on a literature review, and 3) explore the linkages between the two. Based on my findings, I derive four recommendations to mitigate further losses of reef fish and guide current marine and coastal management practices. I hope to fulfill a critical need to address the continued exploitation of coral reef fish communities and ongoing human impacts within the Bay Islands.

2. METHODOLOGY

2.1 Study Area

The Bay Islands archipelago extends over 500km^2 in the Western Caribbean Sea, 30 - 50 km north of the mainland of Honduras in Central America and forms the southernmost end of the Meso-American Barrier Reef System (MAR) (Figure 1) (Harborne et al., 2001; Brown and Caldwell 2002; Gobert et al. 2005). The Bay Islands includes three large islands: Utila (45km^2), Roatan (83km^2), and Guanaja (50km^2), a smaller, less populated group of islands called Cayos Cochinos (2km^2), and over 60 small uninhabited cays (Forest 1998; Gobert et al., 2005). The islands formed a few thousand years ago from uplift along a fault system between the North American and Caribbean plates and consist primarily of uplifted limestone, later colonized by extensive mangrove wetlands (Harborne et al. 2001; Sutton 2015). The two largest islands, Roatan and Guanaja emerge atop the Bonacca Ridge on the south side of the Cayman Trench (Harborne et al., 2001), while Utila and Cayos Cochinos lie on the continental shelf (Figure 2) (Gobert et al. 2005). Each of the Bay Islands are surrounded by fringing coral reefs, seagrass meadows in nearshore lagoons, and extensive mangrove forests (Harborne et al. 2001).

Figure 1: The largest reef system in the Western Hemisphere, the Meso-American Barrier Reef (in green) in the Caribbean Sea (Andrefouet et al. 2002). The location of the Bay Islands is highlighted with a black circle.

The Meso-American Barrier Reef System (MAR) is the largest reef complex in the Americas, and it encompasses over 1000km of Caribbean coastline, islands, cays, atolls, and offshore banks of Mexico, Belize, Guatemala, and Honduras (Figure 1) (Canty et al. 2018; Kjerfve et al. 2021). This reef complex includes barrier reef, fringing, patch, and pinnacle reefs, inner- barrier reef rhomboid shoals, and several atolls off the continental shelf (Kjerfve et al. 2021). In addition to coral reef, the MAR contains widespread mangroves, wetlands, and seagrass beds, as well as numerous underwater seamounts (Harborne et al. 2001). Due to the region's high biodiversity and high cultural and economic value, substantial efforts have endeavoured to increase conservation and support the nearly two million people that rely on the MAR across the four countries (Chollett et al. 2017). A significant portion of the MAR is protected by Honduran legislation in the Bay Islands (ICF, 2013).

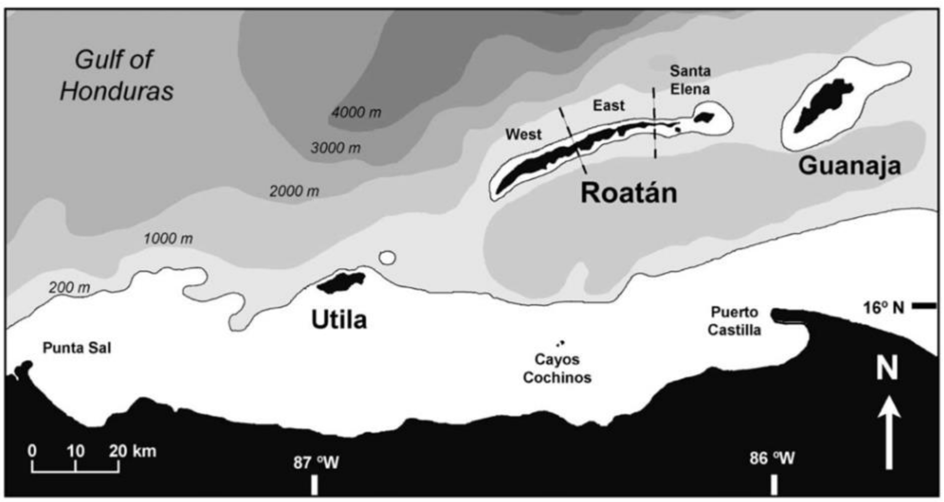


Figure 2: Bathymetry of the Bay Islands. Utila and Cayos Cochinos sit atop the continental shelf and Roatan and Guanaja sit on the Bonacca Ridge (Gobert et al. 2005).

Marine ecosystems across each of the four subregions of the Bay Islands (Cayos Cochinos, Guanaja, Roatan, and Utila) are within protected areas. The Bay Islands National Marine Park (BINMP) contains a large, continuous space surrounding the coastal and marine waters of Utila, Roatan, and Guanaja of approximately 6471.5 km^2 (Figure 3). It contains various zones (e.g., no wake zone, no take zone), and one other smaller protected area: the Cordelia Banks Site of Special Importance (~63,440m long) (Canty et al. 2021). The Cayos Cochinos National Marine Monument (490km^2*)* surrounds three inhabited islands and 14 smaller cays, as well as numerous underwater seamounts (Figure 4) (Gombos et al. 2011). These MPAs encompass diverse and rich marine ecosystems, with estimations of species diversity ranging from 185 to 500 species of fishes, over 125 different coral species, various reptiles (e.g., sea turtles, crocodiles) and marine mammals (e.g., dolphins, whales) (Doiron and Weissenberger 2014; Funes et al. 2015). The region's climate is tropical, with sea surface temperatures ranging from 27-31°C, and a nearby upwelling zone generates productive waters (Harborne et al. 2001; Doiron and Weissenberger 2014). For much of each year, the south-eastern (windward) side of each island is heavily exposed, while the north-west (leeward) side is protected from constant wave action except during the rainy season (October to January) where winds shift from the east and come from the north-west (Brown and Caldwell 2002; Chollett et al. 2014). Most of the reef slope on both northern and southern shores across Roatan and Guanaja continues to >100m, but in some sites in Utila and Cayos Cochinos, it reaches a maximum depth of 40-60m where the seabed levels off stretching to mainland Honduras (Andradi-Brown et al. 2016). Despite close proximity, the marine ecosystems throughout the Bay Islands are associated with different bathymetries, and terrestrial and oceanic inputs (Canty et al. 2018).

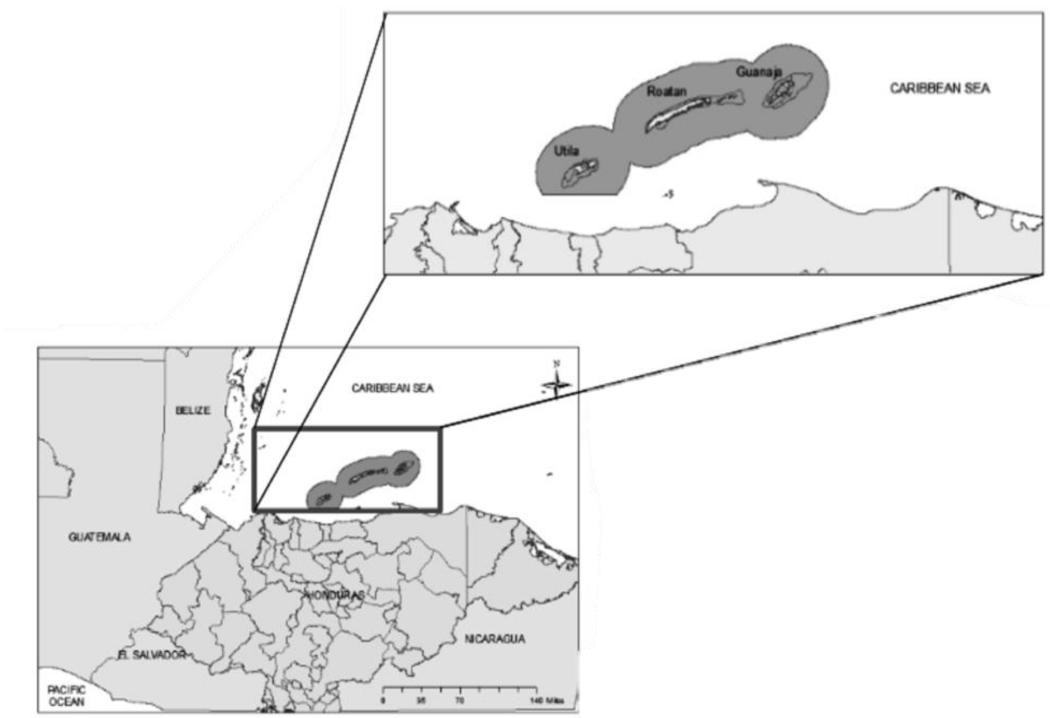


Figure 3: The Bay Islands National Marine Park, which encompasses coastal and marine space (6471.5 km^2) surrounding Utila, Roatan and Guanaja (Zepeda, 2018).

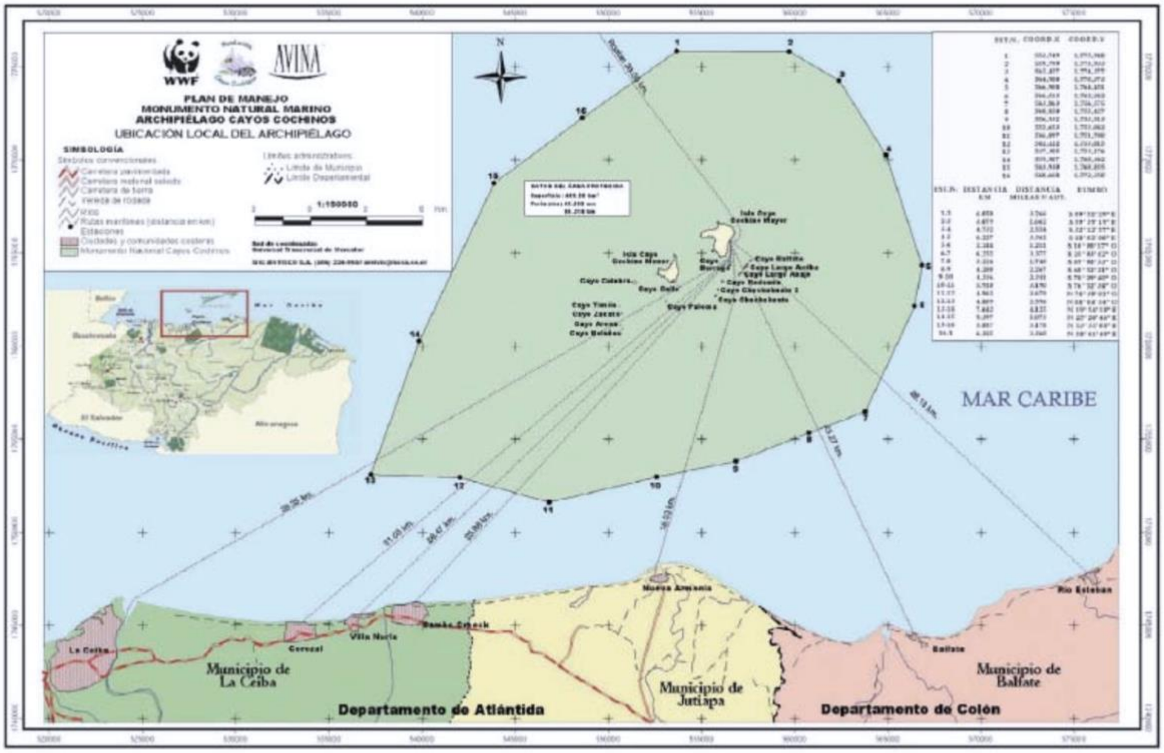


Figure 4: The Cayos Cochinos National Marine Monument (Gombos et al. 2011).

2.2 Field Surveys

Underwater visual surveys (UVS) were conducted at 83 coral reef sites across the Bay Islands by the Healthy Reefs Initiative in 2006, 2010, 2011, 2012, 2014, 2016, and 2018 (HRI, 2018). The number of sites varied across each of the Bay Islands (Utila n = 9; Roatan n = 25; Guanaja n = 13; Cayos Cochinos n = 14) (Figure 4) and there were slight variations in the sites visited throughout the study period. In 2021, I conducted UVS using the same Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology (AGRRA, 2016) that has been used by HRI across the MAR for the past 15 years. I collected abundance and length data on 77 reef fish species (Appendix I) on SCUBA in shallow coral reefs, between 0 to 30 meters. A total of 23 sites were sampled in the Roatan (n = 21) and Cayos Cochinos (n = 2) subregions from April 24th to June 7th, 2021.

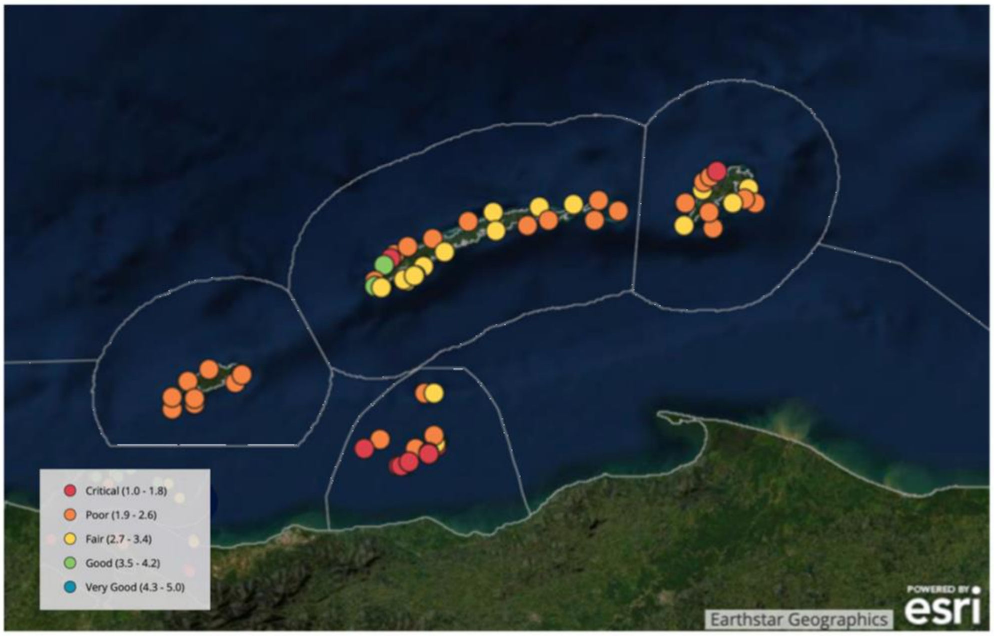


Figure 4: Study sites withing the Bay Islands that were surveyed from 2006 to 2021. The map shows overall scores for the 4 Reef Health Indicators across the BINMP in 2018. Adapted from: Healthy Reefs Data Explorer (www.healthyreefs.org/dataexplorer) (HRI, 2020).

In total, 4,101 transects were completed from 2006 to 2021 in the Bay Islands. Divers recorded the abundance (# of fish) and their estimated size (in cm) along 30m long and 2m wide transects, from the bottom substrate to the top of water column. Transects were placed haphazardly on the reef at differing depths at each site, and at least 10 fin kicks occurred between the starting point of each transect, so that each transect did not cover the same area as another. Each transect was 1 pass of the tape length (i.e. 30m), and post-pass recordings were allowed only for hidden/cryptic fish species (e.g., *Pterois* spp.) (AGRRA, 2016). The number of transects per site differed across data collection year (in 2006: 10 to 15 transects/per site; 2010 to 2018 10 transects/ per site). In 2021, six transects were completed at each site between depths of 0-30 m (0-100 feet) instead of ten, due to time constraints to stay out of decompression on open-circuit SCUBA. Total fish size was estimated using the 10-cm increments on a T-bar with markings for scale and recorded on waterproof paper attached to a slate. Size classes include: 0-5cm; 6-10cm; 11-20cm; 21-30cm; 31-40cm; any fish above 40cm in size was written with the number (abundance) x nearest size estimate (e.g. 2@50cm).

2.3 Fish Data

Fish biomass data from 2006 – 2018 was obtained from the Healthy Reefs Initiative (HRI) dataset (available from www.healthyreefs.org/dataexplorer). This data is collected via a collaboration of over 70 organizations across the MAR, including sites in Belize, Guatemala, Honduras and Mexico, and led by the Smithsonian Institution (Kjerfve et al. 2021). The HRI dataset includes information on four Reef Health Indicators (Table 1), two of which were used in this study: #3) Herbivorous fish - an estimate of the biomass (g/100 m^2) of parrotfish and surgeonfish families and #4) Commercial fish - an estimate of the biomass (g/100 m^2) of snapper and grouper families (Kjerfve et al. 2021). For the scope of this project, only the fish biomass data and the fish family composition data from HRI's database were utilized.

Table 1: Threshold Values for the 4 Reef Health Indicators (RHI) by the Healthy Reefs Initiative (HRI, 2020). Adapted from HRI's 2020 Meso-American Reef Report Card.

Indicator Score	**Indicator Rank**	**RHI #1: Coral Cover**	**RHI #2: Fleshy Macroalgae Cover**	**RHI #3: Herbivorous fish biomass ($g/100m^2$)**	**RHI#4: Commercial fish biomass ($g/100m^2$)**
5	Very Good	40%	1%	3,290	1,620
4	Good	20%	5%	2,740	1,210
3	Fair	10%	12%	1,860	800
2	Poor	5%	25%	990	390
1	Critical	<5%	>25%	<990	<390

To calculate fish biomass from the abundance and length data, I used the same methodology as applied in previous analyses by HRI and AGRRA, where the biomass for each individual fish was calculated as:

$$A*(S*TL2FL)^B$$

where A and B = species biomass curve coefficients, S = size, and TL2FL = total length to fork length conversion factor (AGRRA, 2016). The A and B species-specific conversion constants (Appendix II) were obtained from AGRRA (P. Kramer, pers. comm.), and were originally derived from Fishbase in 2013 (Froese and Pauly 2017). Fish biomass estimations were calculated for each individual fish counted, then summed at the fish family group level per transect, not at the species level (Appendix III). The total biomass per fish family group was normalized using:

(Biomass / (2 * Transect Length (m))) * 100

to produce biomass in grams per 100m. Three additional summations for fish biomass were done for each transect: 1- total fish biomass (all fish families), 2- herbivorous fish biomass (surgeonfishes and parrotfishes), and 3 – biomass of commercially valuable fish (snappers, groupers, jacks, grunts).

Trends of total fish biomass, the herbivorous fish biomass, and the biomass of commericiallly valuable fish over time were analyzed across the four subregions in the BINMP (Cayos Cochinos, Guanaja, Roatan, and Utila). Initial data visualizations were created using the "ggplot2" package (Wickham 2016) and the "tidyverse" package (Wickham et al. 2019) to observe overall trends throughout the study period (2006 to 2021). Linear mixed-effects models were completed using the "lme4" package (Bates et al. 2015) in R statistical software (R Core Team 2020) with the RStudio interface (RStudio Team 2020). Models were plotted using color-scale "viridis" (Garnier et al. 2021). The best fit model was determined using an information crierion approach, an AIC comparison. The linear mixed-effect model used was:

lmer(log(FishBiomass+1)~ Year*Subregion + (Subregion|Site) + (1|Depth)

The log of all fish biomass values was used to increase heterogenetity across residuals and satisfy statistical assumptions (Appendix V). Fixed effects include the interaction of Year and Subregion (Year*Subregion) and the Random effects taken into account into the model computations were Site and Depth. Because depth was taken into account in the linear mixed effects model, all data points without depth information (data from 2006) were not utilized for modelling trends in fish biomass. Thus, the declines in total, herbivorous, and commerically valuable fish biomass were modelled from 2010 to present, and 95% confidence intervals were calculated.

In addition, fish community composition was examined across the four subregions of the Bay Islands (Cayos Cochinos, Guanaja, Roatan, and Utila) from 2006 to 2021. A Bray-Curtis dissimilarity matrix based on fish family biomass was used to generate a cluster dendogram to identify the similarities between fish compositions of subregions across years. Stacked bar graphs were generated in Excel using color-scale "viridis" (Garnier et al. 2021) to illustrate the changes in fish community compositions across time for each subregion (Utila & Guanaja: 2006 – 2018; Roatan & Cayos Cochinos: 2006 – 2021).

2.4 Literature Review

An extensive literature review was conducted to compile information and data regarding marine and coastal management of the Bay Islands, as well as the anthropogenic impacts occuring within the region. The current management practices of the park were reviewed via official governmental legislation (e.g., Plan de Manejo del parque nacional marino Islas de la Bahia) and public access data (e.g., webpages of local non-governmental organizations (NGOs)). In addition, quantitative estimations of anthropogenic impacts were collected via an in-depth literature review of scientific journal articles and grey literature using Google Scholar and Dalhousie Libraries. Key search-words included: “Bay Islands”, “Roatan”. “Utila”, “Guanaja”, “Cayos Cochinos”, “fisheries”, “population”, “coastal development”, “pollution”, “tourism”, “bleaching”, “hurricanes”, “run-off”, “sedimentation”, etc. Impacts were categorized into 6 themes: 1) fisheries, 2) coastal development, 3) increasing population, 4) land-based pollution, 5) tourism, and 6) climate change. Examples of gathered impact data include artisanal fisheries catches, land use change, mangrove clearing, rates of coastal development, population demographics, number of tourists per year, boat traffic, percentage of communities with wastewater infrastructure, bleaching events, and estimations of tonnes of plastic entering the marine environment.

3. RESULTS

3.1 Fish data

3.1.1. Decline of total reef fish biomass

Total reef fish biomass declined throughout the Bay Islands over the past decade (Figure 5). Rates of modelled decline differed across the subregions, with two groupings observed (Guanaja & Roatan; Cayos Cochinos & Utila) (Figure 5). The greatest declines in total reef fish biomass were detected in Guanaja (-1.14578g/100m^2/year) and Roatan (-1.10261g/100m^2/year), while rates of biomass decline in Utila (-1.07387g/100m^2/year) and Cayos Cochinos (-1.034833 g/100m^2/year) were less pronounced. Linear mixed effects model with an interaction between year and subregion (Year*Subregion) was best fit for this highly varied data across transects (n = 2,541) (Appendix VI). Declines in total fish biomass were significant in Guanaja (p=.008), Roatan (p=.05), and Cayos Cochinos (p<.001) but not in Utila (Table 2).

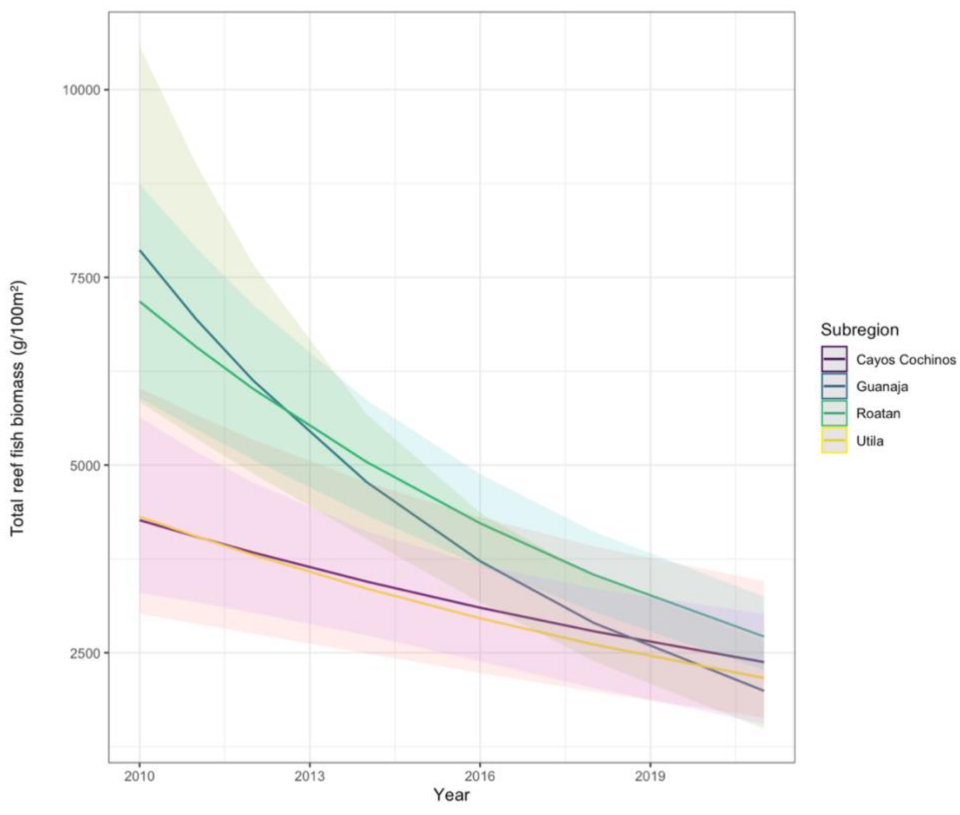


Figure 5: Trends in total reef fish biomass (g/100m^2) across the four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 - 2021. Linear mixed effects model fitted to total fish biomass data; 95% confidence intervals shown by shading.

Table 2: Effects of Year and Subregion on total reef fish biomass (g/100m^2) across the four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 – 2021.

	Effects of Year and Subregion on Total Fish Biomass		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	115.33	59.42 – 171.25	**<0.001**
Year	-0.05	-0.08 – -0.03	**<0.001**
Subregion [Guanaja]	144.40	37.49 – 251.31	**0.008**
Subregion [Roatan]	71.18	-0.04 – 142.40	**0.050**
Subregion [Utila]	19.13	-78.02 – 116.29	0.699
Year * Subregion [Guanaja]	-0.07	-0.12 – -0.02	**0.008**
Year * Subregion [Roatan]	-0.04	-0.07 – 0.00	0.051
Year * Subregion [Utila]	-0.01	-0.06 – 0.04	0.699
Random Effects			
σ^2	1.06		
$\tau_{00\ \mathrm{Depth}}$	0.01		
$\tau_{00\ \mathrm{Site}}$	0.43		
$\tau_{11\ \mathrm{Site.SubregionGuanaja}}$	0.48		
$\tau_{11\ \mathrm{Site.SubregionRoatan}}$	0.54		
$\tau_{11\ \mathrm{Site.SubregionUtila}}$	0.29		
$\rho_{01\ \mathrm{Site.SubregionGuanaja}}$	-0.93		
$\rho_{01\ \mathrm{Site.SubregionRoatan}}$	-0.89		
$\rho_{01\ \mathrm{Site.SubregionUtila}}$	-0.88		
ICC	0.14		
N_{Site}	75		
N_{Depth}	179		

While modelled declines consider the data from each transect, average total reef fish biomass at the subregion levels also declined throughout each subregion in the Bay Islands from 2006 to 2018 (Table 3). At the beginning of the Healthy Reefs Initiative's study period in 2006, subregions Cayos Cochinos and Roatan had the highest average total reef fish biomass (11,896.8g/100m^2 +/- 14,941.0g/100m^2, and 11,896.8 g/100m^2 +/- 20,104.1g/100m^2, respectively) and Utila and Guanaja had lower average total reef fish biomass (7418.8 g/100m^2 +/- 7637.8g/100m^2, and 6161.1g/100m^2 +/- 6292.8g/100m^2 respectively). At the end of the study period in 2018, average total reef fish biomass was fairly similar across all subregions (ranging from 2747g/100m^2 to 4188g/100m^2) (Table 3).

Table 3: Average total reef fish biomass (g/100m^2; mean +/- standard deviation(SD)) across the four subregions of the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from the Healthy Reefs Initiative database from 2006 to 2018.

	CAYOS COCHINOS			**GUANAJA**			**ROATAN**			**UTILA**		
YEAR	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
2006	*92*	11896.8	14941.0	*115*	6161.1	6292.8	*411*	11868.9	20104.1	*155*	7418.8	7637.8
2010	*193*	6643.8	8136.6	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	*198*	9078.0	19632.0	*64*	4271.8	5238.6
2012	*58*	7330.7	8234.2	*88*	6844.4	8995.9	-	-	-	*90*	9198.0	16078.0
2014	*90*	13945.0	17381.8	*103*	6920.0	5269.1	*113*	11774.7	12854.4	*80*	6924.0	5314.0
2016	*112*	11120.5	11098.7	*187*	6308.9	5159.5	*555*	8609.0	8398.0	*97*	8269.2	13845.9
2018	*136*	2747.4	2650.5	*129*	4001.4	6338.9	*562*	3938.0	4949.9	*335*	4188.0	4449.8

3.1.2. Trends in Herbivorous fishes

Herbivorous fish biomass declined throughout the Bay Islands over the past decade (Figure 6). Similar to the total fish biomass, the modelled rates of decline of herbivorous fish biomass had two groupings (Guanaja & Roatan; Cayos Cochinos & Utila). The greatest rates of decline were found in reefs around Guanaja (-1.1584g/100m^2/year) and Roatan (-1.1519g/100m^2 /year), while less severe declines were observed in Cayos Cochinos (-1.0567g/km^2/year) and Utila (-1.0773g/km^2/year). Linear mixed effects model with an interaction between year and subregion (Year*Subregion) was best fit for this highly varied data across transects (n = 2,541) (Appendix VI). Declines in herbivorous fish biomass were significant in Roatan (p=.002), and Cayos Cochinos (p<.001) but not in Utila or Guanaja (Table 4).

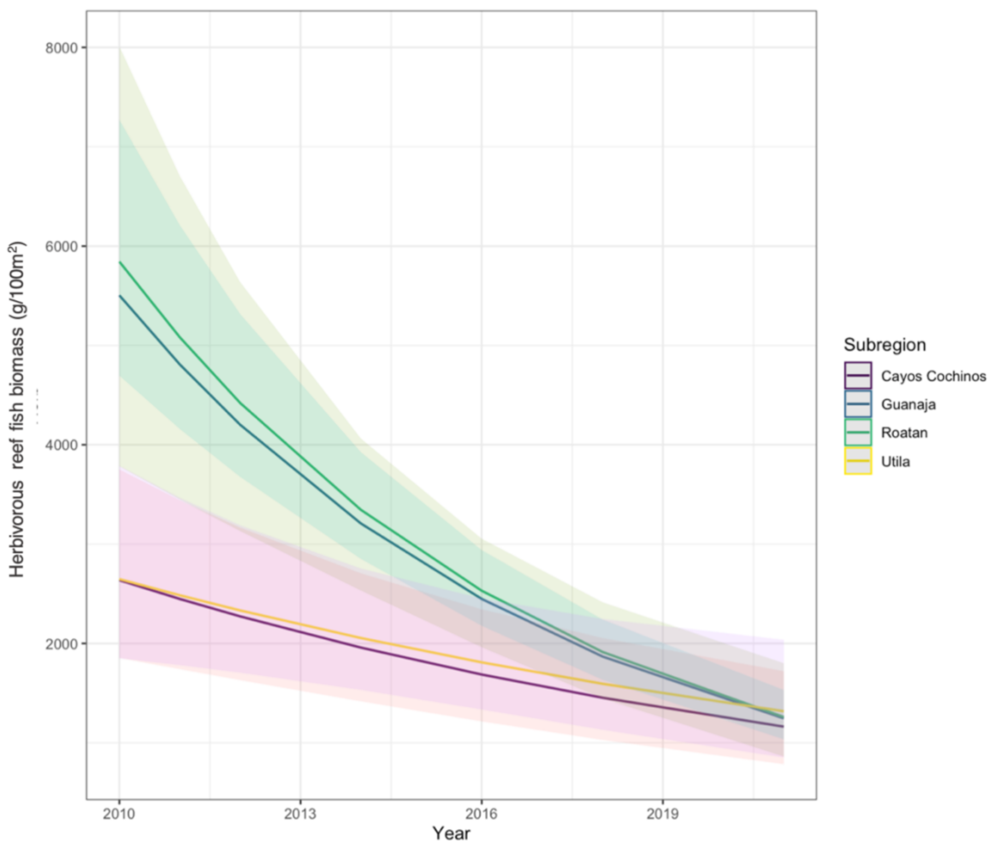


Figure 6: Trends of herbivorous reef fish biomass (g/100m^2) across four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 to 2021. Linear mixed effects model fitted to herbivorous fish biomass data; 95% confidence intervals shown by shading.

Table 4: Effects of Year and Subregion on herbivorous fish biomass (g/100m^2) across the four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 – 2021.

	Effects of Year and Subregion on Herbivorous Fish Biomass		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	157.46	91.00 – 223.91	**<0.001**
Year	-0.07	-0.11 – -0.04	**<0.001**
Subregion [Guanaja]	122.50	-5.51 – 250.50	0.061
Subregion [Roatan]	131.53	47.06 – 216.00	**0.002**
Subregion [Utila]	-22.15	-139.24 – 94.93	0.711
Year * Subregion [Guanaja]	-0.06	-0.12 – 0.00	0.062
Year * Subregion [Roatan]	-0.07	-0.11 – -0.02	**0.002**
Year * Subregion [Utila]	0.01	-0.05 – 0.07	0.710
Random Effects			
σ^2	1.51		
τ_{00} Depth	0.02		
τ_{00} Site	0.40		
τ_{11} Site.SubregionGuanaja	0.60		
τ_{11} Site.SubregionRoatan	0.90		
τ_{11} Site.SubregionUtila	0.65		
ρ_{01} Site.SubregionGuanaja	-0.88		
ρ_{01} Site.SubregionRoatan	-1.00		
ρ_{01} Site.SubregionUtila	-0.81		
N_{Site}	75		
N_{Depth}	179		

The average herbivorous reef fish biomass at the subregion levels also declined throughout each subregion in the Bay Islands from 2006 to 2018 (Table 5). At the beginning of the Healthy Reefs Initiative's study period in 2006, subregions Roatan and Cayos Cochinos had the highest average herbivorous reef fish biomass (8189.9g/100m^2 +/- 18,567.6g/100m^2, and 7471.2g/100m^2 +/- 10,630.4g/100m^2, respectively) and Utila and Guanaja had lower average total reef biomass (4820.3g/100m^2 +/- 6272.9g/100m^2, and 4380.1g/100m^2 +/- 5591.3g/100m^2 respectively). At the end of the study period in 2018, Guanaja, Roatan, and Utila had similar average herbivorous reef fish biomass (ranging from 2607g/100m^2 to 2835 g/100m^2) while Cayos Cochinos had lower biomass by approximately 1000g/100m^2 (1769g/100m^2 +/- 1863.8 g/100m^2) (Table 5).

Table 5: Average herbivorous fish biomass (g/100m^2; mean +/- standard deviation(SD)) across the four subregions of the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from the Healthy Reefs Initiative database from 2006 to 2018.

	CAYOS COCHINOS			**GUANAJA**			**ROATAN**			**UTILA**		
YEAR	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
2006	*92*	7471.2	10630.4	*115*	4380.1	5591.3	*411*	8189.9	18567.6	*155*	4820.3	6272.9
2010	*193*	4819.7	6684.2	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	*198*	7165.0	19271.0	*64*	2368.5	3415.2
2012	*58*	4155.1	4365.1	*88*	4894.4	7394.5	-	-	-	*90*	7201.0	13972.0
2014	*90*	8463.7	8498.0	*103*	5174.3	4726.9	*113*	8171.8	10180.1	*80*	5559.0	4742.0
2016	*112*	6302.2	5978.4	*187*	4439.6	3328.3	*555*	5950.0	5975.0	*97*	5622.3	9531.5
2018	*136*	1769.7	1863.8	*129*	2673.5	5178.3	*562*	2607.0	4053.3	*335*	2835.0	3643.7

3.1.2. Trends in Commercially valuable fishes

Commercially valuable reef fish biomass declined in all four subregions in the Bay Islands over the past decade (Figure 7). Unlike the trends in total and herbivorous reef fish biomass, there were no observable groupings between the different rates of decline across the four subregions, and none of the modelled declines were found to be significant (Table 6). The biomass of commercial valuable fishes was highly varied across transects (n = 2,541) (Appendix VI), and many transects had zero biomass recorded. The change in the scale of this model reflects the much lower overall biomass of commercially valuable fish than herbivorous or total reef fish biomass (Figure 7).

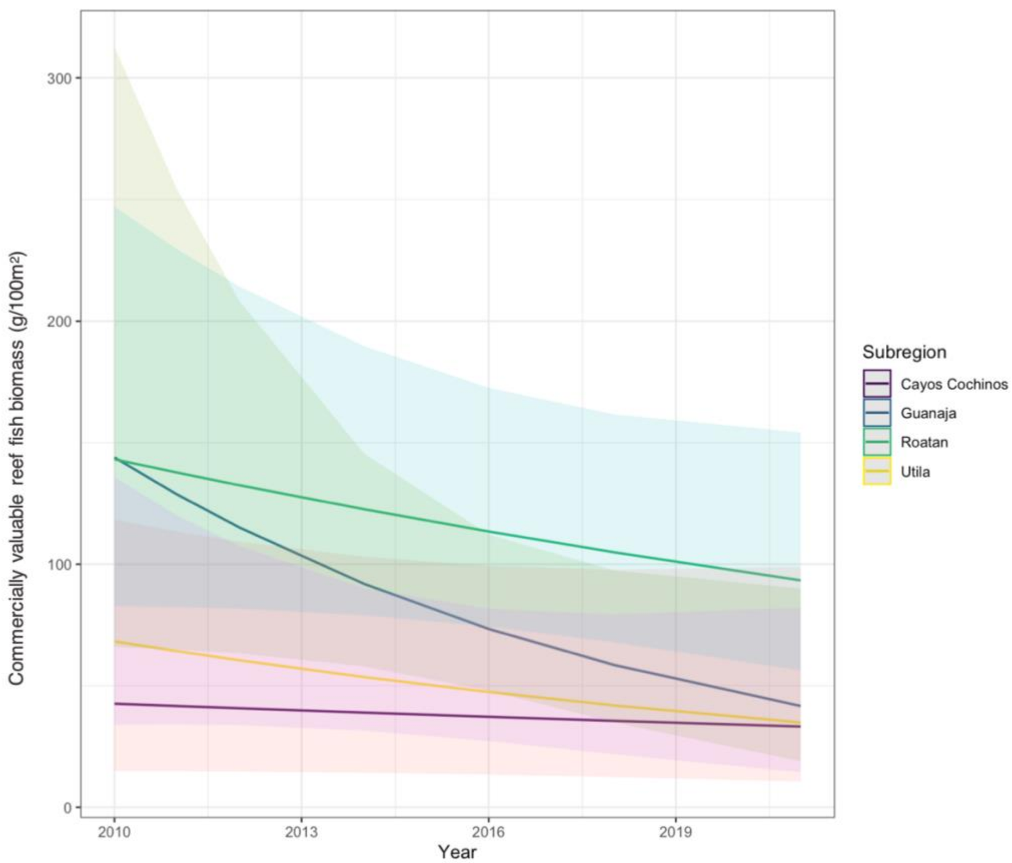


Figure 7: Trends of commercially valuable reef fish biomass (g/100m^2) across four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 to 2021. Linear mixed effects model fitted to fish biomass data; 95% confidence intervals shown by shading.

Table 6: Effects of Year and Subregion on commercial fish biomass (g/100m^2) across the four subregions in the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from 2010 – 2021.

	Effects of Year and Subregion on Commercial Fish Biomass		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	47.99	-96.12 – 192.10	0.514
Year	-0.02	-0.09 – 0.05	0.547
Subregion [Guanaja]	180.39	-94.32 – 455.09	0.198
Subregion [Roatan]	34.46	-148.82 – 217.75	0.712
Subregion [Utila]	76.31	-172.47 – 325.09	0.548
Year * Subregion [Guanaja]	-0.09	-0.23 – 0.05	0.200
Year * Subregion [Roatan]	-0.02	-0.11 – 0.07	0.721
Year * Subregion [Utila]	-0.04	-0.16 – 0.09	0.549
Random Effects			
σ^2	6.87		
$\tau_{00\ Depth}$	0.16		
$\tau_{00\ Site}$	3.82		
$\tau_{11\ Site.SubregionGuanaja}$	3.78		
$\tau_{11\ Site.SubregionRoatan}$	8.06		
$\tau_{11\ Site.SubregionUtila}$	5.46		
$\rho_{01\ Site.SubregionGuanaja}$	-0.94		
$\rho_{01\ Site.SubregionRoatan}$	-0.99		
$\rho_{01\ Site.SubregionUtila}$	-0.95		
ICC	0.19		
N_{Site}	75		
N_{Depth}	179		

The average of commercially valuable reef fish biomass at the subregion levels also declined throughout each subregion in the Bay Islands from 2006 to 2018 (Table 7). At the beginning of the Healthy Reefs Initiative's study period in 2006, subregions Cayos Cochinos had the highest average commercially valuable reef fish biomass (2092.8g/100m^2 +/- 4617.3g/100m^2), followed by Roatan (1760.5g/100m^2 +/- 3754.2g/100m^2) and Utila (1356.4g/100m^2 +/- 3040.1g/100m^2). In 2006, Guanaja had the lowest average of commercially valuable reef fish biomass (518.4g/100m^2 +/- 1065.2g/100m^2). At the end of the study period in 2018, Roatan and Utila had similar average commercially valuable reef fish biomass (ranging from 649 - 685g/100m^2, respectively) while Cayos Cochinos and Guanaja had similarly lower biomass by approximately 200g/100m^2 (432.9 to 431.3g/100m^2, respectively) (Table 7).

Table 7: Average commercially valuable fish biomass (g/100m^2; mean +/- standard deviation (SD)) across the four subregions of the Bay Islands (Cayos Cochinos, Guanaja, Roatan, Utila) from the Healthy Reefs Initiative database from 2006 to 2018.

	CAYOS COCHINOS			GUANAJA			ROATAN			UTILA		
YEAR	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
2006	*92*	2092.8	4617.3	*115*	518.4	1065.2	*411*	1760.5	3754.2	*155*	1356.4	3040.1
2010	*193*	861.9	2145.7	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	*198*	1216.0	2134.0	*64*	1428.6	3597.0
2012	*58*	1646.4	3866.7	*88*	813.3	1822.3	-	-	-	*90*	1023.0	3413.0
2014	*90*	2634.9	7557.4	*103*	665.1	1001.5	*113*	2171.4	4576.4	*80*	554.0	1118.0
2016	*112*	2317.8	6109.0	*187*	690.7	1257.6	*555*	1257.0	3256.0	*97*	1769.6	5660.9
2018	*136*	432.9	1152.1	*129*	431.3	888.6	*562*	649.0	1604.4	*335*	685.0	1868.2

3.1.4. Fish Community Composition

Table 8: Top ten fish families contributing to reef fish community composition in the Bay Islands from 2006 to 2021.

Fish Family (Common Name)	Fish Family (Latin Name)	Fish Family Code	Average Contribution to Community Composition (%)
Parrotfishes	*Scaridae*	PARR	41
Surgeonfishes	*Acanthuridae*	SURG	15
Snappers	*Lutjanidae*	SNAP	8
Grunts	*Haemulidae*	GRUN	6
Chubs	*Kyphosidae*	CHUB	5
Triggerfishes	*Balistidae*	TRIG	5
Angelfishes	*Pomacanthidae*	ANGE	4
Groupers	*Serranidae*	GROU	4
Barracuda	*Sphyraenidae*	BARR	2
Wrasses	*Labridae*	WRAS	2
		Total	**91**

Reef fish family composition across the four subregions of the Bay Islands was examined from 2006 to 2021. Of 20 fish families recorded, ten families contributed 91% towards the total reef fish community biomass with parrotfish having the greatest contribution (Table 8). However, percent contribution varies for each year and subregion (Figure 8- 11).

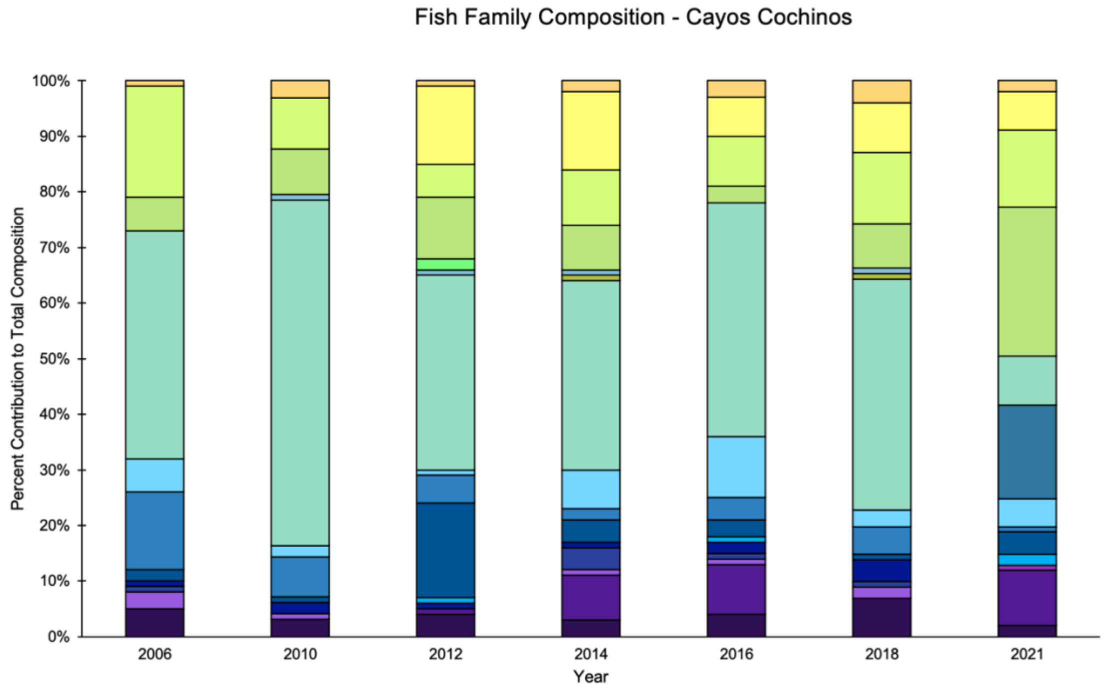
In Cayos Cochinos, snappers increased by 24% between their lowest contribution to the community composition in 2016 (3%) and their highest in 2021 (27%) (Figure 8). There was also a 52% decrease in the contribution of parrotfish from their highest in 2010 (61%) and their lowest in 2021 (9%) (Figure 8). The contribution of some fish families stayed steady over time, such as angelfish (~4%), surgeonfish (~12%), and wrasses (~2%) (Figure 8).

In Guanaja, the fish family composition remained relatively stable throughout the entire period and was dominated by herbivorous fish, like parrotfish (~42%) and surgeonfish (~20%) (Figure 9). Contributions from the angelfish and grunt families (both ~6%) were also very stable, and the percent contributions of the snapper and grouper families were consistently low (~3% and ~4%, respectively) (Figure 9).

In Roatan, parrotfish (~37%), surgeonfish (~17%), snappers (~9%), grunts (~5%), and groupers (~4%) all remained relatively stable (Figure 10). Other families experienced large declines in percent contribution (e.g., chubs contributed 27% in 2006 down to 1% in 2021) (Figure 10).

In Utila, there was greater variance in contributions of parrotfish to overall composition (36% to 62%) but overall, they remained dominant (~47%) (Figure 11). There was also greater variance in the snappers and surgeonfish families; overall snappers contributed an average of ~9% though this ranged from 18% in 2011 to 3% in 2012, while surgeonfish ranged from 20% in 2006 to 8% in 2012 for an average of ~12% over the study period (Figure 11).

Reef fish family composition similarities in the four regions of the Bay Islands were examined from 2006 to 2021 (Figure 12). The fish family composition of Cayos Cochinos in 2021 was most different than any composition of any year and subregion (Year*Subregion) because of the high contribution of snappers and the low contribution of parrotfish. In 2021, the only sampled sites in the Cayos Cochinos subregion were offshore seamounts, thus the composition there was substantially different than others. All four subregions were grouped together in the left-most cluster suggesting similarities of fish family composition in 2018 across the whole Bay Islands region. Three subregions (Roatan, Utila, and Cayos Cochinos) showed similarities in the large middle cluster during the early 2010s (e.g., 2010, 2011, 2012, 2014, and 2016). In contrast, the fish family composition in Guanaja is not as alike to the other three subregions as it has its own cluster (e.g., 2006G, 2012G, 2014G, and 2016G). Lastly, Roatan's fish family composition in 2006 was similar to composition recorded in Cayos Cochinos in 2012, which could be due to lower contributions of parrotfish and snappers in both, and higher percent contributions of other fish families (e.g., chubs, groupers).



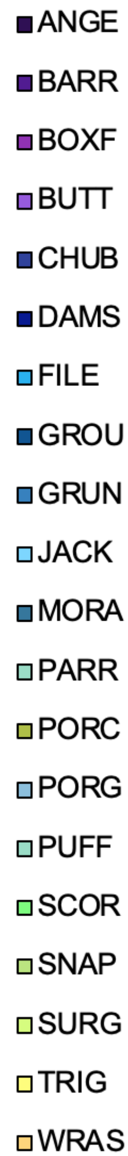


Figure 8: Fish Family Composition in Cayos Cochinos from 2006 – 2021.

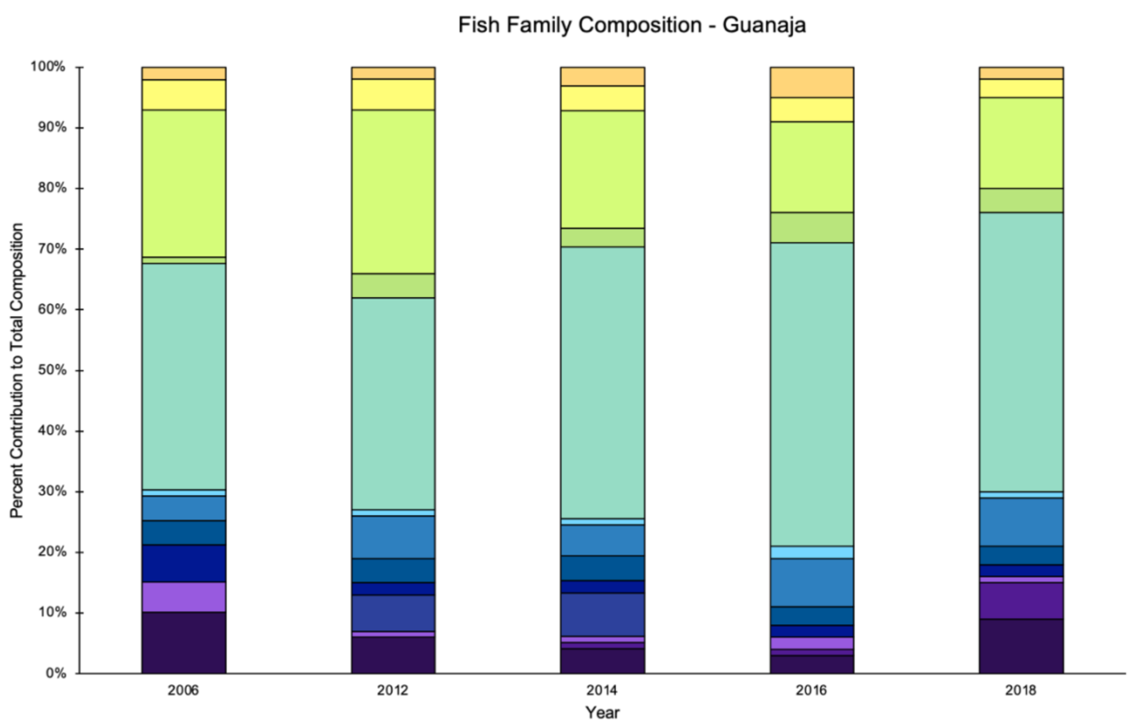


Figure 9: Fish Family Composition in Guanaja from 2006 – 2018.

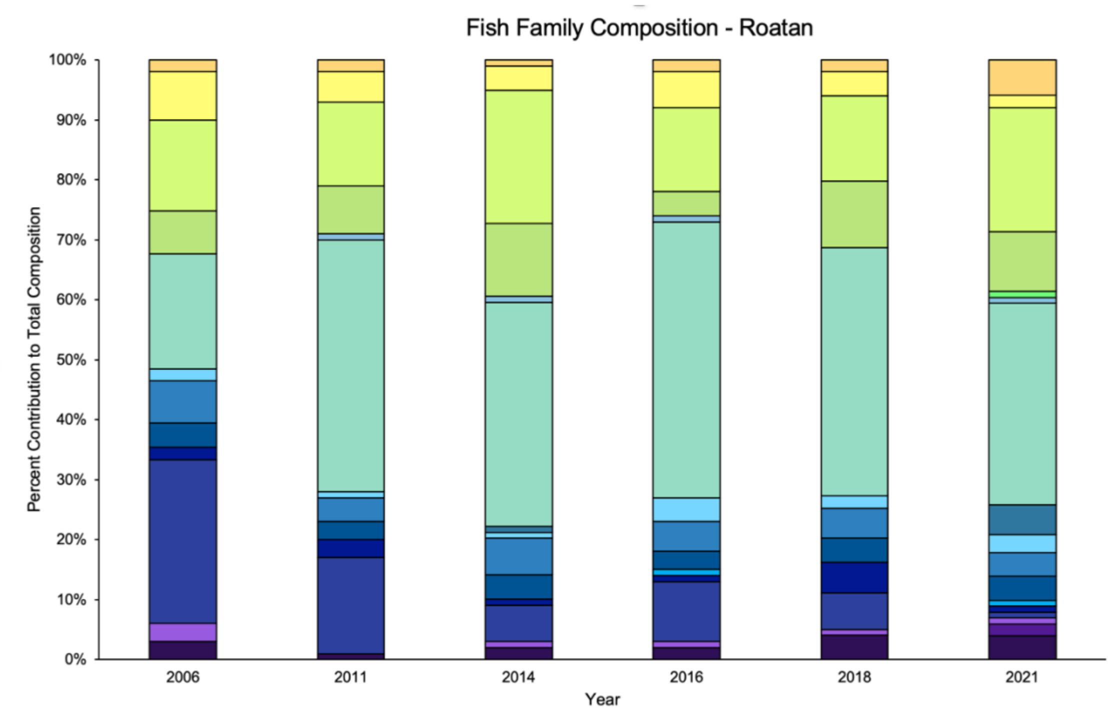
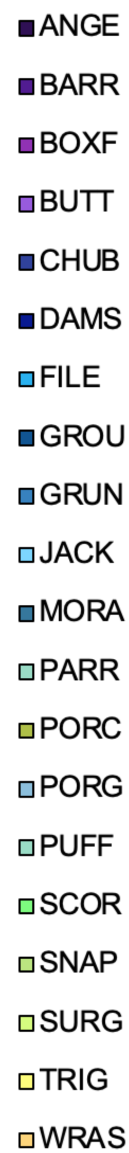


Figure 10: Fish Family Composition in Roatan from 2006 – 2021.



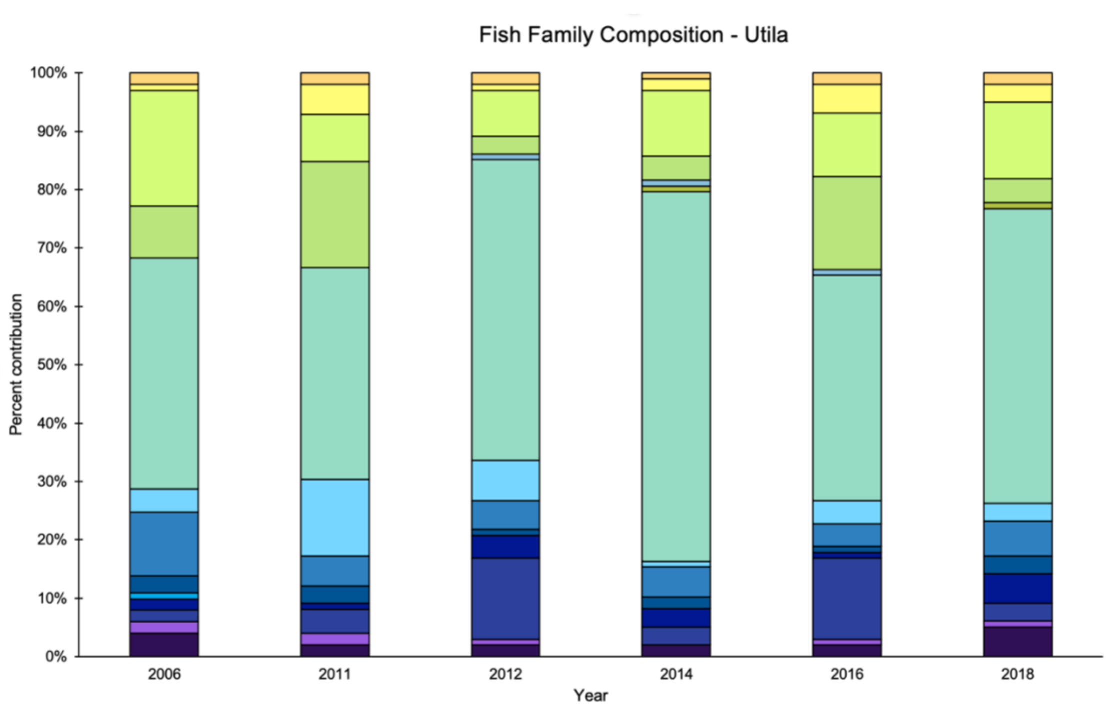


Figure 11: Fish Family Composition in Utila from 2006 – 2018.

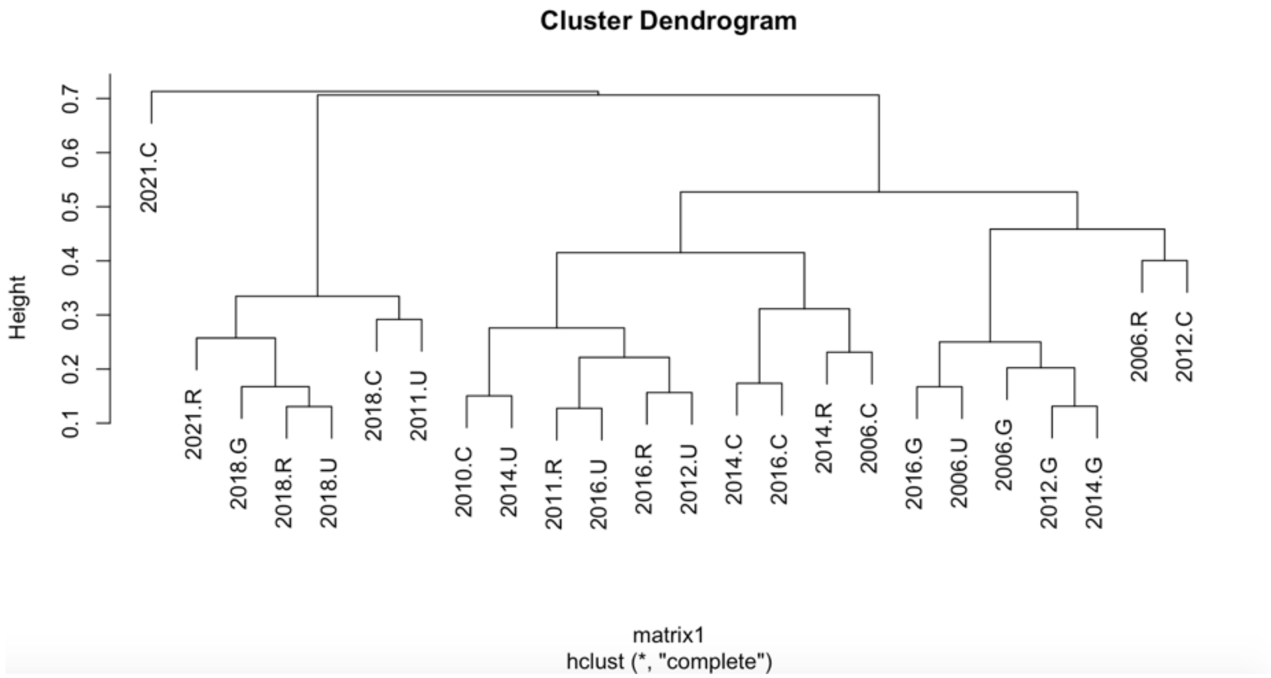


Figure 12: Fish family composition similarities across the four subregions of the Bay Islands (C= Cayos Cochinos, G= Guanaja, R = Roatan, U = Utila) from 2006 to 2021.

3.2 Management in the Bay Islands

Management of coastal and marine ecosystems in the Bay Islands began in the late 1980s when rapid growth in tourism and development, declines in coral reef health, and the lack of government action inspired a grass-roots conservation initative, the Sandy Bay Marine Reserve (SBMR) on Roatan (Luttinger 1997). A wealthy local businessman, Don Julio Galindo, oversaw the establishment of the SBMR in front of his dive operation, Anthony's Key Resort, and of the first conservation association in the region, the Bay Islands Conservation Association (BICA) (Luttinger 1997; Forest 1998). This association collected user fees from local businesses to fund the conservation initiatives in the SBMR, such as enforcement (e.g., guard salaries, boat and engine maintenance, and gasoline) (Luttinger 1997; Forest 1998). Four guards were employed to patrol the reserve and stop non-permissible activities such as anchoring on the reef, spearfishing, collecting coral, net fishing, garbage and sewage dumping (from yachts and sail boats), as well as creating new piers or docks in the area (Luttinger 1997). Notwithstanding, large-scale reef destruction to create nearby channels and construction of piers and docks continued without implementation of the fines for violations of reserve policies (US$100 to $600, and/or a jail sentence) (Luttinger 1997). After several years, local support for the reserve faded with conflicts occurring due to equal user fees for small and large businesses alike, and because a proposal to establish a national park in the Bay Islands hung in the interim for approximately a decade (Luttinger 1997).

Centralization of marine and coastal management in the Bay Islands began in the 1990s, when the first subregion, Cayos Cochinos, was established as a Natural Marine Monument by Presidential order (#1928-93) in 1994 (Cayos Cochinos Foundation, 2015). The ecological significance of this area was recognized internationally at the Earth Summit in 1992 by the Smithsonian Tropical Research Institute, The Summit Foundation, The Nature Conservancy, and World Wildlife Fund, which inspired the creation of the Honduran Coral Reef Fund (HCRF) (Cayos Cochinos Foundation, 2015). Initially, the area (489.25km^2) was managed by the HCRF, and a complete no-take zone was enforced within five miles of the largest island in the archipelago (Bown et al. 2013). This severely affected the Garifuna community living in the subregion, who relied on subsistence and artisanal fishing for food and income and after a few years of conflict and pressure, the no-take zone was removed in 1999 (Bown et al. 2013). In

2003, the area was designated as a MPA again through another presidential order by Porfirio (Pepe) Lobo (Acuerdo #114-2003) (Republic of Honduras, 2003), and HCRF was entrusted with its management for the following decade (Bown et al. 2013).

Partnership between World Wildlife Fund and HCRF led to the subregion's first management plan (2004-2009), which imposed further restrictions on the Garifuna community but chose to allow a reality tv show to film within the protected zone in 2007 (Bown et al. 2013). Because of this exclusive access given to foreigners, local conflict and civil unrest grew, resulting in the change of management plan in 2008 to include an adaptive co-management perspective and allow unrestricted fishing for Garifuna inhabitants (Bown et al. 2013). Presently, the area is managed by the Cayos Cochinos Foundation (which absorved the prior Honduran Coral Reef Fund) and several governmental institutions including the Institute of Conservation and Forestry (ICF), the Institute of Tourism (IHT), Ministry of Environment (Mi Ambiente), Director of Fisheries (DIGEPESCA), the Marine Merchant, and the Naval Force of Honduras (Cayos Cochinos Foundation, 2015). The MPA houses numerous critical resources including coral reefs, seagrasses, mangroves, reef fishes, lobster and conch, terrestrial vegetation, sandy keys, turtle nesting sites, sea birds, snakes and amphibians, and it is primarily used for tourism, fishing, and navigation. (Gombos et al. 2011)

Concurrently, an environmental management project in the other three subregions (Utila, Roatan, and Guanaja) arose in the early 1990s. In 1994, the Bay Islands environmental project (Programa de Manejo Ambiental de Islas de la Bahia) began with the collaboration of numerous organizations including the United Nations Development Programme, the Inter-American Development Bank, and two local NGOs: BICA, and APRODIB (Asociacion pro Desarrollo de las Islas de la Bahia) (Doiron and Weissenberger, 2014). The project was completed in 2008, and a 12 nautical mile zone around Utila, Roatan, and Guanaja was established as the Bay Islands National Marine Park (BINMP) in 2010 (Decreto #75-2010) (Republic of Honduras, 2010; Doiron and Weissenberger, 2014). The BINMP is managed by the same government agencies as in Cayos Cochinos (e.g., IHT, ICF, DIGESPESCA, etc.) as well as several ENGOs (e.g. Roatan Marine Park, BICA) (ICF, 2013). In 2013, the BINMP's management plan was published, and contains an overview of objectives, recommendations, and regulations [Table 9]. The BINMP has no public fisheries regulations (Gobert et al. 2005) or specific fisheries laws to govern management of teleost fishes (Box and Canty 2010), except for regional protection of parrotfishes (Healthy Reefs, 2020) and the proposed exclusion of fishing in a few zones (e.g., Cordelia Banks) (Canty et al. 2021).

Table 9: A list of permissible and non-permissible activities within the BINMP translated from the Marine Management Plan by Institute of Conservation and Forestry (ICF, 2013).

Permitted Activities	Non-permitted Activities
Diving	Aquaculture of non-native species
Snorkeling	Open system aquaculture
Kayaking	Anchoring on top of the coral reef
Environmental education	Capture and sell of marine life species for aquarium trade
Extraction of lionfish (Pterois sp.)	Boating speeds over 20 knots, >5 knots in channels, >10 knots in diving/snorkeling areas, and >15 knots in other nearby reef areas
Scientific monitoring	Cutting, burning or filling in of mangrove forests
Subsistence fishing for a household	Extraction and/or selling of: shells, corals, sea cucumbers, starfish, seahorses, sponges, sea fans, turtles, sharks and any sub-products
	Introduction of non-native species
	Fishing with: harpoon, chemicals, explosis or any other method other than hand or net
	Fishing of herbivorous reef fish species
	Industrial fishing
	Fishing while SCUBA diving
	Fishing/ hunting of endangered species
	Removal and selling of archaeological or heritage artifacts
	Removal / dredging of seagrass or coral
	Capture of all conch species
	Capture and selling of Spiny Lobster or other lobster species
	Fishing at grouper and snapper spawning aggregation sites
	Mooring >2 boats at a buoy
	Anchoring boats without a buoy
	Boating within swimming area or within 100 meters of diving buoy
	Jetskis, parasailing and other water sports within the barrier reef

While the BINMP extends twelve nautical miles around each island from the high tide line (10 meters into land) to a depth of 60 meters, several types of zones exist within its boundaries (Figure 13) (ICF, 2013). These include a buffer zone (ZA), restricted zone (ZR), zone restricted to fishing and agriculture (ZRPA), zone of economic development/multiple use (ZDE-ZUM) and a special marine protection zone (ZPEM) (ICF, 2013). Information about the zones and their various regulations is not readily available, nor are the boundaries physically marked in coastal and marine space. In the legislation of the BINMP, two ZPEMs exist in each subregion: Cordelia Banks and Sandy Bay to West End in Roatan, Turtle Harbour to Rock Harbour and Raggedy Cay in Utila, as well as Half Moon to Southwest Cay and Michael Rock in

Guanaja (Republic of Honduras, 2010). Cordelia Banks was declared a ZPEM due to the large stands of Acropora corals extending over 63,000 meters parallel to the airport on Roatan's southern shore (Canty et al. 2021; RMP, 2021). These shallow banks covered with coral reef are threatened by two surrounding cruise-ship ports, pollution, and over-fishing, though fishing and tourism are technically excluded (Figure 14) (Canty et al. 2021; RMP, 2021). The Sandy Bay to West End ZPEM covers 9.41km^2 along Roatan's western coast (Figure 15) and is an extension of the SBMR that was created in 1989; though, conflict in the area is high due to multiple uses, especially on cruise-ship days (Gombos et al. 2014). The Turtle Harbour to Rock Harbour ZPEM is a wildlife refuge (no-take zone) that covers 8.12km^2 on the northern shore of Utila, while the Raggedy Cay ZPEM cover 27.5km^2 of sandy cays and shallow shoals (Figure 16) (Republic of Honduras, 2010; Gombos et al. 2014). In Guanaja, the Half Moon to Southwest Cay ZPEM covers 25.8km^2 of open marine space, while Michael Rock encompasses 28km^2 of mangroves surrounded by two sandy beaches (Republic of Honduras, 2010, pers. obs. 2019). In addition, Guanaja also has a ZR of 4.8km^2 in between West End and Blue Rock Point (Republic of Honduras, 2010); however, neither a map, nor a list of regulations, or other information regarding this zone was found.

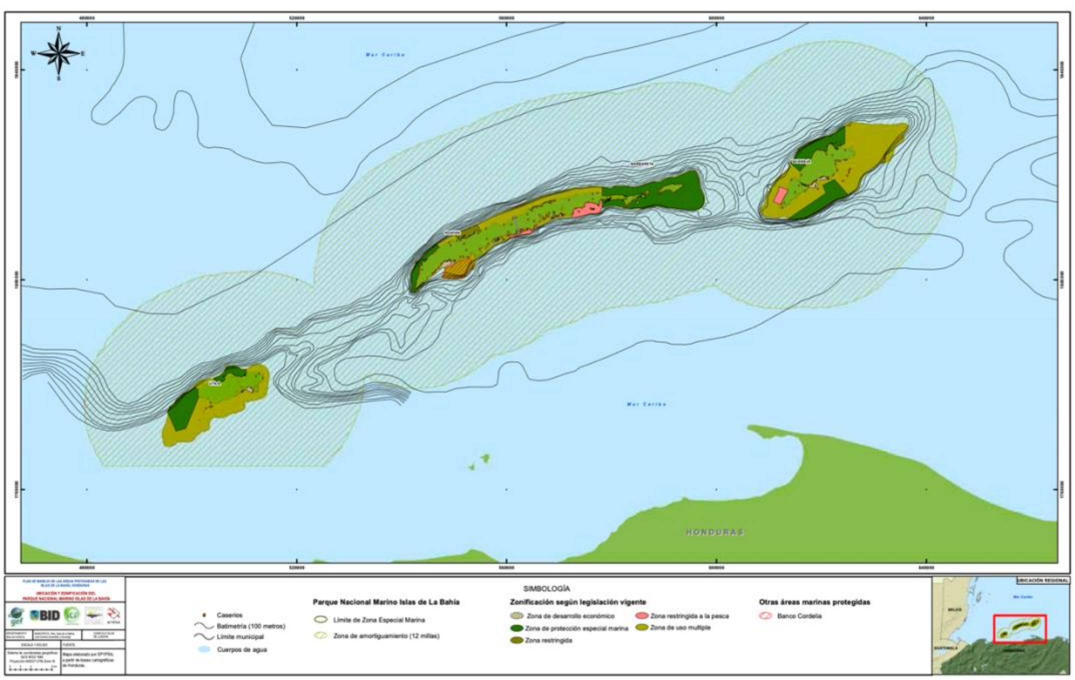


Figure 13: Multiple zones within the Bay Islands National Marine Park (ICF, 2013).

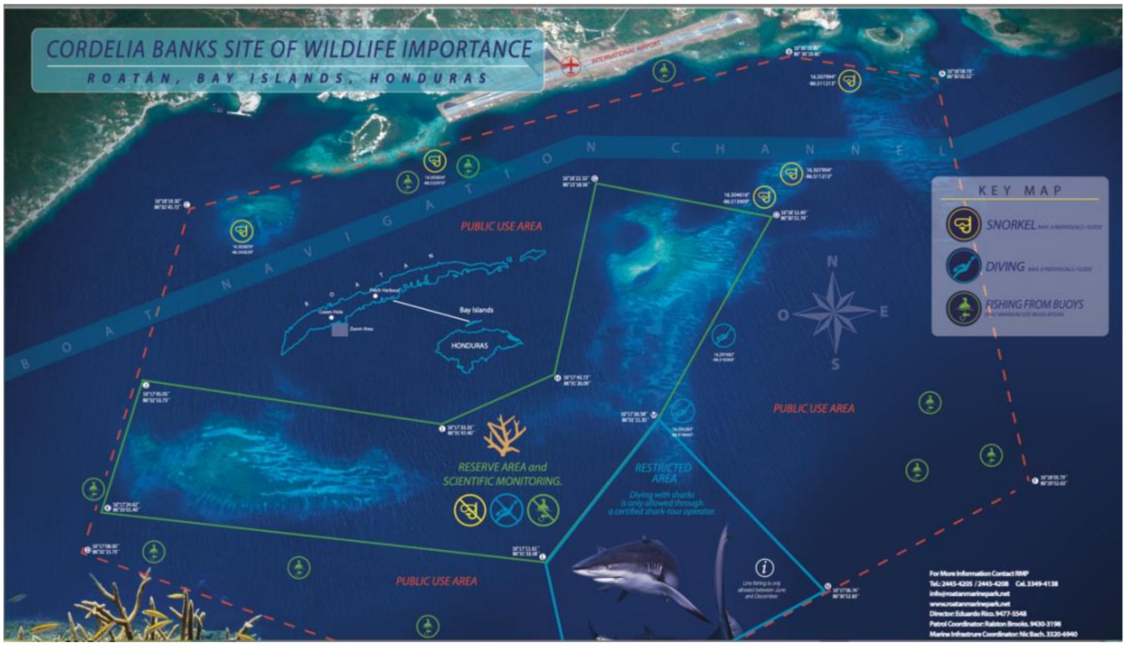


Figure 14: One of the special marine protection zones in the Bay Islands National Marine Park: Cordelia Banks, Roatan, Bay Islands, Honduras (RMP, 2021).

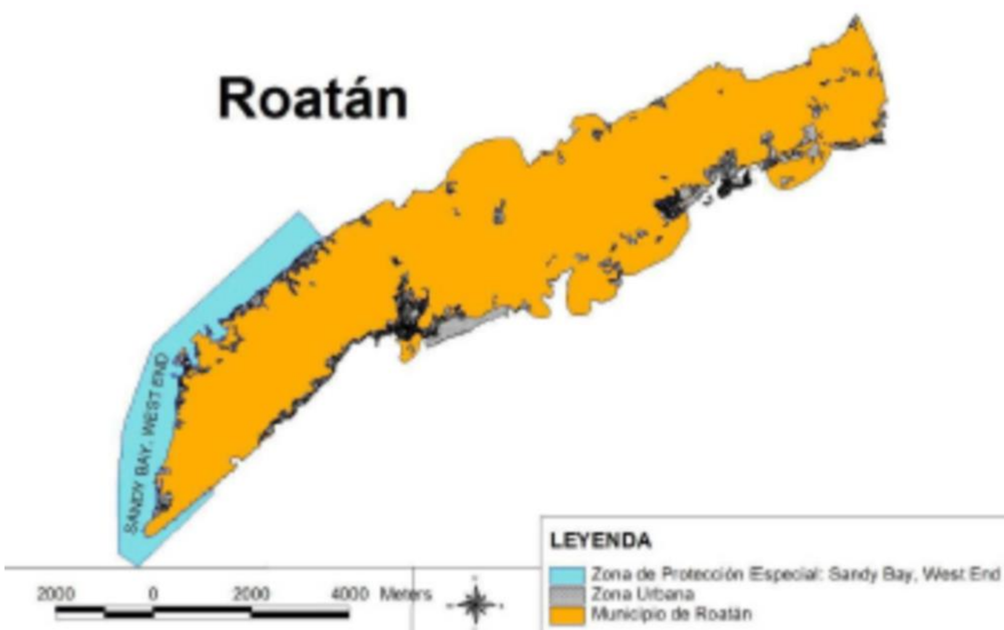


Figure 15: The Sandy Bay to West End special marine protection zones in the Bay Islands National Marine Park: Roatan, Bay Islands, Honduras (Gombos et al. 2014).

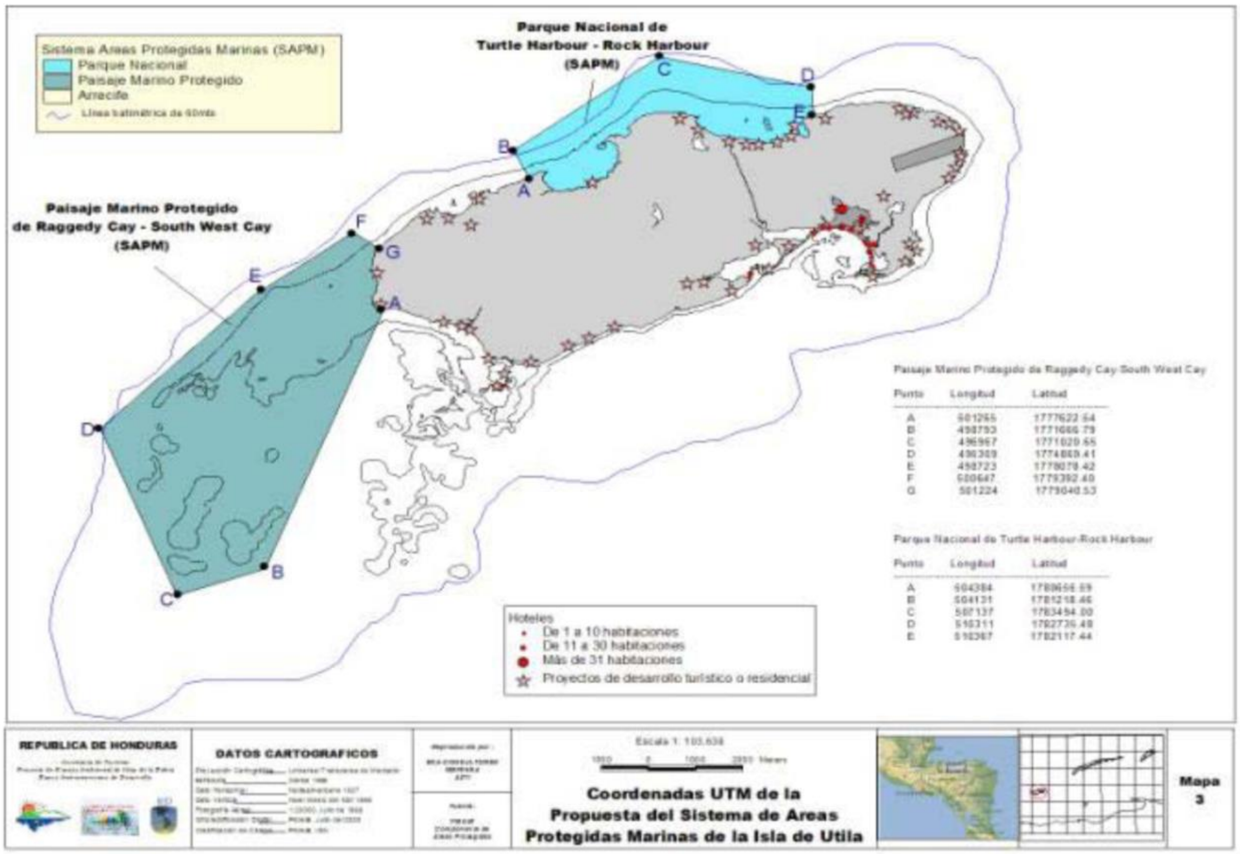


Figure 16: Two special marine protection zones in the Bay Islands National Marine Park on Utila, the Turtle-Rock Harbour, and Raggedy Cay (Gombos et al. 2014).

Despite the centralized nature of marine protection through national legislation passed in the mainland capital (Tegucigalpa) of Honduras, day to day operations in the BINMP are overseen by local ENGOs (Canty et al. 2018; pers.obv.2021). National governance in the park is not present, except for the Honduran Navy members who occasionally accompany patrol boats in Roatan (RMP, 2021; pers.obv.2021). One ENGO, BICA, is present in each subregion of the BINMP, and executes grass-roots initiatives like community education, beach clean-ups, and mangrove re-forestation (BICA, n.d.). Some ENGOs, such as the Roatan Marine Park (RMP), are only established in one subregion but have greater capacity. The RMP has a larger presence in the management and conservation of Roatan's ecosystems. They are responsible for installing marine tourism infrastructure (e.g. dive buoys, channel markers), patrolling against illegal activities, research initiatives (e.g., coral spawning), and community outreach programs (RMP, 2021). The RMP has ~10 fulltime staff members, whose salaries are paid primarily via donations and scientific project grants, as well as a large volunteer base of divers from tourists and dive professionals that live and visit the island. One of RMP's longest-running initiatives is the lionfish spearing license program, which includes an educational course for tourists and dive professionals alike to learn how to reduce the population of this invasive species within the BINMP. Many divers within the park (not just in Roatan) participate in the culling of lionfish, though more are found at deeper aggregate and patch reef habitats where divers have less access (Biggs and Olden, 2011; Andradi-Brown et al., 2017b). In addition to this license, the RMP also provides tourists and local residents with a yearly update to a Bay Islands Responsible Seafood Guide (Figure 17). They adapt their programs frequently, and their most recent conservation project is treating the spread of Stony Coral Tissue Loss Disease with antibiotics at numerous reef sites around the island (RMP, 2021). Public reporting is done primarily via websites and webinars.

Figure 17: The new (2021) Bay Islands responsible seafood guide. Adapted from: Roatan Marine Park (www.roatanmarinepark.org/rsg).

3.3 Anthropogenic impacts

3.3.1. Fisheries

Fishers from the Bay Islands partake in four types of fisheries: industrial, artisanal, recreational, and subsistence. Artisanal and subsistence fisheries began many generations prior to industrial ones, and are presently active throughout all subregions in the Bay Islands. Their expansion, along with the rise of recreational fisheries, rose in the 1970s; however, fisheries have been an important economic sector in Honduras for more than 100 years (Canty et al. 2019). In the early 20th century, prior to national industrial fisheries, other foreign fleets, such as the United States, were fishing along the northern Honduran coast and Bay Islands (Canty et al. 2019). Nationalized industrial fisheries began in the 1950s and continue presently, though no longer within the Bay Islands, and in a reduced capacity due to significant declines in stocks (Funes et al. 2015).

The Bay Islands once held the largest industrial fishing fleet in the Caribbean in the early 1970s, when fishers were forced to move from nearby exploited reefs to further offshore banks to supply the increased export demand to the United States, primarily for shrimp and lobster (Harborne et al., 2001). In the 1980s and 1990s, the highest catch by weight and value were of conch, filling the gap in the United States market from Florida's fishery, which collapsed in 1975 (Funes et al., 2015). Industrial fishing in much of the late 20th century included lobster (Caribbean spiny lobster (*Panulirus argus))*, conch (pink and queen conch (*Lobatus spp.*)), shrimp (southern white shrimp (*Penaeus schmitti*) and northern pink shrimp (*Farfantepenaeus duorarum*)), and finfish (primarily of the snapper (Lutjanidae) and grouper (Serranidae) families) (Funes et al. 2015). Industrial fisheries continue today within FAO Area 31 (Caribbean), with a variety of vessel sizes (4 to 78 m), crew sizes (6 to 85 people), and length of fishing seasons (10 to 90 days) (Canty et al. 2019). Approximately 90% of the catch is exported to the United States, though noticeable declines in industrial fisheries over the past two decades have impacted Bay Islands fishers significantly (Funes et al., 2015).

In 1991, the Honduran government established a fishing and agricultural department, DIGEPESCA, to regulate fishing activities and record catches (Canty et al. 2019). In their records, total industrial catch, total discards, and the number of industrial fleet licenses began to decline in the 1990s and 2000s (Funes et al. 2015). Official Honduran records report total catch in 1950 at 500t, and under 9,000t in 2015, while Funes et al. (2015) estimate total catches in

1950 at 5,000 t and in 2015 at over 26,000 t (Figure 18). Estimations of total catch values from 1950 to 2010 were 2.1 times greater than the quantities previously reported; unreported catches were from discards from the industrial shrimp fishery (45%), and unrecorded catches (artisanal (40%), subsistence (11%), and industrial (4%)) (Funes et al. 2015). According to their catch reconstruction data, the peak of industrial fisheries occurred earlier, in 1987 at US$59 million, and by 2015 declined to under US$13 million (Funes et al. 2015; Canty et al. 2019). However, this decline in industrial fisheries was hidden by the simultaneous increase in artisanal catches, which in 1996 surpassed the industrial catches, and continues to make up most of the total catch in the region (~60%) (Canty et al. 2019).

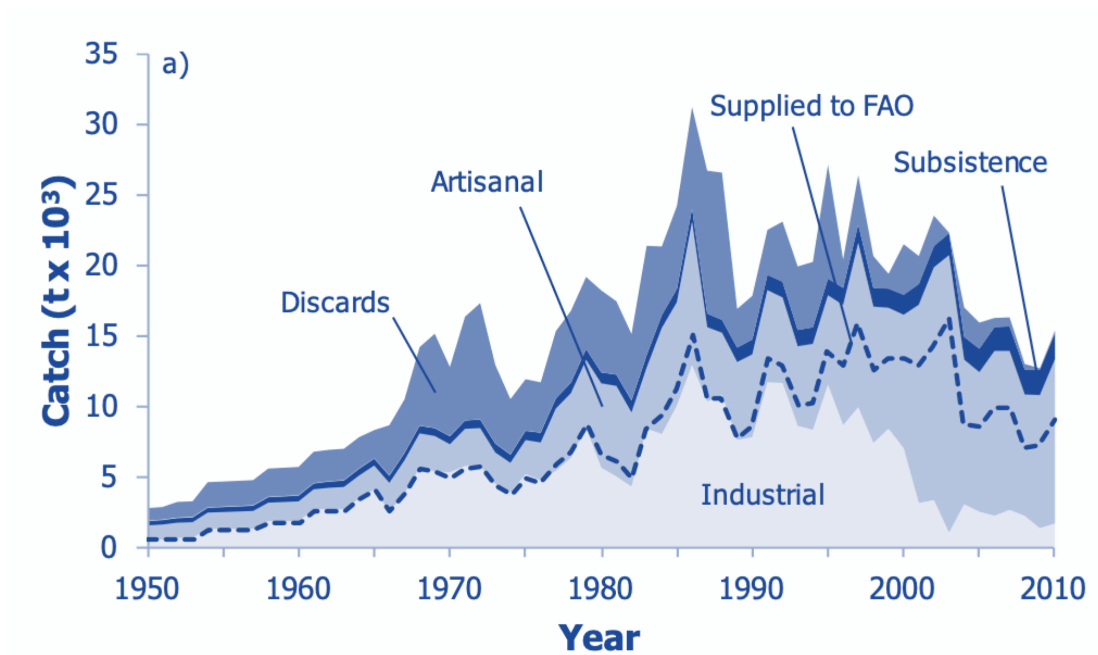


Figure 18: Reconstruction of catch records from 1950 to 2010 in Honduras (Funes et al. 2015).

Artisanal fisheries peaked in 2003 with an estimated value of $US35 million, and total catches remain high (20,000t in 2015) (Canty et al. 2019). Coral reef artisanal fisheries are multi-species and multi-gear, and they exert a high fishing pressure level in Honduras (Teh et al. 2013). As most industrial catch is exported, the demand from artisanal catch continues to increase with increasing local populations and number of tourists, who often request fresh fish (Funes et al. 2015). Over 7,000 artisanal fishers are registered with DIGEPESCA, and more than 135 different fishing communities are in the study region (Canty et al. 2019). Fishers utilize a variety of tools and methods ranging from small-scale hand and line fishers on wooden canoes to fiberglass boats with multiple outboard engines (Gobert et al. 2005; pers. obv. 2017 – 2021). Four distinct types of artisanal fisheries are accessed, including hand-lining for coral reef fishes or deep-water species, trapping during grouper spawning events, trolling for pelagic species, or collecting of invertebrates (lobster and conch) using SCUBA equipment or freediving (Chollett et al. 2014). Fishing pressure varies widely within the Bay Islands; some areas are highly exploited (e.g., west Roatan = 1.6t/km^2) while other areas have lower annual production (e.g., Guanaja = 0.15t/km^2), perhaps due to stocks that have been previously fished out (Gobert et al. 2005). Most fishers target shallow and deep reef species, which together make up 87% of total landed catch (pelagic species are the remaining 13% of catch) (Box and Canty 2010).

Various types of finfish are targeted by artisanal fishers in the Bay Islands, including highly valued coral reef fishes like snappers (Lutjanidae) and groupers (Serranidae), as well as pelagic species such as wahoo (*Acanthocybium solandri*), mahi mahi (*Coryphaena hippurus*), kingfish (*Scomberomorus cavalla*), crevalle jack (*Caranx hippos*) and blackfin tuna (*Thunnus atlanticus*) (Box and Canty 2010; Chollett et al. 2014). Often, smaller snappers, jacks, and grunts are viewed as by-catch only (Gobert et al. 2005). Targeted snappers in the shallows (reef, from 0- 60m) include yellowtail (*Ocyurus chrysurus)*, mutton (*Lutjanus analis)*, dog (*L. jocu)*, shallow red (*L. purpureus)*, grey (*L. griseus)*, lane (*L. synagris)*, schoolmaster (*L. apodus)*, cubera (*L. cyanopterus)*, and mahogany (*L. mahogoni*), while deep-water species (>100m) include clubhead (*Rhomboplites aurorubens*), queen (*Etelis oculatus*) and red (*Lutjanus campechanus*) (Gobert et al. 2005; Box and Canty 2010). Targeted groupers include yellowfin grouper (*Mycteroperca venenosa*), red hind (*Epinephelus guttatus*), Nassau grouper (*E. striatus*), graysby (*Cephalopholis cruentatus*), coney (*C. fulvus*), goliath grouper (*E. itajara*), and black grouper (*M. bonaci*) (Gobert et al. 2005). In 1999, the snapper and grouper families accounted for 50.9-88.3% of the total catch in the Bay Islands (Figure 19) (Gobert et al. 2005).

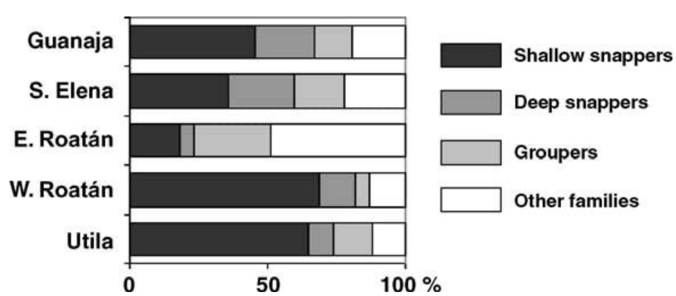


Figure 19: Characteristics of artisanal fisheries catch in various locations in the Bay Islands in 1999 (Gobert et al. 2005).

More recently, declines in large, highly valued snappers and groupers (e.g., mutton snapper, black grouper), have shifted pressures to smaller and faster growing fish (e.g., yellowtail snapper, blackfin tuna) across most of the archipelago (Cholett et al. 2014). The yellowtail snapper (*O. chrysurus*) accounts for ~36% of total fish catch, and tunas (*Thunnus atlanticus*) which were historically used as bait fish and rarely chosen for local consumption (Box and Canty, 2010), are now being sold to local restaurants and contribute towards subsistence (pers.obs 2019 – 2021). Some subregions (e.g, East Roatan, Guanaja) are depleted of snapper and groupers, and intensification is present as most species are being harvested in their juvenile phase (Gobert et al. 2005). For decades, massive yields from fishing events during aggregations and migrations used to supply large influx of income, which would make up for high operating costs (e.g. fuel) (Chollett et al. 2014). Notwithstanding, declines in certain fish stocks has not deterred this practice, as some entire communities rely solely upon the income from artisanal fisheries (e.g., 60% of the Utila cay population) (Box and Canty, 2010; Chollett et al. 2014). For example, in 2009 fishers from the Utila cays landed 17,884 lbs of mutton snapper (*Lutjanus analis)* in one week (Box and Canty 2010).

Recreational fisheries began with the rise in tourism during the 1980s and are presently active in many areas in the Bay Islands (e.g., West Bay, Roatan). This type of fishery is described as the capture and non-release of sport fish species, such as mahi mahi (*Coryphaena hippurus)* or wahoo (*Acanthocybium solandri)*, and over 35 companies offer recreational fishing tours in the Bay Islands (Canty et al. 2019). However, tours in the Bay Islands typically include both trawling for pelagics, as well as deep-water fishing (Enrick Bush, local fisher, pers. comm. 2019). Bay Islands fishers target deep-water snappers and groupers by bottom-fishing if no success was had during the pelagic fishing component of the fishing trip or by request of the charter guest (pers. obs. 2017, 2019, 2021). Occasionally sharks (e.g., silky (*Carcharhinus falciformis*), Caribbean grey (*C. perezi*) are caught, but in most cases, they are released in Roatan (Enrick Bush, local fisher, pers. comm. 2019). The intensity of recreational fishing is highest on one weekend each September, during the annual International Fishing Tournament. Since 1999, this annual tournament attracts dozens of fishing boats that target billfishes (Istiophoridae) and other fish such as Yellowfin tuna, wahoo, and barracuda (Canty et al. 2019; pers. obs. 2018-2019). In 2009, billfishes (e.g., marlin and sailfish) were to be properly released after a photo was taken in order to be eligible to win points in the ‘Billfish’ category of the tournament. Other fish species (e.g., yellowfin tuna) caught during the tournament are not released due to being awarded points in the 'Rodeo' category for the heaviest fish (pers.obv. 2017, 2019, 2021). Other smaller scale fishing tournaments occur nearby in Utila and Guanaja and are also catch and release.

Subsistence catch in the Bay Islands is often caught during artisanal and recreational fishing outings where some of the catch is retained for personal consumption (Canty et al. 2019). Total subsistence catch in the study region is estimated at over 20,000 tonnes per year (Cisneros-Montemayor et al. 2016). The mean fish consumption of Bay Islanders and the northern coast of Honduras is estimated at <30kg/per person/per year (Cisneros-Montemayor et al. 2016).

3.3.2. Coastal development

The un-sustainable pace and method of coastal development in the Bay Islands has been studied for over 20 years (Luttinger 1997; Forest 1998), yet it continues in present day (Kjerfve et al. 2021). In the 1990s, dramatic acceleration of the rate of coastal development was noted to negatively impact water resources (e.g., greater need for sewage treatment and of freshwater) (Harborne et al. 2001). This led to the establishment of the first environmental legislation, "Acuerdo Dos", for the Bay Islands to regulate coastal development (Forest, 1998). Despite extensive regulations (e.g., prohibition of coral extraction and mangrove clearing), rural land was rapidly developed to match the increased tourist demands by creating new roads, an airport, and numerous dive shops and resorts (Luttinger 1997). Many developments that filled in reef, cleared mangroves, or dredged out sensitive beach environments were able to obtain permits, which may have been due to the hastened nature of development and a lack of environmental expertise (Forest, 1998). However, coastal development in the Bay Islands continues to be destructive; permits are almost always approved, and fines are rarely given to offenders, regardless of "Acuerdo Dos" or objections from local islanders (Doiron and Weissenberger, 2014).

This rapid coastal development has fueled an incredulous rate of land use change in the Bay Islands; built and impervious surfaces have increased by 315%, while soil/vegetation cover decreased by 57% from 1985 to 2014 (Tuholske et al. 2015). Land changes occurred from deforestation, clear-cutting, burning, and construction (Forest 1998), which led to extensive sedimentation by coastal erosion (Harborne et al. 2001; Prouty et al. 2008). In addition to the sedimentation from changes occurring on the Bay Islands themselves, marine ecosystems within the study region are impacted by human alteration on the mainland of Honduras, Guatemala, and Belize from deforestation and agricultural practices (Harborne et al. 2001; Prouty et al. 2008). Sedimentation from mainland watersheds into the Gulf of Honduras has increased by 20 times and has been identified using geochemical indicators (Ba and Mn concentrations) in coral skeletons of the Bay Islands (Prouty et al. 2008). Increased Ba/Ca and Mn/Ca levels in corals from the Bay Islands indicated sediment runoff from rivers primarily in northern Honduras (e.g., Ulua, Motagua), which seasonally discharge large flows (Prouty et al. 2008). Most of the sediments originate from highly cultivated lands, and carry high sediment loads along with fertilizers, herbicides, and other pollutants (Kjerfve et al. 2021).

Coastal development has directly impacted critical habitats and ecosystems such as mangroves, coral reefs, and beach dunes (Harborne et al. 2001; Doiron and Weissenberger 2014). Severe losses in mangrove cover (-110,000 ha) were observed across the MAR from 1990 to 2010, with the greatest losses in Honduras and in Mexico (Canty et al. 2018). While mangroves are protected in Honduran legislation and international agreements (Canty et al. 2018), large swathes of mangroves in the Bay Islands have been cut down to make space for residential and tourism infrastructure development (e.g., resorts and marinas) (Doiron and Weissenberger 2014). Multiple beaches in the region have been created by dredging (e.g., Fantasy Island), and rocky shores have been dug out (Forest 1998; Doiron and Weissenberger, 2014). Increased development near beaches (e.g., buildings, lights) result in less pristine coastal ecosystems (Forest 1998). In addition, critical habitats such as coral reefs continue to be highly threatened by coastal development (Doiron and Weissenberger 2014). For example, large areas of coral reefs have been lost during development projects such as the 2019-2020 expansion of the cruise-ship port in Coxen Hole, Roatan (Figure 20).

Figure 20: Expansion of the cruise-ship port in Roatan, Honduras, which has filled in large section of coral reef for development purposes. Photos from Joel Amaya, and the Roatan Tourism Bureau (RTB, 2020).

3.3.3. Changes in population and demographics

The population in the Bay Islands has rapidly increased since the 1970s (Tuholske et al. 2015) and the demographics have changed extensively (Doiron and Weissenberger 2014). Five main community groups live in the Bay Islands including: i) Garifuna (Afro-Indigenous-Garifuna speaking), ii) European descent (Caucasian- English speaking), iii) Afro-Caribbean descent (Black- English speaking), iv) Hispanics (from Central America - Spanish speaking), and v) Ex-patriates (from the U.S.A, Canada, and the Czech Republic) (Pozzi, 2021).

The first historical account of peoples in the Bay Islands was written by Christopher Columbus, who visited Guanaja on his fourth and final voyage in 1502 (Pozzi, 2021). The Indigenous peoples he encountered had well-equipped and spacious boats to travel from the islands and trade with mainlanders (present-day Honduras) (Pozzi, 2021). In 1526, Indigenous peoples on both Guanaja (Los Guenejos) and Utila (Huitila) were mentioned in a letter by Hernan Cortes to the Spanish Emperor Charles V (Pozzi, 2021). Throughout the 16^{th} and 19^{th} century, European exploratory fleets interacted with these Indigenous groups when they stopped for supplies (Harborne et al., 2001). In 1638, an English merchant-landlord, William Clairborne was the first British settler to claim land in the Bay Islands, when he won a concession to establish a colony on Roatan (Rattan), though the Spanish expelled it shortly thereafter in 1642 (Pozzi, 2021). Throughout the 1600s, numerous Spanish and Indigenous settlements on the islands were raided by English, French and Dutch buccaneers, and well-known pirates such as Henry Morgan and Edward Teach (Blackbeard) lived on Roatan (Pozzi, 2021). In 1650, the Spanish removed all Indigenous peoples from the Bay Islands in an effort to expel all other peoples from their settlement (Pozzi, 2021). In the mid 1700s, English settlers from British Honduras (present-day Belize) occupied strategic locations such as Port Royal in Roatan, and the British continued to exercise sovereignty on the Bay Islands for over a century during which many Europeans of Scottish and English origin and Afro-Antillean black slaves immigrated to the Bay Islands (Pozzi, 2021).

In 1797, King George III of England declared the expulsion of Black Caribs (Garifunas) from St. Vincent to be exiled to the Bay of Honduras (Pozzi, 2021). Garifunas are Indigenous Afro-Caribbean peoples that arrived in Punta Gorda, Roatan after being taken from the West Coast of Africa, enslaved on St. Vincent & the Grenadines, then expelled to Roatan by the British (Doiron and Weissenberger, 2014). The Garifuna community and culture remains strong on Roatan, and other Garifuna settlements occurred shortly after in Cayos Cochinos, along the north coast of Honduras, and in some areas of Belize (Pozzi, 2021).

In 1859, a treaty was signed between Great Britain and Honduras (Pozzi 2021), and the British formally ceded the Bay Islands to Spanish Honduras in 1860 (Doiron and Weissenberger, 2014). Throughout the 1800s, English-speaking islanders of Afro-Caribbean descent from Jamaica and white Caymanians also emigrated to Roatan, which continued into the early 20th century with the establishment of American banana companies in the region (Pozzi, 2021). At this time, the majority of the population of the Bay Islands were English-speaking islanders (of both European and Afro-Caribbean descent) who resisted language assimilation by the Spanish-speaking Honduran government, and who kept a distinct English-speaking culture for over one hundred years (Doiron and Weissenberger, 2014). Islanders have developed their own distinct language (Island English), culture and traditions (Pozzi, 2021). To this day, the descendants of these European settlers, ‘Caracoles’ remain the highest portion of the population in some areas of the Bay Islands; for example, the Utila cay population consists of 65% white Cayans, Hispanics (25%), Garifuna (8%), and expatriates (2%) (Box and Canty 2010).

However, in recent years a substantial population increase from Hispanic mainlanders have changed the demographic of the Bay Islands. This has become a point of concern for many islanders who would be in favour of restricting immigration to the islands because mainlanders from low socio-economic class are willing to work for lower salaries than islanders (Doiron and Weissenberger, 2014). Lastly, ex-patriates make up the final community group in the Bay Islands and whom have approximately 3,000 homes within the archipelago (Gov. Dino Silvestri, pers. comm.). The majority of ex-pats within the Bay Islands are retirees from the United States, Canada, and the Czech Republic, while others are in real-estate, dive tourism, or are digital nomads (Gov. Dino Silvestri, pers. comm. 2021).

Population estimates for the Bay Islands archipelago are wide-ranging. Estimations range from 13,000 in 1970 (Tuholske et al. 2015), to 48,000 in 2005 (Gobert et al. 2005), to 71,296 in 2013 (Censo Nacional de Poblacion y Vivenda 2013), to over 100,000 people in 2015 (Tuholske et al. 2015). Roatan is the most populous, with an estimated population of 61,000, while Guanaja has an estimated population around 5,700, and Utila around 4,500 (INE, 2018). Most of Guanaja's population >5,000 people live on a small low-lying cay called Bonacca (UNEP-CEP 2021). Private organizations like Brown and Caldwell (2002) estimated that Utila had a higher population of approximately 7,800 residents 17 year prior in 2001. More recent estimations by local authorities noted a large decline in the population during the covid-19 pandemic to approximately 60,000 people throughout the department in 2020, including 48,000 in Roatan, 7,000 in Utila, 5,000 in Guanaja, and around 150 people in Cayos Cochinos (Gov. Dino Silvestri, pers. comm. 2021). The demographics in each subregion of the Bay Islands differ. The highest proportion of islanders (both Afro-Caribe and European descent) to mainlanders (Hispanic descent) occurs in Utila (70:30), whereas in other subregions the communities are more evenly mixed (Guanaja: 60:40, West Roatan 50:50, and East Roatan 60:40), and in Cayos Cochinos nearly all of the community members are Garifuna (Gov. Dino Silvestri, pers.comm. 2021). The population of cays in Cayos Cochinos is highly variable, as most community members live some parts of the year on the mainland of Honduras (Canty et al. 2018). Chachahuate is the main inhabited cay in Cayos Cochinos with approximately 50 wooden homes (Figure 21) (pers. obv. 2018, 2019).

Figure 21: Chachahuate Cay, in Cayos Cochinos, Honduras. Photo: F. Krysiak (2019).

3.3.4. Land-based pollution

Land-based pollution exist in the Bay Islands in three main forms: 1) wastewater discharge, 2) plastic waste, 3) chemicals. Wastewater includes discharges of sewage (black waters), wash water (grey water), and agricultural runoff (Degeorges et al. 2010). Since the late 1980s, traditional sewage treatment and disposal across coastlines of Caribbean islands were inadequate to prevent inputs of land-sourced nutrient pollution and eutrophication to coral reefs (Degeorges et al. 2010). Estimations of treated wastewater in Honduras currently range from 1.8% (HRI, 2020) to 3.2% (Nature Conservancy, 2021). These estimations are the lowest of any region across the MAR (e.g., Mexico = 46.5% treated) (HRI, 2020). The majority of wastewater sources found directly in the Bay Islands is from sewage discharge and grey-water, while indirect sources of agricultural runoff are from mainland watersheds (Brown and Caldwell 2002; UNEP-CEP 2021; CORAL, 2021; Kjerfve et al. 2021).

Sewage discharge (black waters) is a major pollutor in marine and coastal ecosystems across the Bay Islands. In Roatan, the largest and most populated subregion, only a few communities have access to proper wastewater treatment and disposal. In 2012, the Coral Reef Alliance assisted local organizations (Polo's Water Association and Roatan Marine Park) in the community of West End, Roatan by connecting 137 out of 360 homes and businesses to a small-scale treatment plant (Summit Foundation, 2017). This plant is estimated to divert between 14 million gallons of raw sewage per year (Summit Foundation, 2017) to 28 million gallons of wastewater per year (Nature Conservancy, 2021). Residential and commercial users of the West End treatment plant increased from 37% in 2012 to 98% in 2018 (HRI, 2020). In contrast, there is no wastewater collection, nor treatment system for any communities in Utila; all wastewater is discharged directly into the marine environment, or into non-engineered septic tanks that discharge into the soil, or onto the ground, which drains along streets (Brown and Caldwell 2002; CORAL, 2021). In Guanaja, the situation is similar and approximately 70% of the population's sewage (>5,000 people) is dumped directly into the marine environment, while the other 30% have a septic type of system with no concrete bottom (UNEP-CEP 2021). No information on waste-water treatment was found for communities in Cayos Cochinos, however from personal observations made in this subregion, no wastewater treatment facility exists, and sewage is discharged directly into the sea.

Another form of wastewater discharge that impacts the Bay Islands is agricultural runoff.. There are no local agricultural installations, except for a small-scale eco-friendly hydroponic farm on Roatan, the Blue Harbour Plantation. Runoff from this hydroponic farm is estimated to be minimal, as their sustainable farming practices utilize rainwater and no pesticides (Blue Harbour, 2020). However, agricultural runoff from sources on the nearby mainland of Honduras does occur. Freshwater from mainland watersheds flows through vast areas of banana, pineapple, palm-oil, and coffee plantations, with high inputs of fertilizers, herbicides, and other agricultural pollutants before it enters into the Gulf of Honduras near the Bay Islands (Kjerfve et al. 2021). While there are no direct sources of this type of discharge found on the islands, marine and coastal ecosystems are impacted by these indirect sources.

Plastic waste is prevalent throughout the Bay Islands and can be seen in all coastal and marine environments (e.g., mangroves, reef, beaches) in both macroplastic and microplastic form. The majority of plastic waste originates from urban areas in the mainland of Honduras & Guatemala, where waste management is limited. There is no policy or system for waste management in most of Guatemala, while in Honduras, just 28% of domestic waste is collected, and less than 4% (3.7%) of the total waste ends up in a controlled landfill (Kikaki et al. 2020).

Due to the lack of waste systems in place for millions of people, open-air waste burning, uncontrolled dumping on land and in water bodies are common disposal activities across the region (Kikaki et al. 2020). Frequent discharges of plastic waste enter the marine environment from the Motagua River (Guatemala) as well as the Ulua, Tinto, Cangrejal and Aguan rivers (Honduras); the plastic waste travels over 200 km from urban sources and arrives along coastal environments across the Bay Islands due to dynamic surface circulation in the Gulf of Honduras (Kikaki et al. 2020). Massive floating plastic aggregations of an average of 6km in length x 1-40 m in width travels an average speed of 6 km d^{-1} in a southwest to northeast direction, driven by sea surface currents (Figure 22) (Kikaki et al. 2020). Each of the 20 major plastic discharge events that occurred between 2014 – 2019 resulted in 400 +/- 250 tonnes of plastic waste entering the marine environment and totalling an estimated 8,015 tonnes over the 5 year period studied (Kikaki et al. 2020).

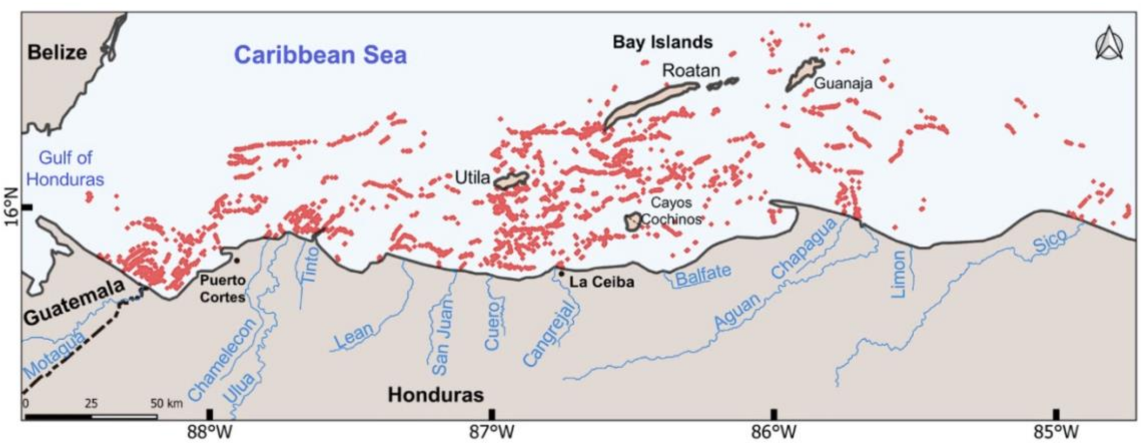


Figure 22: Total plastic debris (red dots) from 2014 – 2019 in the southern Gulf of Honduras. Rivers transport plastic waste from the mainland to the ocean, and prevailing winds and currents deposit the debris throughout the region (Kikaki et al. 2020).

Chemical pollution occurs in marine ecosystems of the Bay Islands primarily from shipping and tourism industries in the form of trace metal contamination (Prouty et al. 2008). Industrial shipping one of the largest industries in the Gulf of Honduras, and multiple sites in subregions Utila and Cayos Cochinos have elevated Cu/Ca and Sb/Ca levels (Prouty et al. 2008). The most likely source of these trace metals is the copper–antimony additives found in anti-fouling paints used on boat hulls, which has been shown to be detrimental to coral reef development (Prouty et al. 2008).

3.3.5. Tourism

Since the collapse of industrial fisheries, tourism has become the primary industry in the Bay Islands, which has driven a rapid boom of economic development since the 1980s (Doiron and Weissenberger, 2014; Pozzi 2021). Prior to this boom, early estimates of tourist visitors were as low as 900 per year in 1969 (Forest 1998), a time when no roads, telephones, or electricity existed within the region (Pozzi, 2021).

"In the 1960s, there was no airport, no roads, no cars, no electricity, no phones, and no tv. Paradise!" – Eric Anderson (Prominent land owner, conservationist, and founder of Port Royal National Park on Roatan) [Excerpt from ROATAN – by Lizette Pozzi]

In the early 1990s, the number of annual visitors increased to 30,000; the majority of whom were scuba-divers who were drawn by coral reefs and beaches (Luttinger 1997; Forest 1998). Estimates of annual visitors jumped to 100,000 in 2000, and to over a million people per year by 2010 (The Guardian, 2017). The number of visitors to the subregion of Roatan in particular has increased by 80 times since the 1990s, which over-shadows its local population by almost 20 times (Tuholske et al. 2015). The majority of the growth within this subregion has been attributed to the cruise ship industry (The Guardian, 2017), which carries over 1.1 million passengers to Roatan's two ports each year (Poitevien, 2018).

Since 2000, the number of ships visiting the subregion each year has increased by 4 times, and 18 different cruise ship lines call to port in Roatan (The Guardian, 2017; Poitevien, 2018). While the number of cruise ship tourists diminished during the covid-19 pandemic, ships returned to regular visits in July, 2021 and Roatan currently receives between 4 to 10 ships per week (Gov. Dino Silvestri, pers.comm.). In addition to cruise-ships, tourists can access each of the four subregions via the sea and air; three of four (Roatan, Utila, and Guanaja) have airports and Cayos Cochinos has a helicopter landing pad (pers. obs. 2021). Tourists contribute over US$ 500 million to the Bay Islands each year from marine and coastal based activities (The Nature Conservancy, 2021).

The Bay Islands are renowned as a scuba-diving and sport-fishing destination. Numerous dive centers, hotels, and marinas offer scuba-diving, snorkeling, and boating activities for the millions of tourists that visit the region each year (Wright et al. 2020). The highest intensity of marine tourism occurs in West Roatan (West Bay, West End) where over 30 dive centers operate within 8km of coastline, as well as sport-fishing boats, and dozens of water taxis (Wright et al.

2020). Dive centers operate in each of the four subregions in the Bay Islands, with over 60 in Roatan, 16 in Utila, 4 in Guanaja, and 1 in Cayos Cochinos (RTB, 2020). Many of these dive operators adopt responsible practices, and it is difficult to distinguish between normal diving tourism and diving eco-tourism (Doiron and Weissenberger 2014). Tourists also participate in sport-fishing tours year-round, including private day charters (e.g., Ruthless Roatan Charters), and the annual International Fishing Tournament mid-September, which attracts hundreds of fishers from many countries to the Bay Islands (pers. obs. Sept. 2017- Sept. 2021). The tourism industry also includes numerous hotels, hostels, rental properties, restaurants, bars, shops, and other establishments, which provide logistical support for these marine-based activities (Wright et al. 2020).

3.3.6. Climate change

In addition to the afore-mentioned impacts, climate change is currently impacting the entire Caribbean region in numerous ways such as increasing mean temperatures, increasing rainfall, rising sea level, ocean acidification, and extreme weather events (e.g., heatwaves, tropical cyclones) (IPCC, 2021). Mean temperatures and ocean acidification are very likely to continue increasing, while extreme events like marine heatwaves and tropical storms are all very likely to increase in intensity and duration (IPCC, 2021). Relative sea level rise contributes to increased flooding in low-lying coastal areas and shoreline retreat along sandy coasts (IPCC 2021), which will impact coastal ecosystems like the coral reefs, seagrasses, mangroves, and beaches found in the study area (Doiron and Weissenberger 2014). The region is particularly susceptible to climate change (Glenn et al. 2015), especially from two impacts from climate change: increasing sea temperatues, and increasing frequency and intensity of storms. This was exemplified in 1998 when hurricane Mitch followed a massive bleaching event that left coral reefs decimated (Kramer and Kramer 2002).

Sea surface temperature (SST) is the main predictor of coral bleaching (Doiron and Weissenberger 2014), and temperatures in the Caribbean are rising faster than the global average (IPCC, 2021). In the study region, SST ranges from 28°C to 32°C, though it has been warming significantly over a 31-year period from 1982 to 2012, and the greatest changes occurred in the latter 15 years (Figure 23; Figure 24) (Glenn et al. 2015). Warmer than normal SST for extended periods of time is known as a marine heatwave, which can result in mass coral-bleaching events.

Prior to the mid-1990s, documentation of bleaching events in the study region is limited (Harborne et al. 2001). However, severe bleaching events affecting the Bay Islands were studied in 1995 (Harborne et al. 2001), 1998 (Kramer and Kramer, 2000), 2005, and 2010 (Doiron and Weissenberger 2014), 2015, and 2017 (Kjerfve et al. 2021). During these events, coral mortality ranged between 19% (Kramer and Kramer 2000) to over 90% (Harborne et al. 2001). Increasing frequency and intensity of these events place coral reef ecosystems at greater risk (Kramer and Kramer 2002).

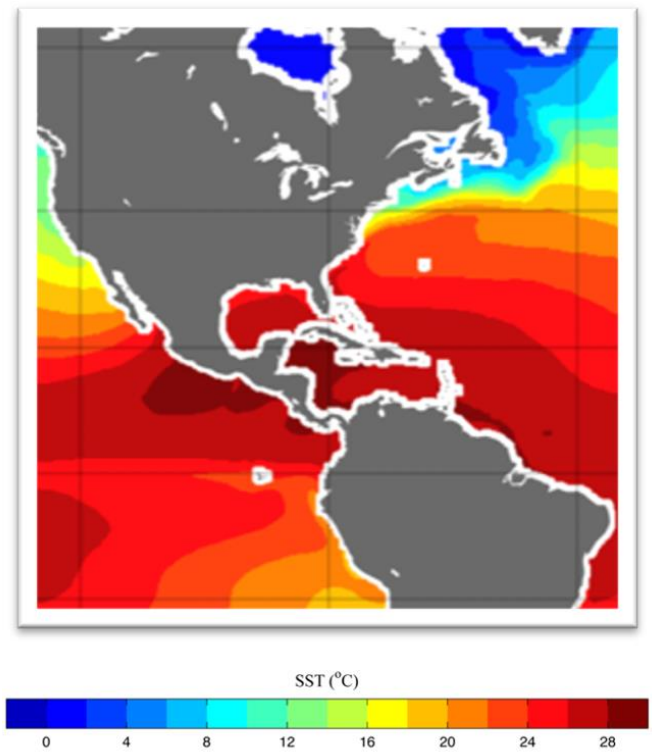


Figure 23: The ten year daily average sea surface temperature around Central America (1998 to 2007) (Clayson et al. 2016).

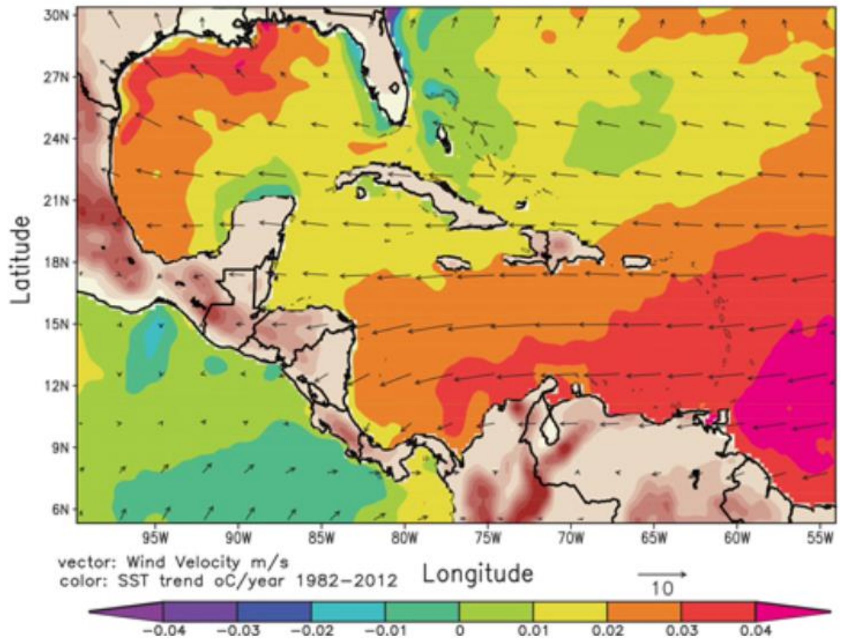


Figure 24: Trends in sea surface temperature and prevailing winds in the Caribbean Sea from 1982 to 2012 (◦C/year) (NOAA- CREST, 2015).

In addition to increasing sea surface temperatures, the Bay Islands are highly susceptible to disturbances like hurricanes (Kramer and Kramer 2002), and storms within the region are expected to become more extreme (IPCC, 2021). The region experiences hurricanes frequently, mostly from the east south-east (Figure 24) (Kjerfve et al. 2021). Strong winds and waves cause damage to coastal ecosystems from a combination of impacts including breakage, flooding, changing water transparency and nutrient inputs, and reduced herbivory by reef fishes (Kjerfve et al. 2021). For example, Hurricane Mitch was a category 5 storm that hovered over Guanaja for two days in 1998 (Erdman, 2020). This storm damaged 50 to 70% of coral reefs in the Bay Islands from breaking, overturning, and burying many corals (Kramer and Kramer 2000). Destruction from hurricanes and other storms can also occur from longer-term ecological shifts beginning with areas of dead coral being colonized by turf algae, macroalgae, and sponges, leading to area wide destruction of reef ecosystems (Kjerfve et al. 2021).

Figure 25: Hurricane Mitch hovering over Guanaja, Bay Islands in October 1998 (NOAA).

4. DISCUSSION

4.1 Trends of reef fishes in the Bay Islands over the past decade

Over the past fifteen years, assessments of reef fish biomass in the Bay Islands via UVS have recorded significant declines in overall biomass as well as herbivorous fish biomass, and low levels of commerically valuable fishes. Obtaining fish biomass estimates from UVS combines abundance and size data to provide a holistic assessment of fish assemblages (Wilson et al. 2018), determine ecological functions (Andradi-Brown et al. 2016), and can be related to herbivory, predation, overall trophic structure, and ecosystem state (Barnes et al. 2019). In this study, we observe declines in three categories of reef fish biomass: total, herbivorous, and commericially valuable, as well as changes within reef fish assemblages throughout the Bay Islands.

Our findings show declines in total reef fish biomass in all four subregions (Table 3), despite regional protection in two nationalized MPAs. Rates of declines differed across the Bay Islands, most likely because of varying levels of anthropogenic pressures in each subregion driving the declines. For example, the average total reef fish biomass in Roatan declined by 66.8% from 2006 to 2021 (n= 1839), while in Utila it declined by 43.5% during the same period (n = 821). Predictions generated by our linear mixed effects model suggest that total reef fish biomass throughout the Bay Islands will continue decreasing. While significant losses in biomass are projected for about half of the global ocean (40%-57%) (Boyce et al. 2020), effective MPAs have been shown to have up to five times more reef fish biomass (Edgar et al. 2014). In protected areas that allow fishing, Edgar et al. (2014) recorded a great decline in overall fish biomass (-63%), including larger reductions for vulnerable groups like large fish (-80%), sharks (-93%), jacks (-85%) and groupers (-84%). The decline in overall fish biomass observed by Edgar et al. (2014) of -63% is comparable to overall declines examined in recent years of the Bay Islands, suggesting the ineffectiveness of these marine parks.

Our results show a decline in herbivorous reef fish biomass throughout the Bay Islands in the past fifteen years. According to HRI's indicator scale (Table 1), all four subregions had "Very Good" scores (>3,290g/100m^2) at the start of the study period in 2006. In 2018, Utila scored "Good" (mean = 2,835g/100m^2) while Guanaja and Roatan scored "Fair" (1,860- 2,740 g/100m^2). Only Cayos Cochinos scored "Poor" (mean =1769.7g/100m^2) (Table 7). Predictions generated by our linear mixed effects model suggest that herbivorous fish biomass throughout the Bay Islands will continue decreasing and reach the "Poor" score (990- 1,860g/100m^2) in the near future (Figure 6). Nevertheless, these estimates are higher than in other coral reefs in the Eastern Caribbean which ranged from 944g to 1,736g/120m^2 in fished and non-fished marine reserves, respectively (Steneck et al. 2018). This suggests that herbivorous reef fishes in the Bay Islands may not experience as much fishing pressure than in other areas of the Caribbean. Biomass estimates varied extensively throughout the region, with multiple transects with zero herbivorous fish recorded to some reaching over >50,000g/100m^2 (Appendix VI).

Commercially valuable reef fish biomass has also declined throughout the Bay Islands in the past fifteen years. According to HRI's indicator scale (Table 1), two subregions (Cayos Cochinos and Roatan) had "Very Good" scores (>1,620g/100m^2) at the start of the study period, while Utila ranked "Good" (mean = 1356.4g/100m^2), and Guanaja ranked "Poor" (mean = 518.4g/100m^2). In 2018, all four subregions in the Bay Islands had lower biomass values associated with the second lowest score ("Poor" = 390-800g/100m^2) (Table 7). Predictions generated by our linear mixed effects model suggest that commercially valuable fish biomass throughout the Bay Islands will continue decreasing towards "Critical" levels (<390g/100m^2) (Figure 7). These biomass levels are comparable to other coral reefs in the Eastern Caribbean. Steneck et al. (2018) assessed the predatory fish biomass (also just snappers and groupers) in fished and non-fished marine reserves and recorded values from 290g to 728g/120m^2, respectively. The average commercially valuable reef fish biomass in the Bay Islands falls within this range, however, it is important to note that many sites surveyed in the study region throughout the Bay Islands had zero commercially valuable biomass (e.g., George Cay, Guanaja). Commercially valuable fish biomass varied extensively throughout the Bay Islands, ranging from zero in many transects across all four subregions to >30,000g/100m^2 in some subregions (e.g., Cayos Cochinos, Utila, and Roatan) (Appendix VI). In contrast, Guanaja did not have any transects with commercially valuable fish biomass values over 10,000g g/100m^2 (Appendix VI).

Reef fish assemblages were also examined in the Bay Islands over the past fifteen years (Figures 8-12). Herbivorous fishes, including parrotfish (41%) and surgeonfish (15%), dominated fish assemblages throughout the study period across the Bay Islands. This explains large similarities between our results of total reef fish biomass and of herbivorous reef fish biomass. On average, commercially valuable fish contributed much less to the overall fish community (8% and 4%, respectively) (Table 8). Differences in the percent contributions of each of the twenty fish families recorded was varied across subregions. For example, Cayos Cochinos experienced large variations in the percent contribution of some families (e.g., snappers and parrotfish), most likely due to a smaller number of sites sampled in 2021. Some regions (e.g., Guanaja) experienced relatively stable fish family compositions throughout the entire study period (Figure 9; Figure 12). Our results of reef fish assemblages in marine parks in the Bay Islands can be compared to those recorded in the Exuma Cays reserve, which established a no-take zone in 1986 (Mumby et al. 2006). Contributions towards predatory fish assemblages were particularly high for Nassau groupers (45%), tiger groupers (27%), and a combination of barracuda, morays, and large snappers (28%) (Mumby et al. 2006). This exemplifies how fish assemblages can recover to pre-exploited distributions if fishing pressure reduces. If protection increases and human impacts decrease in the Bay Islands, fish assemblages in the study region may include greater contributions from highly targeted fish families, like snappers and groupers.

4.2 Linking anthropogenic impacts to the decline of reef fishes

Fisheries

Our results suggest that impact from fisheries has the greatest linkage to the declines of reef fish in the Bay Islands. The greatest direct threat to coral reefs is overfishing (Jackson et al. 2001; Teh et al. 2013) which can be assessed by using biomass as an indicator for gradients of fisheries exploitation (Darling and D'agata 2017). High levels of exploitation in the Bay Islands have reduced overall fish biomass, and caused population collapses in some reef fishes (e.g., Nassau groupers (*Epinephelus striatus*)) and in other species (e.g., lobster, conch) (Funes et al. 2015). While industrial fisheries have been in decline since 1986, pressures from artisanal, recreational, and subsistence fisheries continue to rise (Canty et al. 2019). Barnes et al. (2019) state that all coral reef fisheries have faced the tragedy of the commons. This is applicable in the Bay Islands, because the MPAs that exist have offered little protection to the reef fish populations in the face of the open access laws of Honduran fisheries. Multiple fisheries in the area have declined sharply within the past 20 years, which local fishers have attributed to juvenile overfishing, habitat destruction, and in the industrial fishery – the use of harmful gear (e.g., bottom trawl) (Funes et al. 2015). Presently, high fishing pressures (from artisanal, recreational, and subsistence) are unregulated and unreported, which threatens the populations of reef fishes themselves, the entirety of coastal ecosystems in region, and the thousands of people that rely upon them for various needs (e.g., food provision, livelihoods, cultural heritage).

Exploitation of reef fish was noticed as early as the 1970s, when fishing fleets moved to offshore banks because nearby reefs could not produce sufficient yield for export markets. The rapid reduction of community biomass from industrial fisheries has been demonstrated by Myers and Worm (2003) who found that these fisheries can reduce biomass by 80% within 15 years. This type of reduction typically occurs before scientific monitoring begins (Myers and Worm 2003). As seen in the Bay Islands, monitoring of reef fish populations that overlap with industrial fisheries (e.g., snappers and groupers) began decades later in 2006. At the beginning of this study period, subregions such as Guanaja already had low commercially valuable reef fish biomass (mean = 518.4g/100m^2) compared to other parts of the Bay Islands (e.g., Cayos Cochinos: mean = 2,092.8g/100m^2), which suggests that some areas had already been depleted from over-fishing. Localized ecological extinction from over-fishing pre-dates other human impacts such as water quality degradation and climate change (Jackson et al. 2001). The subregion of Guanaja was the first area within the Bay Islands to have seafood packing plants over fifty years ago, which could have resulted in an earlier collapse of some vulnerable reef fish species. The decline in coral reef fish biomass from over-fishing is common in other regions; for example, 55% of island-based coral reef fish communities are over-fished (Newton et al. 2007), and almost 90% of artisanal coral reef fisheries list overfishing as a concern (Nash & Graham 2016).

Throughout the Caribbean, the biomass of some reef fish (e.g., groupers, snappers, parrotfish, and surgeonfish) has fallen drastically (order-of-magnitude differences) from intensive fishing practices (Hawkins and Roberts 2004). Nevertheless, 94% of marine reserves (e.g.., the Virgin Islands National Park and the Bonaire marine park) still allow fishing within boundaries (Hawkins and Roberts 2004; Sala et al. 2021). The decline of reef fish biomass in the Bay Islands is comparable to other regions like Jamaica and the Caribbean as a whole (Canty et al. 2019). In addition to the direct loss of reef fish and the decline in overall populations, fisheries can also induce species-specific characteristics. For example, fishing can change the physiology and behaviour of targeted reef fish like sex change dynamics (e.g., parrotfish), and flight responses (Williams et al. 2019). These minute changes can, at a larger scale, have other implications like the loss of ecosystem functions that reef fishes perform (Williams et al. 2019). The large-scale loss of ecosystem functions in the Bay Islands is not considered in this study, but further research in this area could emphasize the importance of mitigating further losses of reef fish in the region.

Another important aspect to consider when examining the impact of fisheries on reef fish biomass in the Bay Islands is the preservation of cultural heritage in the region. Bay Islanders have a right to fish for culturally appropriate food (i.e., snappers and groupers). These reef fish are highly vulnerable to exploitation for several reasons (e.g., old age of maturity, large gatherings), and for economic reasons have been over-harvested during aggregation events. Fishers in the region are at risk from further decline in fish biomass. For example, fishers utilize local ecological knowledge daily to select fishing sites, bait, and inform their decisions, but if declines are severe enough costs outweigh the potential benefits of catch and fishers may choose to fish elsewhere or leave the fishery entirely (Woodhead et al. 2021). These decisions impact coastal communities who rely on fish for consumption and alter fishing pressures within a region (Woodhead et al. 2021). These changes can also drive illegal fishing activity, increase spatial competition between fishers, and increase resource depletion in specific areas (Chollett et al. 2014). Chollett et al. (2014) suggests the decline of reef fish biomass in Utila follows a 'Gaussian effort allocation model' where fishing grounds closer to port are depleted first because of low travel time and high fuel costs followed by progressively further distances and expanded exploitation area. This can also be exemplified throughout the Bay Islands region with recent trends of fishing deeper (e.g., deep-water snappers and groupers) and targeting offshore species (e.g., wahoo, tuna, mahi mahi). Though outside the scope of this paper, the vulnerability of deep-water reef fish to fishing pressures was demonstrated in the collapse of deep-water snapper fishery (e.g., *Etelis oculatus*) 2 years after it began in 1990 in Bermuda (Stefanoudis et al. 2019). Preventing further decline of reef fish communities in the Bay Islands is integral to sustaining fisheries for the benefit of local communities (Aronson and Precht, 2006).

Coastal development

Intense and rapid development of coastal ecosystems in the Bay Islands has changed land use, increased sedimentation, and led to the generalized destruction of coral reef fish habitat. In the past several decades, these changes have occured throughout the study region, but have been most pronounced in Roatan. Sedimentation has multiple lethal and sublethal consequences on reef fishes and on their surrounding ecosystem, including reduction of light, smothering of organisms, and increased turbidity (Chase et al. 2020). These consequences have a number of obvious impacts for corals, but they also impact coral reef fishes at the individual and population level.

Reefs with high sedimentation are linked to declines in species richness (Moustaka et al. 2018) and in fish abundance, as well as shifts in species distributions (Wenger et al. 2012). Because fish rely on visual cues for many functions (Wenger et al. 2012), sedimentation can lead to reduced feeding and foraging behaviours and decreased predator avoidance, as well as numerous physiological changes at the individual level like gill damage and altered metabolic performance (Moustaka et al. 2018). The seemingly small impact of behaviour and physiological changes at the individual fish level can have major impacts in overall populations, because sediments can significantly increase juvenile mortality rates which reduces the number of fish that reach reproductive age (Wenger et al. 2012). Some fish families experience greater impacts from these consequences. For example, the abundance and biomass of herbivorous scrapers (e.g., parrotfish) is lower at turbid reef sites, perhaps due to decreased feeding rates (Moustaka et al. 2018). Damselfish have also decreased feeding success (Moustaka et al. 2018), which can in turn create negative feedback loops with host coral colonies because colonies with symbiont fishes were shown to have 10 times less mortality, and higher chlorophyll and protein concentrations (Chase et al. 2020). Larger reef fish can also be directly impacted by sedimentation on reefs by having a decreased food supply (e.g., sponges) (Rogers 1990). In the Bay Islands, these consequences of excessive sedimentation are expected to have similar impacts on reef fishes. Sedimentation in the study region occurs frequently, as many new roads have been developed into cliffsides the past decade (Tulhoske et al. 2015). Each year, sedimentation on the reef is highly noticeable during the rainy season months when runoff is increased (October to January) (pers.obs. 2017, 2018, 2019, 2021). Typically, visibility is reduced in the first ten meters of water column (0-10m), which suggests that impacts of sedimentation on reef fish in the Bay Islands could potentially have greater consequences for shallow reef fish. Moreover, it is extremely common to see reef fish (e.g., angelfishes) feeding on large barrel sponges throughout the study region, which are also threatened from excessive sediments.

Coastal development also contributes to the decline of reef fish populations by degrading critical habitat. Reef fish in the Caribbean vary extensively in their extent of reef habitat use; while no Caribbean fish species relies exclusively on one live coral (compared with some in

Indo-Pacific), many clearly associate with reef structure (Alvarez-Filip et al. 2015). Reef fishes in the region associate predominately with large branching corals (e.g., *Acropora*, *Porites*) (Coker et al. 2013) that provide structural complexity and support higher abundance and species richness (Alvarez-Filip et al. 2015). As such, the loss of reef habitat from degradation by sedimentation decreases species richness and overall abundance of reef fish (Moustaka et al. 2018). It can also decrease density of reef fish, homogenise previously diverse species assemblages, and alter community composition by favoring populations of generalist fish species (Alvarez-Filip et al. 2015). For example, herbivorous fishes can receive short-term benefits from increased algae on degraded reefs (Hempson et al. 2017). In the Bay Islands, this type of short-term benefits for parrotfish may explain why the majority of fish biomass is from this family (Scaridae). In some sites with very low coral cover (e.g., Bucanero in Roatan), parrotfishes dominate the reef fish assemblage (average of 55.4% in 2021, n = 6), whereas other sites that experience less sedimentation and have higher coral cover (e.g., seamounts in Cayos Cochinos), are less dominated by parrotfish (average of 11.1% in 2021, n = 6).

In contrast, most reef fish decline in abundance with loss of coral cover; Coker et al. (2013) recorded a loss of 62% reef fish with just a 10% loss in coral cover. Declines are particularly apparent for small coral-dwelling and coral-feeding fishes (Coker et al. 2013); for example, extensive coral loss from siltation in Johnston Atoll contributed to the local extinction of 12 species of butterflyfishes (Chaetodontidae) (Rogers 1990). Damselfishes also have strong adverse effects to habitat degradation: they can lose the ability to identify alarm cues and have much greater mortality in degraded coral habitats than in pristine ones (McCormick et al. 2017). The impacts of habitat loss on medium and large reef fishes are less understood; however, Hempson et al. (2017) found that some species of mesopredators (e.g., Serranidae, Lutjanidae) suffer from decreased prey biomass and must shift their dominant prey species. This can result in reduced nutrition, increased energy costs, which lead to reduced fecundity, growth rates, or delayed age of maturity (Hempson et al. 2017). These long-term impacts can present with declines in abundance and diversity years after degradation of their habitat occurs (Hempson et al. 2017). Habitat loss from the ongoing degradation of coral reefs is likely negatively impacting reef fish populations throughout the study region. The high sedimentation rates that occur throughout the study region from multiple sources (on-island and mainland Central America) may be significantly contributing to our results in fish biomass decline. This impact warrants further examination to determine the consequences of sediment-driven habitat degradation on multiple reef fish families in the Bay Islands.

Changing population & demographic

Increases in the population of the Bay Islands impacts reef fish communities by increasing anthropogenic pressures because humans greatly depend on goods and services from the marine and coastal environment (Halpern et al. 2008). One human pressure has existed for centuries as Indigenous peoples in the region have exerted fishing pressures since the Mayan era (Canty et al. 2019). However, this pressure intensified exponentially from exploitation during the 20^{th} century (Funes et al. 2015) while other stressors also accumulated (e.g., pollution), as seen in other coastal regions during this time (Jackson et al. 2001; Lotze et al. 2006). In present day, thousands of people living in the Bay Islands depend on declining coral reef resources for food provision (e.g., reef fish), livelihoods (e.g., tourism), and for regulative processes (e.g., herbivory, sand creation) (Woodhead et al. 2019). This problem is exasperated further because an accurate estimate of the Bay Islands population does not exist. Population estimates vary greatly from national projections to private companies and local authorities; therefore, it is difficult to ascertain exactly how many people rely on reef resources in the Bay Islands. This is challenging for researchers who aim to stress the importance of conserving these resources for the benefit of many people, and for decision-makers to incorporate their needs into management policies (Newton et al. 2007).

In addition to increases in the overall population living in the Bay Islands, the demographic has also transformed in recent decades. In general, islanders, including communities from Afro-Caribe, European, and Garifuna descent, have a higher reliance on reef resources because of generations of cultural heritage. Bay Islanders are coastal Indigenous peoples (CIPs) who rely heavily on their coasts and seas for social, economic, and cultural purposes, as well as overall well-being (Cisneros-Montemayor et al. 2016). These communities are particularly vulnerable because CIPs link closely with marine ecosystems as a way of preserving cultural heritage and achieving food sovereignty (Cisneros-Montemayor et al. 2016), which is threatened in the Bay Islands from the decline of reef fish populations, pollution, and climate change. CIPs have a right to culturally appropriate food (Cisneros-Montemayor et al.

2016). For Bay Islanders, the preferred source of protein is majorly reef fish (snappers and groupers), though more and more fishers are targeting pelagics (wahoo, mahi mahi). Other community groups such as mainlanders and ex-patriates often don't have cultural heritage that ties them to the reef, and their immigration is seen by the majority of islanders as a trade-off for increased wealth and development on the island (Doiron and Weissenberger, 2014). Peoples who have recently migrated to the island may not have experienced the islands' ecosystems in their pristine state or possess local ecological knowledge, and therefore, may have a greater social acceptance for environmental degradation. Moreover, the influx of workflow from the mainland raises concerns amongst islanders from a cultural perspective, but it can also have unexpected ecological impacts. For example, the lack of employment alternatives can lead to greater pressure on local fish stocks (Singh et al. 2021). These socio-economic and environmental changes are not welcomed by all islanders, as the welfare of Bay Islanders ultimately depends upon their coastal and reef resources (Doiron and Weissenberger, 2014; pers. obs. 2018, 2019, 2021).

Human population density can predict the direct and indirect effects on coral reef fisheries (Newton et al. 2007), and this parameter can predict coral reef ecosystem state over biophysical drivers (Williams et al. 2019). Newton et al. (2007) found that densely populated islands have unsustainable coral reef fisheries footprints, and those footprints are projected to increase by 160% by 2050. In the Bay Islands, Roatan has the largest population density (543 people/km^2) and Utila and Guanaja are less densely populated (156 people/km^2 and 100 people/km^2, respectively). Cayos Cochinos has the lowest population density (75 people/km^2), however it is important to note that not all islands that contribute to the overall size of this subregion are inhabited. In other Caribbean regions, such as Barbuda, lower population density (10.2 people/km^2) corresponds with higher biomass of predatory reef fish (119g/120 m^2) and of parrotfish (672g/120 m^2) (Steneck et al. 2018). In contrast, higher population densities in Antigua (289 people/km^2) correspond to lower biomass of predatory fish (84.5g/120 m^2) and parrotfish (339g/120 m^2) (Steneck et al. 2018). Interestingly, this trend does not occur in the Bay Islands. High population densities in Roatan do not correspond with lower levels of predatory reef fish or of parrotfish, nor vice versa in Utila, Guanaja, and Cayos Cochinos. This may be attributed to other impacts (e.g., fisheries) and not human population.

In addition to human population density as a predictor of coral reef ecosystem state, another factor to consider is the measure of accessibility for communities within the study region. This can be measured with a metric, ‘gravity’, which combines the travel time to reefs with population sizes within a given distance (Cinner et al 2018; Williams et al. 2019). This metric is a stronger predictor of exploitation than human population density alone (Williams et al. 2019), even in areas where there is high compliance within marine reserves (Cinner et al. 2018). Throughout all subregions in the Bay Islands, reefs are widely accessible from shore and travel times range from seconds to minutes. In most locations, reefs can be accessed year-round by nearby communities within walking or boating distance, as well as by the thousands of visitors. Many islanders access reefs with simple wooden canoes (cayucos), whereas ex-patriates and foreign visitors access the reef within seconds from engine-powered dive and sport-fishing boats. While Cinner et al (2016) estimate the ‘gravity’ of the Bay Islands and other areas within the MAR at a medium level, our results demonstrate a high level of human impact and low travel times, resulting in a high level of gravity. Even in areas with high compliance for MPA regulations, high gravity may impede conservation initiatives significantly and reduce overall levels of fish biomass (Cinner et al. 2016). If the Bay Islands continue to experience high gravity, even increased management may not have a significant impact on increasing reef fish biomass while pressures continue. Gravity is primarily driven by fishing pressure (not sedimentation, or climate change), which is influenced by the socio-economic climate in the surrounding populations (Cinner et al. 2016).

Many ecological issues are reinforced by complex socio-economic drivers and interactions (Barnes et al. 2019); for example, trade, consumer demands, and human migration (Williams et al. 2019). During this time in the Anthropocene, natural biophysical processes are being over-powered by socio-economic and cultural norms because human activities are the main drivers of change (Williams et al. 2019). The circumstances of individuals and their behavioral choices dictate their impacts; thus, it is integral to understand the interactions between socio-cultural and ecological systems (Woodhead et al. 2019) and be able to understand what will enable or impede effective management action (Barnes et al. 2019). Effective conservation and management of coastal ecosystems, even as fragile as coral reefs, is possible, but only if socio-economic drivers are also addressed (Newton et al. 2007). Understanding current and predicting future socio-economic changes, like population growth, affects the effectiveness of reef conservation (Cinner et al. 2020), but it is a challenge for ecological researchers who must also delve into the human dimensions of coastal ecosystems (Woodhead et al. 2019). In the Bay Islands, the diverse communities have different uses of reef resources (e.g., food provision, leisure, cultural significance), but all communities depend on the coast in some form. The sharing of coastal and marine space and resources leads to increased conflict, which inhibits shared vision and cooperation, and in turn achievement of conservation goals. Addressing the socio-economic inequalities and local conflicts over reef resource use in the Bay Islands with an interdisciplinary socio-ecological approach will contribute towards achieving ecological recovery, sustainable development, and the well-being of communities that all depend on these threatened ecosystems (Boyce et al. 2020; Eddy et al. 2021).

Land-based pollution

Land based pollution causes direct and indirect impacts on coral reef ecosystems by altering habitat structure (Pandolfi et al. 2003), changing marine biodiversity (Worm et al. 2006), increasing coral stress and disease prevalence (Williams et al. 2019), and by posing a risk to fishery productivity (Singh et al. 2021). In the Bay Islands, wastewater transports harmful bacteria and nutrients to the reef, decreasing water quality (CORAL, 2021), which acts synergistically with coastal development impacts like sedimentation to stress corals (Harborne et al. 2001) and have numerous adverse effects to overall reef health (Prouty et al. 2008). This contributes to ecological shifts which degrade fish habitat. Moreover, some forms of pollution (e.g., chemicals, plastics) directly threaten reef fish from ingestion, contamination, and entanglement which contributes to the overall decline of coral reef fish biomass.

Land-based pollution has caused substantial and accelerating declines in the abundance of coral reef species, triggering widespread changes in reefs over the past two centuries (Hughes et al. 2003). Firstly, natural habitats are removed, altered, or destroyed from the runoff of nutrient-rich pollutants, like sewage discharge (Halpern et al. 2008). Runoff can bury and smother corals, reduce their recruitment and calcification rates, and lead to reduced depth distributions, increased diseases, and the proliferation of algae (Prouty et al. 2008). In the Bay Islands, nutrient pollution has caused ecological and public health problems, such as the transformation of coral reefs to algal lawns, which added to fisheries collapse previously caused by over-fishing (DeGeorges et al. 2010). Loss of suitable habitat for reef-associated species can contribute to further declines in reef fish biomass in the Bay Islands. Localized efforts to lessen sewage discharge (e.g., West End treatment plant) may have contributed to the recent increase in coral cover (22% to 27%) and the decrease in fleshy macroalgae (27% to 24%) from 2018 to 2020 (HRI, 2020). However, this type of pollution from expanding tourist resorts remains a threat (Prouty et al. 2008; pers. obs. 2021) and most communities in the Bay Islands still lack the infrastructure to collect and treat wastewater (CORAL, 2021). For example, Cordelia Banks is one of the ZPEMs in Roatan closed to marine-based tourism (e.g., diving) but it remains threatened by untreated wastewater from nearby Coxen Hole (Canty et al. 2021), the largest and most densely populated community in the Bay Islands.

Other forms of land-based pollutants, including macro-plastics, micro-plastics, and chemicals, also threaten reef fish in the Bay Islands. Massive floating aggregations of macro-plastics, as well as micro-plastics, are found ubiquitously throughout the marine and coastal space in the Bay Islands, including shallow coral reefs, deep coral reefs (>60m), seagrass meadows, mangroves, and beaches (pers.obs.2021). Macro-plastics cause direct physical damage to coral reef species, and can entangle and entrap reef fish (e.g., plastic fishing line) (Diez et al. 2019). The thousands of tonnes of plastic waste (8,015 tonnes in five years) found floating in the study region (Kikaki et al. 2020) may also be concentrating toxic chemicals and acting as pathogenic vectors (UNEP, 2019; Diez et al. 2019).

Firstly, plastics can concentrate toxic chemical pollutants 1 million times the amount in surrounding seawater (Diez et al. 2019). When reef fish ingest these plastics they can absorb leaching UV stabilisers, polychlorinated biphenyls, polycyclic aromatic hydrocarbons, metals, and pesticides, which can then bio-accumulate up the food chain (UNEP, 2019). This is particularly significant because trace metals in the study region include the copper–antimony additives (Cu/Ca and Sb/Ca) found in anti-fouling paints used on boat hulls. Secondly, plastic pollution promotes disease-causing bacteria and viruses, increases coral disease, and restructures microbial communities on reefs (Williams et al. 2019). Coral-reef associated fishes like corallivores (e.g., butterflyfishes), may be more susceptible to this form of pollution.

In addition, microplastics are also impacting reef fish in the Caribbean from ingestion (Diez et al. 2019) and have been found in over 20% of reef fish (UNEP, 2019). Micro-plastics (<5mm) have a 0.25 probability of being ingested by reef fish and cause false satiation and changes in buoyancy (Diez et al. 2019). Contamination may also occur through ingestion of micro-plastics or be integrated into fishes through their gills (Diez et al. 2019). These impacts can decline individual fish health and given the scale of plastic pollution occurring in the Bay Islands region, whole populations. As seen in other regions (Duarte et al. 2020), municipal efforts to ban single-use plastic in Roatan did reduce the amount of plastic entering the marine environment in 2019, however, the massive plastic aggregations that bring the vast majority of waste originate in the mainland (Kikaki et al. 2020) and are outside of the single-use plastic ban. The removal of pollution is a critical step in the recovery of coral reefs, seagrass meadows, and kelp forests (Duarte et al. 2020).

Tourism

Tourism in the Bay Islands impacts reef fish communities and their surrounding coastal ecosystems by increasing pollution and disturbance, and by both intensifying and alleviating fishing pressure. It also initiates destructive coastal developments (e.g., the expansion of the Coxen Hole cruise-ship port over live coral reef). Cruise-ship tourism directly impacts the subregion of Roatan, and it primarily contributes to increased pollution and disturbance at large scales along the southern shore. Ships discharge wastewater, physical waste, hydrocarbons, and ashes, which have unmonitored impacts on nearby coral reef ecosystems like that of Smith and Cordelia Banks (Doiron and Weissenberger, 2014). Cruise-ship tourists may also create a greater demand for reef resources by requesting fresh seafood lunches, however this may impact invertebrate populations (e.g., lobster, shrimp) more than reef fish (e.g., groupers) and typically originates from offshore fishing banks outside of the study region. Alternatively, cruise-ship tourism can also alleviate fishing pressure because it provides hundreds of job opportunities to local communities which may have previously relied on income from industrial and artisanal fisheries. The wide-spread economic shift from traditional fisheries to tourism began in the 1990s in Roatan (Luttinger 1997). Despite the lower revenue that cruise-ship tourists typically produce compared with those who stay over-night (Doiron and Weissenberger, 2014), the subregion of Roatan's economy is highly reliant on this type of tourism. For example, when tourism during the covid-19 pandemic was put on pause, illegal fishing activities identified by the RMP rose by 50% in comparison to the previous year (RMP, 2021). This example demonstrates how the consequences of rapid touristic development can have indirect ecological impacts. The Bay Islands would benefit from diversification away from cruise-ship tourism, which could strengthen the region's environmental, economic, and social resilience (Doiron and Weissenberger, 2014), particularly in the face of global crises with unpredictable effects.

The other predominant form of the tourism industry in the Bay Islands is marine-based, including millions of scuba-divers, free-divers, snorkelers, and boaters, that visit each subregion annually. Much like cruise-ship tourism, marine-based tourism has complex impacts on fisheries (both intensification and alleviation), and contributes towards land-based pollution (e.g., sewage discharge), and coastal development (e.g., hotels, roads). However, some impacts on reef fish communities are directly related to this specific type of tourism, including increased noise disturbance on the reef (e.g., boat traffic), strengthened conservation efforts (e.g., coral restoration efforts by volunteer divers), decreases in invasive species populations (e.g., from lionfish spearing), and alterations in animal behaviour (e.g., from diver presence). Some negative impacts from marine-based tourism no longer occur within the Bay Islands; for example, anchoring directly on the reef, and localized spearing of reef species (e.g., lobster, conch, reef fish) (Luttinger 1997). Diver presence can affect the activities, behaviours, and habitat uses of reef fish (Titus et al. 2015), while dive boats above cause extensive noise and vibrations that can saturate the reef for kilometers (Wright et al. 2020). For example, reef fish can either avoid or aggregate towards divers, snorkelers, and free-divers, altering natural behaviours (Simmons et al. 2021). Both physical and noise disturbances from diving activities are most prevalent where numerous dive centers occupy small areas, such as in certain touristic areas within the Bay Islands (e.g., west Roatan and southern Utila) (pers.obs 2017, 2019, 2021). Moreover, boating activities (from fishing, leisure, or water transportation) can increase stress and injure several aquatic animals (Wright et al. 2020), including reef fishes. Just one zone in the entire Bay Islands, Cordelia Banks, is off limits for all forms of marine-based tourism and only scientific diving is allowed (Canty et al. 2021).

Climate change

Wide-ranging changes in climate, such as warming oceans and intensifying storms, are increasingly likely to alter tropical coral reef ecosystems from global and localized stressors (Woodhead et al. 2019). Increasing SST and frequent marine heatwaves cause mass coral bleaching events and increase their vulnerability, which in some cases, can transform the benthos from a coral-covered environment to macro-algal one (Williams et al. 2019). This type of benthic regime shifts can prevent the new growth of corals and change the diversity and abundance of reef-associated organisms like reef fish (Williams et al. 2019). In the Bay Islands, this regime shift has not yet occurred despite high coral mortality (19% - 90%) during past bleaching events. Climate change and marine disease is a greater threat to corals than the loss of reef fish, because even remote, unfished reefs suffer from mass bleaching events (Aronson and Precht, 2006). However, high populations of herbivorous reef fish can control macroalgal growth after a large-scale climate event (like bleaching or a hurricane) (Aronson and Precht, 2006). In the Bay Islands, herbivorous fishes may contribute to the control of fleshy macroalgae, which covers approximately one fourth of the benthos (HRI, 2020). Recently, declines in coral cover in the Bay Islands from Stony Coral Tissue Loss Disease may have been worsened from warm summer temperatures with little rainfall, but high herbivorous fish populations in the region could increase coral resilience. The negative impacts of marine heatwaves on coral reef ecosystems throughout the region may be temporarily mitigated by high herbivorous biomass; however, reef fish themselves are also impacted by increasing SST.

Rising temperatures can impact fish populations directly by changes in individual fish characteristics such as growth, survival, and reproduction, or in whole populations like connectivity or habitat loss (Chollett et al. 2014). The functional diversity of reef fish can decline with severe heat stressors, and whole communities may change (Woodhead et al. 2019). Increases in SST can cause re-distributions of reef fish, ranging from large-scale movements towards the poles to smaller-scale movements to deeper waters, which can result in overall shifts in species ranges, abundances, and assemblages (Chollett et al. 2014). Predicting the climate-induced changes to fish biomass is necessary to mitigate potential issues with increased conflict and a decline in food security (Boyce et al. 2020). In small islands states, climate-driven reductions in biomass are expected severely disrupt fishery-dependant economies and increase malnutrition (Boyce et al. 2020). Further reductions in reef fish biomass due to climate stressors like increasing temperatures or re-distributions of populations (either to deeper waters, or outside of the region) would negatively impact communities throughout the Bay Islands. All fisheries (industrial, artisanal, recreational, subsistence) would be negatively impacted by increased effort per catch from higher fuel costs to travel longer distances or run longer fishing days. Ongoing warming could also increase conflict between fishers who exploit shared marine space resulting in reduced catch. Moreover, declines in artisanal and subsistence catch from climate change would be socio-culturally and economically harmful to Bay Islanders. Further loss of reef fish biomass may result from not only increased ocean warming, but also from the increase in storms in the region.

Intensifying storms produce greater rainfall, fluvial runoff, winds, and wave destruction which can impact reef populations directly by altering behaviour (e.g. reduced herbivory) (Kjerfve et al. 2021) or indirectly by damaging their habitat (Kramer and Kramer 2000). As storms within the region become more extreme (IPCC, 2021), threats to coral reef ecosystems are increasing and the entirety of the MAR is critically endangered (Canty et al. 2021). Storms such as hurricanes can disrupt and reduce coral reef ecosystem functions and services and decrease the 3D structure of the reef which can impact reef fish populations and their fisheries (Simmons et al. 2021). Impacts of hurricanes on reef fish can be both short-term, and long-term. In the short-term, hurricanes can change food web structure (Ibarra-García et al. 2020), reduce herbivory (Steneck et al. 2019), and alter fish communication because their sounds occupy the low-frequency spectrum, which competes with background wind and wave noise (Simmons et al. (2021). In contrast, long-term changes in fish assemblages can appear years later (Ibarra-García et al. 2020). After a great disturbance, larger transient reef fish (e.g., snappers) have a greater ability to find refuge or relocate to a more desirable habitat (Simmons et al. 2021). However, many reef fish are unable to travel large distances and may be highly vulnerable to predation. In the Bay Islands, the intermittent effects of hurricane waves are less pronounced than other impacts (e.g., over-fishing, pollution) (Kjerfve et al. 2021), but the impact of increasing storms due to climate change may in fact have a positive effect on reef fish biomass because of reduction in fishing days. As storms intensify and occur more frequently, this region is expected to have more rainfall which can limit fishing activity for more days of the year (Chollett et al. 2014). The impacts of climate change on reef fish communities in the Bay Islands is complex and warrants further research on projected marine biomass declines due to climate change (Boyce et al. 2020).

4.3. Current Management approaches and their gaps

Numerous limitations exist in the current management of coastal ecosystems, including coral reefs and associated fishes, in the Bay Islands. A top-down centralized approach with decision-making power residing in the capital of Honduras excludes the local needs of Bay

Islanders. Several governmental agencies are charged with different facets of management but provide little on-the-ground support, culminating in a fragmented system with little responsibility assumed. Complex zoning with little to no enforcement of regulations leaves marine space users free to utilize ecosystems and their resources as desired. Fisheries remain open access with the majority of catch not reported and unlimited. A lack of communication between municipal and national levels of government results in wide-spread land-based impacts (e.g. land clearing, sedimentation, plastic waste). Finally, low capacity of island ENGOs and lack of authority inhibits local governance despite best efforts.

In the Bay Islands, initial grass-roots marine reserves were replaced with a top-down centralized approach, which outlined several MPAs in national decrees (*Acuerdo* #114-2003; *Decreto* #75-2010). A lack of transparency and communication, in conjunction with little understanding and incorporation of the local needs of Bay Islanders into these MPAs, has resulted in over seven thousand square kilometers (7,259km^2) of paper parks. An over-abundance of government agencies is responsible for various management components in parks, but none are actively present in the study region, except for the occasional presence of the Honduran Navy (Gombos et al. 2011). National legislative documents highlight numerous types of zones and different zoning within the Bay Islands, but the zones are not physically marked or widely recognised. Access to these documents is limited for most Bay Islanders because they obtained online, and many do not have computer access. In addition, the management plans (one for BINMP, one for Cayos Cochinos) are available only in Spanish (ICF, 2013), which contradicts the cultural heritage of most Bay Islanders, who's primary (or only) language is English. Communities throughout the study region feel mis-represented, not consulted, unfamiliar and puzzled with ongoing management, especially when the few known regulations are consistently ignored in favor of foreign interests (Doiron and Weissenberger, 2014). In general, stakeholders in the Bay Islands are not bound by any of the policies or plans provided by the Honduran government because enforcement of environmental legislation in both coastal and marine ecosystems in the Bay Islands is virtually nonexistent (Doiron and Weissenberger, 2014). This is attributed to the lack of resources and lack of political will (Canty et al. 2018), lack of cooperation from local police (Luttinger 1997), low financial stability (Gill et al. 2017), and remoteness (Chollett et al. 2017). The lack of enforcement in the region is comparable to the rest of the Honduran Caribbean coast (Chollett et al. 2014) and elsewhere. Only 2.7% of the 7% of global ocean area that is currently an MPA is fully or highly protected (Sala et al. 2021) and wide-spread shortages in enforcement leads to less than intended protection occurring in most MPAs (Wright et al. 2020).

Another issue with current management in the Bay Islands is that fisheries remain open access in all subregions without limitations (e.g., catch sizes, catch limits), and the majority of catch (artisanal, recreational, and subsistence) is not reported (Cholett et al. 2014). Minimum catch sizes of finfish do not exist in government mandated legislation for the MPAs (Cholett et al. 2014), whereas other nations with Caribbean fisheries have had minimum sizes implemented since the 1980s. For example, the United States have included yellowtail snapper in a management plan since 1985 and regulates the fishery with minimum sizes and annual catch limits (NOAA Fisheries, 2020). In some cases, minimum catch size can increase discards and discard mortality (e.g., deep water snappers like queen and silk), but in the majority of cases of shallow reef fish (<60m) it decreases harvesting of fishes in their juvenile stage (NOAA and NMFS, 2020). The Bay Islands seafood guide published by the RMP recommends a minimum catch size for only one species of fish: barracuda (Sphyreana barracuda) (91cm), though it also discourages the consumption of groupers, snappers, and parrotfish (RMP, 2021). Bag limits are also in place for other reef fish included a combined limit of 5 fish/person/day for snappers, groupers, and parrotfishes, or 15 per vessel per day (NOAA Fisheries, 2020). In the Bay Islands, it is common for small-scale fishers to catch hundreds of snappers per day, especially during fish spawning aggregations, where catches can reach five figure weights in a few days (e.g. >19,000 lb of mutton snapper in one week in Utila) (Box and Canty 2010). Moreover, there are no official catch records for ongoing coral reef fisheries in the Bay Islands, which results in the underestimation of their importance to communities and island economies (Canty et al. 2019). In general, these issues are common in most coral reef fisheries where knowledge gaps regarding fishing effort, production, markets and value, are unknown (Kittinger et al. 2015). These gaps threaten the ecological and socio-economic sustainability of reef fish resources as well as the implementation of effective marine management practices (Kittinger et al. 2015).

Management of the Bay Islands does not consider the high levels of sedimentation and land-based pollutants that the MPAs are subject to. Destructive land-clearing and rapid coastal development (e.g., roads, buildings) on the islands, as well as increased runoff from the mainland has led to excessive sediments and pollutants being deposited on coral reefs and reef fishes in the study region. In addition, thousands of tonnes of plastic waste are spread across the marine and coastal ecosystems annually. The protective legislation of both the BINMP and the Cayos Cochinos reserve do not acknowledge these harmful inputs or attempt to mitigate them, despite extensive documentation of negative consequences on reef fishes and their surrounding environments. National regulations in 'Acuerdo Dos' are not enforced, and municipal work permits for environmentally damaging development projects continue to be provided (Doiron and Weissenberger, 2014; pers. obs. 2019). The lack of infrastructure regarding waste seems to be the result of a large disconnect between the municipal and central government, who both claim the task of creating a waste management facility is the responsibility of the other (Gov. Dino Silvestri, pers. comm. 2021). This results in nation-wide issues in disposal of physical waste (e.g., plastics) and wastewater (e.g., sewage). Moreover, the plastic pollution crisis in the Bay Islands is an international issue because much of the plastic waste entering the Gulf of Honduras is traced back to Guatemalan dumps (Kikaki et al. 2021). The lack of management of land-based pollutants is a common issue across Central America and the Caribbean and marine pollution poses a direct and immediate threat to the USD $57 billion of tourism revenue that the region brings in annually (Diez et al. 2019). Addressing this gap in current management could improve the lives of islanders, conserve natural capital, and enable continued economic growth from tourism (Diez et al. 2019).

The final issue observed in the current management of the Bay Islands is low capacity, particularly in financial, physical, and technological aspects (Box and Canty 2010). This gap is common in the management of coral reef ecosystems because they are often located in areas with high poverty (Barnes et al. 2019), like in Honduras. This issue has been present in the region for nearly three decades; in 1996, the greatest environmental impact was identified as the lack of institutional capacity in governing agencies (Forest 1998). Due to the lack of government-run management of MPAs in the region, ENGOs are left with the duty of executing conservation programs and initiatives, installing marine infrastructure, consulting communities through outreach, and patrolling coastal ecosystems in an attempt to increase compliance. These efforts are limited by lack of funding and support from the government agencies who are supposed to be managing the area. For example, ENGOs in the Bay Islands are limited by number of patrol boats, materials for coral restoration projects (RMP, 2021), and funding for staff salaries (Gombos et al. 2011). In addition, the ENGOs lack authority and are unable to enforce governmental regulations such as illegal fishing within the restricted zones of the parks (Canty et al. 2018). The lack of capacity limits the positive impacts that conservation initiatives could have in the Bay Islands region.

4.4 Management recommendations

4.4.1. Begin government-led enforcement of environmental regulations

Our results highlight a decline in reef fish biomass, various ongoing and increasing human pressures, and several gaps in the current management of the Bay Islands, including the lack of enforcement. Compliance with rules and regulations is essential to achieve successful realisation of environmental management policies. Increasing the enforcement of existing regulations in the study region is a critical step towards preventing continued habitat degradation and further loss of reef fish biomass. Without enforcement, other recommendations to prioritize conservation objectives and improve management practices in the study region are unlikely to succeed. For example, recommendations to decrease exploitation of fish aggregations from fishing pressure is not viable unless enforcement is also implemented. The lack of enforcement in the Bay Islands may be due to low political will and stability. The Honduran government established legislative protection for marine ecosystems around each subregion in the Bay Islands over a decade ago. However, the government has not yet allocated substantial funding into the conservation of the critical ecosystems nor enforced their legislated regulations, despite substantial financial gains from the tourism industry in the area.

Though thousands of people in the Bay Islands benefit from marine ecosystems (e.g. private sector businesses, government) (Forest, 1998), the responsibilities of enforcement within the national parks falls primarily on ENGOs. However, the sheer size of the two MPAs across large distance around multiple islands requires a much stronger enforcement effort. The Healthy Reefs Initiative, who has over 15 years of experience working on conservation across the MAR, have also highlighted the need to protect important habitats via enforcement, enlist the help of the Honduran Navy for patrols, and increase the severity of penalties for non-compliance (e.g., increasing fines) to reduce exploitation rates (HRI, 2020). Enforcement could particularly aid in the clarification of numerous unmarked zones and boundaries, which generate confusion for locals and foreigners alike (HRI, 2020). Citizens can help by reporting illegal fishing activities with website forms and a phone app (RMP, 2020), but it is truly the Honduran government's responsibility to protect its natural resources for the benefit of all, including future generations.

Increasing enforcement in the Bay Islands can result in numerous positive benefits for coral reef fishes, surrounding marine and coastal environments, and those who rely upon them. Greater investment in presently established MPAs through improvements to enforcement and compliance can increase the benefits they produce (Sala et al. 2021). While the MPAs in the Bay Islands (both BINMP and Cayos Cochinos) currently have three of five NEOLI features (they are old >10 years, large >100km^2, and isolated by deep-water), they are not no-take nor enforced. In order for MPAs to be effective they must have at least four out of five essential features (Edgar et al., 2014). Due to islanders' high reliance on coral reef fisheries for socio-economic and cultural reasons, I cannot advocate for a complete no-take zone throughout the region (>7,000km^2), nor would it be feasible. However, the fourth and final NEOLI feature within the Bay Islands should be government-led enforcement because it can lead to higher fish biomass and an increased number of large (>25cm) fish (Edgar et al. 2014). High MPA enforcement has also been found to have benefits for small-scale fisheries management by increasing health of fish stocks and the incomes of fishers (Di Franco et al. 2016). Short-term adjustments can be outweighed by ecological and socio-economic advantages from increased fish biomass in the long-term.

4.4.2. Implement size and catch restrictions & record- keeping

Recovery of fish populations in the Bay Islands is inhibited by the continued intensification of fishing pressure from the open-access nature of artisanal and recreational fisheries. The decline in reef fish biomass highlights a need to curb over-harvesting of reef fish species, particularly during their juveniles stages. Regulations for catch limits and minimum sizes of reef fish do not exist in the study region, but could be beneficial, especially for commercially valuable long-lived species like snappers and groupers. In addition to lack of minimum catch sizes and daily or weekly catch limits, there is no closed season for harvesting of groupers or snappers, which jeopardises them during vulnerable aggregations and migrations. Removing high quantities of long-lived reef fish in a short period of time threatens entire generations of island communities by pre-maturely harvesting over the maximum sustainable yield. A daily or weekly limit for specific species or fish families (e.g., 5 snapper/person/day) could allow the over-exploited fish populations in the Bay Islands to recover. In some cases, lightly fished reefs can create concave trophic pyramids which can maintain essential ecological functions and support reef fisheries suggesting that reduced fishing effort can be successful (Darling and D'agata 2017). While current management promotes irresponsible fishing practices and allows for continued demise of reef fish populations, the implementation of a simple daily or weekly catch limit and minimum catch sizes of highly vulnerable species could enable management to meet ecological and economic objectives while avoiding collapse (Darling and D'agata 2017).

Coral reef fisheries in the Bay Islands are highly underestimated in terms of their importance to communities and island economies and their impacts on the decline of reef fish populations. Multiple knowledge gaps (e.g., lack of catch records, unknown fishing effort and value of the fishery (Kittinger et al. 2015)) and the lack of a fisheries management program (Canty et al. 2019) is threatening the ecological and socio-economic sustainability of reef fish resources in the Bay Islands. Creating a baseline of information by improving data collection (e.g., determining the number of participants in a reef fishery) is essential in addressing overfishing (Teh et al. 2013; Canty et al. 2019). Due to the extensive cultural heritage and local ecological knowledge of fishers in the Bay Islands, I support Chollett et al. (2014)'s suggestion of developing a participatory, community-led system where fishers are involved in the collection and use of fisheries data. This can inform local management strategies that can ensure the sustainability of the fishery they depend on (Chollett et al. 2014). These types of co-management approaches can increase transparency, facilitate shared vision, decrease conflict, and increase compliance (Mcconney and Pena 2012), which could highly increase both ecological and socio-cultural benefits throughout the study region.

4.4.3. Reduce sedimentation and land-based pollution

The influx of sediments and multiple types of pollutants into the coastal and marine environments in the Bay Islands continues to threaten coral reef fishes in the region. Though the impacts from sedimentation and land-based pollution are not considered in MPA management plans or in national legislation, there are numerous environmental regulations in Honduras that could apply to preventing some of these issues (e.g., Acuerdo Dos). Because land-based stressors often influence nearshore MPAs (Gill et al. 2017), mitigation strategies or active attempts to reduce the influx of sediments and pollutants into critical ecosystems in the Bay Islands are necessary. Curbing destructive coastal development practices and creating municipal level waste management infrastructure (e.g., wastewater treatment, organized landfill, recycling station, etc.) could promote increased health of coastal ecosystems and their associated assemblages. Foreign investors that obtain great financial gain from the area should be required to install appropriate waste treatment plants that support the millions of visitors that frequent their installations annually. While localized efforts such as beach clean-ups in the Bay Islands are common, the scale of the plastic pollution crisis requires the implementation of high-levels solutions on the mainland and national and international co-operation. A reduction in the land-based pollutants could support recovery of reef fish populations and have multiple benefits for coral reef ecosystems in the region.

4.4.4. Increase capacity for local organizations

Increased realisation of conservation objectives could be achieved by increasing the financial (e.g., funding), physical (e.g., workspace), and technological (e.g., equipment) capacity of ENGOs in the Bay Islands. Numerous ENGOs in the Bay Islands (e.g., RMP, BICA, Utila Coral, Bay Island Reef Restoration, Cayos Cochinos Foundation, etc.) could benefit from an increase in staff, budget, and supplies. Since staff and budget capacity is the strongest predictor of conservation impact, MPAs with low capacity are often ineffective; MPAs with high capacity produced 2.9 times greater positive ecological effects than those with low (Gill et al. 2017). In both the BINMP and in the Cayos Cochinos reserve, staff and budget capacity are an issue (Gombos et al. 2014; RMP, 2021); for example, ENGOs will often create social media campaigns to ask for donations of marine management supplies. The protective legislation of many MPAs is weakened by inadequate human and financial capacity (Duarte et al. 2020); these gaps in capacity hinder local management's ability to meet multiple conservation objectives and implement an ecosystem-based approach (Cinner et al. 2020). Building capacity at the local level can have several benefits. For example, it can develop participatory processes (Dalton et al. 2012), increase stakeholder participation and cohesion (Chollett et al. 2014), facilitate results-based decision-making (Canty et al. 2018), and improve ecological conditions of coral reef fisheries by increasing communication and trust (Barnes et al. 2019). By increasing capacity of ENGOs, local communities could re-gain an important role in managing their coastal ecosystems (Ferse et al. 2010), protection for coral reef fishes and their environments could increase, and positive ecological outcomes could expand in the Bay Islands.

5. CONCLUSION

In summary, coral reef fish in the Bay Islands remain threatened from numerous anthropogenic stressors despite legislative protection in national marine parks. Unrestricted open-access fisheries, destructive coastal development, a changing demographic, and massive increases in tourism without proper infrastructure for waste management (e.g., sewage, plastic) all contribute to the continued degradation of coral reef fish communities in the region. Increasing SST and intensifying storms from climate change also threaten the vulnerable coastal ecosystems and their species assemblages. Our results highlight drastic declines in total and herbivorous reef fish biomass, as well as low quantities of snappers and groupers overall. Fish assemblages in the Bay Islands are dominated by herbivorous fishes, which may be experiencing short-term benefits from changes in the benthos, and overall contributions from targeted fish species that are commercially valuable is very low (<5%). The loss of reef fish biomass threatens their surrounding ecosystems and the thousands of community members in the Bay Islands that rely upon them. Reef resource reliance in the study region is high, and islanders have important socio-cultural and economic ties to their coastal and marine space. Several factors limit effective protection of reef fish in the Bay Islands including a fragmented centralized government system with little to no support, substantial fisheries that are unlimited and unreported, high influx of land-based sediments and pollutants, and low capacity for local ENGOs that are attempting to manage the region. To prevent further loss of reef fish biomass, four recommendations are provided for incorporation into current management efforts. Ongoing and expanded initiatives to reduce human impacts that are degrading coral reef fish communities are integral to allow the recovery of fish populations and to sustain communities in the Bay Islands for years to come.

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APPENDIX

I. List of fish species & fish family groups recorded

Appendix I: List of fishes surveyed across the Meso-American Barrier Reef from 2006 – 2021. Adapted from the Atlantic Gulf and Rapid Reef Assessment's Fish Protocol (AGRRA, 2016). Each fish was identified at the species level during UVS, except where noted (*). The (*) denotes all fish in the group are recorded at the genus level (i.e., *Kyphosus* - CHUB).

Family Code	Fish Family (Common)	Fish Species (Latin name)	Fish Species (Common Name)
ANGE	Angelfish	*Holocanthus tricolor*	Rock Beauty
ANGE	Angelfish	*Holocanthus cilaris*	Queen Angel
ANGE	Angelfish	*Pomacanthus paru*	French Angel
ANGE	Angelfish	*Pomacanthus arctutus*	Grey Angel
BARR	Barracuda	*Sphyreana barracuda*	Barracuda
BOXF	Boxfish	*Lactophrys bicaudalis*	Spotted Trunkfish
BUTT	Butterflyfish	*Chaetodon capistratus*	4 eyed butterflyfish
BUTT	Butterflyfish	*Chaetodon striatus*	Banded butterflyfish
BUTT	Butterflyfish	*Chaetodon ocelatus*	Spotfin butterflyfish
BUTT	Butterflyfish	*Chaetodon aculeatus*	Longsnout butterflyfish
CHUB	Chubs	**Kyphosus spp.*	Chubs
DAMS	Damselfish	*Stegastes planifrons*	Three-spot damselfish
DAMS	Damselfish	*Microspathodon chrysurus*	Yellowtail damselfish
FILE	Filefish	*Aluterus scriptus*	Scrawled Filefish
FILE	Filefish	*Cantherhines pullus*	Orange filefish
FILE	Filefish	*Cantherhines macrocerus*	While filefish
GROU	Groupers	*Cephalopholis cruentata*	Graysby
GROU	Groupers	*Cephalopholis fulva*	Coney
GROU	Groupers	*Epinephelus adscensionis*	Rock Hind
GROU	Groupers	*Epinephelus guttatus*	Red Hind
GROU	Groupers	*Epinephelus striatus*	Nassau Grouper
GROU	Groupers	*Mycteroperca bonaci*	Black Grouper
GROU	Groupers	*Mycteroperca tigris*	Tiger Grouper
GROU	Groupers	*Mycteroperca venenosa*	Yellowfin Grouper
GRUN	Grunts	*Anisotremus surinamensis*	Black Margate
GRUN	Grunts	*Anisotremus virginicus*	Porkfish
GRUN	Grunts	*Haemulon album*	White Margate
GRUN	Grunts	*Haemulon aurolineatum*	Tomtate
GRUN	Grunts	*Haemulon carbonarium*	Caesar grunt
GRUN	Grunts	*Haemulon chrysargyreum*	Small-mouth grunt
GRUN	Grunts	*Haemulon flavolineatum*	French grunt
GRUN	Grunts	*Haemulon macrostomum*	Spanish grunt
GRUN	Grunts	*Haemulon melanurum*	Cottonwick
GRUN	Grunts	*Haemulon parra*	Sailors choice
GRUN	Grunts	*Haemulon plumerii*	White grunt
GRUN	Grunts	*Haemulon sciurus*	Blue-striped grunt

JACK	Jacks	*Caranx ruber*	Bar Jack
JACK	Jacks	*Trachinotus falcatus*	Permit
MORA	Morays	*Gymnothorax funebris*	Green Moray
MORA	Morays	*Gymnothorax miliaris*	Goldentail Moray
MORA	Morays	*Gymnothorax moringa*	Spotted Moray
PARR	Parrotfish	*Scarus coelestinus*	Midnight Parrotfish
PARR	Parrotfish	*Scarus guacamaia*	Rainbow Parrotfish
PARR	Parrotfish	*Scarus iseri*	Striped Parrotfish
PARR	Parrotfish	*Scarus taeniopterus*	Princess Parrotfish
PARR	Parrotfish	*Scarus vetula*	Queen Parrotfish
PARR	Parrotfish	*Sparisoma aurofrenatum*	Redband Parrotfish
PARR	Parrotfish	*Sparisoma chrysopterum*	Redtail Parrotfish
PARR	Parrotfish	*Sparisoma rubripinne*	Yellowtail Parrotfish
PARR	Parrotfish	*Sparisoma viride*	Stoplight Parrotfish
PORC	Porcupinefish	*Diodon holocanthus*	Balloonfish
PORC	Porcupinefish	*Diodon hystrix*	Porcupinefish
PORG	Porgies	*Calamus bajonado*	Jolthead Porgy
PORG	Porgies	*Calamus calamus*	Saucereye Porgy
PORG	Porgies	*Calamus penna*	Sheepshead Porgy
PORG	Porgies	*Calamus pennatula*	Pluma Porgy
PUFF	Pufferfish	*Sphoeroides spengleri*	Bandtail Puffer
SCOR	Scorpionfish	*Pterois spp.*	Lionfish
SNAP	Snappers	*Lutjanus analis*	Mutton Snapper
SNAP	Snappers	*Lutjanus apodus*	Schoolmaster
SNAP	Snappers	*Ocyurus chrysurus*	Yellowtail Snapper
SNAP	Snappers	*Lutjanus cyanopterus*	Cubera Snapper
SNAP	Snappers	*Lutjanus griseus*	Grey Snapper
SNAP	Snappers	*Lutjanus jocu*	Dog Snapper
SNAP	Snappers	*Lutjanus mahogani*	Mahogany Snapper
SNAP	Snappers	*Lutjanus synagris*	Lane Snapper
SURG	Surgeonfish	*Acanthurus coeruleus*	Blue Tang
SURG	Surgeonfish	*Acanthurus chirurgus*	Doctorfish
SURG	Surgeonfish	*Acanthurus tractus*	Surgeonfish
TRIG	Triggerfish	*Balistes vetula*	Queen Triggerfish
TRIG	Triggerfish	*Melichtyes niger*	Black Durgon
TRIG	Triggerfish	*Canthidermis sufflamen*	Ocean Triggerfish
WRAS	Wrasse	*Bodianus rufus*	Spanish Hogfish
WRAS	Wrasse	*Lachnolaimus maximus*	Hogfish
WRAS	Wrasse	*Halicoeres garnoti*	Yellowhead Wrasse
WRAS	Wrasse	*Halicoeres radiatus*	Puddingwife
WRAS	Wrasse	*Halicoeres bivittatus*	Slippery Dick

II. Species-specific biomass conversion values

Appendix II: Species-specific information used for fish biomass estimations (AGRRA, 2016; P.Kramer, pers.comm.) Biomass for each individual fish was calculated as $A*(S*TL2FL)^B$, where A and B = species biomass curve coefficients, S = size, and TL2FL = total length to fork length conversion factor.

Code	Common Name	Fish Family	TL2FL	A	B
SURG	Surgeonfishes	Acanthuridae	0.93	0.04	2.83
TRIG	Triggerfishes	Balistidae	0.79	0.05	2.78
JACK	Jacks	Carangidae	0.84	0.02	2.99
BUTT	Butterflyfishes	Chaetodontidae	1	0.05	2.86
PORC	Porcupinefishes	Diodontidae	1	0.16	2.4
GROU	Groupers	Serranidae	1	0.02	2.93
GRUN	Grunts	Haemulidae	0.86	0.01	3.16
CHUB	Chubs	Kyphosidae	0.91	0.02	3.08
WRAS	Wrasses	Labridae	1	0.01	3.37
SNAP	Snappers	Lutjanidae	0.98	0.02	2.98
FILE	Filefishes	Monacanthidae	1	0.07	2.56
MORA	Morays	Muraenidae	1	0.001	3.16
BOXF	Boxfishes	Ostraciidae	0.84	0.12	2.63
ANGE	Angelfishes	Pomacanthidae	1	0.04	2.86
DAMS	Damselfishes	Pomacentridae	0.88	0.02	3.08
PARR	Parrotfishes	Scaridae	1	0.02	3.02
SCOR	Scorpionfishes	Scopaenidae	1	0.02	2.89
PORG	Porgies	Sparidae	0.95	0.04	2.8
BARR	Barracudas	Sphyraenidae	0.94	0.01	3.08
PUFF	Pufferfishes	Tetraodontidae	1	0.01	3.27

III. Biomass estimations (in g) of fish family groups

Appendix III: Biomass estimations (in g) of each fish family per size class.

Family Group	3cm	8cm	15cm	25cm	35cm	40cm	50cm	60cm	70cm	80cm	90cm	100cm	180cm
ANGE	0.9	15.3	92.4	398.3	1042.6	1527.4	2891.5	4870.5	NA	NA	NA	NA	NA
BARR	0.3	5.0	34.7	167.1	470.9	710.5	1412.7	2477.1	3982.3	6008.3	8635.8	11946.3	0.0
BOXF	1.4	18.0	94.0	360.3	872.9	1240.1	NA	NA	NA	NA	NA	NA	NA
BUTT	1.2	19.1	115.5	497.8	1303.2	NA	NA	NA	NA	NA	NA	NA	NA
CHUB	0.5	9.1	62.7	302.4	852.3	1286.0	2556.9	NA	NA	NA	NA	NA	NA
DAMS	0.4	8.2	56.6	272.7	768.7	NA	NA	NA	NA	NA	NA	NA	NA
FILE	1.2	14.4	71.8	265.4	627.9	883.8	1564.8	NA	NA	NA	NA	NA	NA
GROU	0.5	8.9	55.9	249.5	668.6	988.7	1901.1	3243.5	5095.3	7535.0	10640.5	14488.7	NA
GRUN	0.2	4.4	32.3	162.4	470.2	717.0	1451.3	NA	NA	NA	NA	NA	NA
JACK	0.3	6.0	39.0	179.7	491.4	732.5	1427.4	2462.1	3903.6	5819.2	NA	NA	NA
MORA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	28189.0
PARR	0.6	10.7	71.3	333.3	920.7	1378.0	2703.5	4688.6	7468.4	NA	NA	NA	NA
PORC	2.2	23.5	106.4	362.4	812.6	1119.6	1912.7	NA	NA	NA	NA	NA	NA
PORG	0.8	11.7	68.0	284.4	729.6	1060.4	NA	NA	NA	NA	NA	NA	NA
PUFF	0.4	9.0	70.1	372.6	1119.7	NA	NA	NA	NA	NA	NA	NA	NA
SCOR	0.5	8.2	50.1	219.3	580.0	853.1	NA	NA	NA	NA	NA	NA	NA
SNAP	0.5	13.3	60.2	275.9	752.0	1119.5	2176.8	3747.8	5933.0	8832.7	12546.6	17174.5	NA
SURG	0.7	11.7	69.4	294.5	763.1	1113.5	NA	NA	NA	NA	NA	NA	NA
TRIG	0.6	8.4	48.3	199.8	509.2	738.1	1372.5	NA	NA	NA	NA	NA	NA
WRAS	0.4	11.1	91.9	514.1	1597.8	2505.8	NA	NA	NA	NA	NA	NA	NA

IV. List of sites sampled across the Bay Islands

Appendix IV: List of sites sampled from 2006 to 2021 across the Bay Ialands

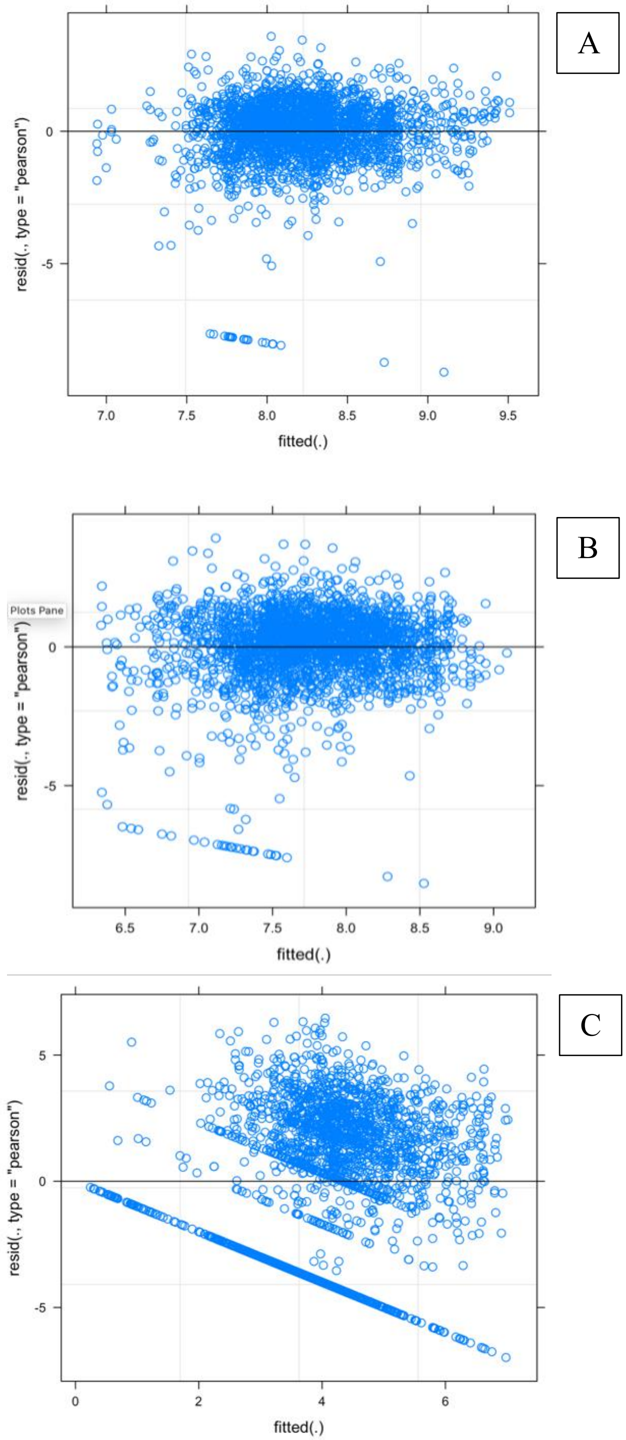
Code	Site	Latitude	Longitude	Zone	Subregion	Shelf
HNCYC001	Caballeros 1	15.97270	-86.59276	Bank	Cayos Cochinos	Bay Islands
HNCYC002	Caballeros 2	15.95457	-86.62655	Bank	Cayos Cochinos	Bay Islands
HNCYC003	Cayo Culebra	15.95399	-86.51929	Fore	Cayos Cochinos	Bay Islands
HNCYC004	Tariagagu	15.91957	-86.55431	Fore	Cayos Cochinos	North Honduras
HNCYC005	Voitague	15.91946	-86.54763	Bank Crest	Cayos Cochinos	North Honduras
HNCYC006	Cayo Cordero	15.95947	-86.47297	Patch	Cayos Cochinos	Bay Islands
HNCYC007	Atkins Bight	15.96647	-86.47972	Patch	Cayos Cochinos	Bay Islands
HNCYC008	Cayo Mayor	15.96377	-86.47610	Patch	Cayos Cochinos	Bay Islands
HNCYC009	Lion's Paw / Pelican 4	15.98111	-86.47856	Fore	Cayos Cochinos	Bay Islands
HNCYCZA001	Bajo Malaca	15.91781	-86.38764	Fore	Cayos Cochinos	North Honduras
HNCYCZA002	Bajo Bululo	15.87149	-86.36769	Fore	Cayos Cochinos	North Honduras
HNCYCZA003	Roatan Banks 1	16.06445	-86.49831	Fore	Cayos Cochinos	Bay Islands
HNCYCZA004	Roatan Banks 2	16.06433	-86.47906	Fore	Cayos Cochinos	Bay Islands
HNCYCZA005	Bajo Tano	15.89740	-86.43987	Fore	Cayos Cochinos	North Honduras
HNCYCZA006	Santa Maria	15.79586	-86.34880	Patch	Cayos Cochinos	North Honduras
HNGUA001	Eel Garden	16.47025	-85.92023	Patch	Guanaja	Bay Islands
HNGUA002	Captain Crack	16.39414	-85.89658	Bank	Guanaja	Bay Islands
HNGUA003	West End Reef Patches	16.39906	-85.95850	Fore	Guanaja	Bay Islands Shelf
HNGUA004	Baalmorales	16.42489	-85.90453	Patch	Guanaja	Bay Islands
HNGUA005	Rock Caves	16.44394	-85.95537	Fore	Guanaja	Bay Islands
HNGUA006	West Peak	16.48613	-85.91708	Fore	Guanaja	Bay Islands
HNGUA007	Allerson Wall	16.49697	-85.90324	Fore	Guanaja	Bay Islands
HNGUA008	Graham Cay	16.46074	-85.82514	Fore	Guanaja	Bay Islands
HNGUA009	George Cay	16.47248	-85.82225	Crest	Guanaja	Bay Islands
HNGUA010	Shark Alley	16.44352	-85.80896	Bank	Guanaja	Bay Islands
HNGUA011	Well Roy	16.45228	-85.83158	Crest	Guanaja	Bay Islands

HNGUA012	Mayra's Thunder	16.52301	-85.85322	Fore	Guanaja	Bay Islands
HNGUA013	Calaway	16.50801	-85.88915	Fore	Guanaja	Bay Islands
HNGUA014	Shark Stop	16.44486	-85.85587	Fore Inner	Guanaja	Bay Islands
HNGUA015	Long Reef	16.41377	-85.90294	Fore Inner	Guanaja	Bay Islands
HNGUA016	Chele's Last Day	16.47828	-85.82875	Subtidal Crest Bank	Guanaja	Bay Islands
HNBAR001	Shark Shoal	16.42967	-86.09623	Fore	Roatan	Bay Islands
HNBAR002	Boomerang Point	16.41108	-86.14527	Fore	Roatan	Bay Islands
HNBAR003	McNab Reef	16.42173	-86.12995	Patch	Roatan	Bay Islands
HNBAR004	Trunk Turtle	16.45107	-86.13706	Fore	Roatan	Bay Islands
HNMOR001	Rita´s Scary Wall	16.44242	-86.18790	Fore	Roatan	Bay Islands
HNROA001	Palmetto Bay	16.37378	-86.48286	Fore:Inner	Roatan	Bay Islands
HNROA001X	Shallow Sea Quest	16.28918	-86.60270	Subtidal Crest	Roatan	Bay Islands
HNROA002	Tree House	16.27845	-86.60387	Bay	Roatan	Bay Islands
HNROA002X	Turtling Bay	16.36675	-86.50686	Fore	Roatan	Bay Islands
HNROA003	El Bucanero	16.34750	-86.45660	Fore	Roatan	Bay Islands
HNROA004	Las Palmas	16.31880	-86.50160	Fore	Roatan	Bay Islands Shelf
HNROA004X	Wrasse Hole	16.34072	-86.56174	Fore	Roatan	Bay Islands Shelf
HNROA005	Man of War	16.35788	-86.53368	Fore	Roatan	Bay Islands Shelf
HNROA005X	Front Porch	16.33441	-86.57124	Fore	Roatan	Bay Islands Shelf
HNROA006	Politilly Bight	16.40841	-86.40711	Fore	Roatan	Bay Islands Shelf
HNROA006X	Overheat Reef	16.32145	-86.58442	Fore	Roatan	Bay Islands Shelf
HNROA007	Palmetto Bay	16.37351	-86.48902	Fore	Roatan	Bay Islands Shelf
HNROA008	Camp Bay East	16.43680	-86.26131	Fore	Roatan	Bay Islands Shelf
HNROA009	Punta Gorda Bay	16.42614	-86.35575	Subtidal Crest	Roatan	Bay Islands
HNROA010	Smith Bank	16.29008	-86.53690	Bank Crest	Roatan	Bay Islands
HNROA011	Key Hole Bay	16.27498	-86.58928	Subtidal Crest	Roatan	Bay Islands
HNROA012	Cliff	16.41113	-86.23973	Fore	Roatan	Bay Islands
HNROA013	Port Royal	16.40030	-86.28360	Fore	Roatan	Bay Islands
HNROA014	Oak Ridge	16.38838	-86.35029	Fore	Roatan	Bay Islands
HNROA015	Cordelia	16.29285	-86.54411	Bank Crest	Roatan	Bay Islands

HNROA017	Cordelia Banks	16.29071	-86.54292	Bank	Roatan	Bay Islands
HNROA018	Blue Hole Cordelia Banks	16.29843	-86.51913	Bank	Roatan	Bay Islands Shelf
HNROA019	Cordelia 2	16.30007	-86.52129	Bank	Roatan	Bay Islands
HNROA020	Cordelia 3	16.28987	-86.54247	Subtidal Crest Bank	Roatan	Bay Islands
HNROAPP	Pirate's Point (First Bight)	16.35835	-86.41237	Fore	Roatan	Bay Islands
HNROASHARK	Shark Dive	16.28550	-86.52002	Fore	Roatan	Bay Islands
HNUTA001	Carrie's Bay	16.10483	-86.97240	Fore	Utila	Bay Islands
HNUTA002	Paraiso	16.08995	-86.99433	Fore: Front	Utila	Bay Islands
HNUTA003	The Maze	16.11180	-86.94998	Fore	Utila	Bay Islands
HNUTA004	Joshua Swash	16.11880	-86.94077	Fore	Utila	Bay Islands
HNUTA005	Rock Harbour	16.12157	-86.91516	Fore	Utila	Bay Islands
HNUTA006	SouthWest Cay	16.07962	-87.01417	Fore	Utila	Bay Islands
HNUTI001	Tom Howell's Shoal	16.03252	-87.02547	Fore :Outer	Utila	Bay Islands
HNUTI002	José Ramón Shoal	16.05797	-87.02756	Bank	Utila	Bay Islands
HNUTI003	Moon Hole	16.08498	-86.89317	Fore (Front)	Utila	Bay Islands
HNUTI004	Salmedina's Cay	16.04326	-86.98087	Subtidal Crest	Utila	Bay Islands
HNUTI005	Little Cay	16.05409	-86.97887	Fore: Front	Utila	Bay Islands
HNUTI006	Ron´s Hole	16.08495	-86.89407	Fore	Utila	Bay Islands
HNUTI007	The Maze	16.11266	-86.94912	Fore: Front	Utila	Bay Islands
HNUTI008	Linda's Wall	16.10348	-86.87947	Fore: Front	Utila	Bay Islands
HNUTI009	Mangrove Bight	16.10096	-86.88094	Fore: Front	Utila	Bay Islands
HNUTI010	Anchor Bank	15.96638	-87.14321	Bank	Utila	North Honduras
HNUTI011	Banco Salmedina	15.89436	-87.04620	Bank	Utila	North Honduras
HNUTI012	Perez Corner	15.86143	-86.95560	Bank	Utila	North Honduras
HNUTI013	Ana´s Backyard	15.88291	-86.87875	Bank	Utila	North Honduras
HNUTI014	Jenny´s Garden	15.98502	-86.92270	Bank	Utila	North Honduras
MARUTA002	Paraiso	16.08995	-86.99433	Fore: Outer	Utila	Bay Islands

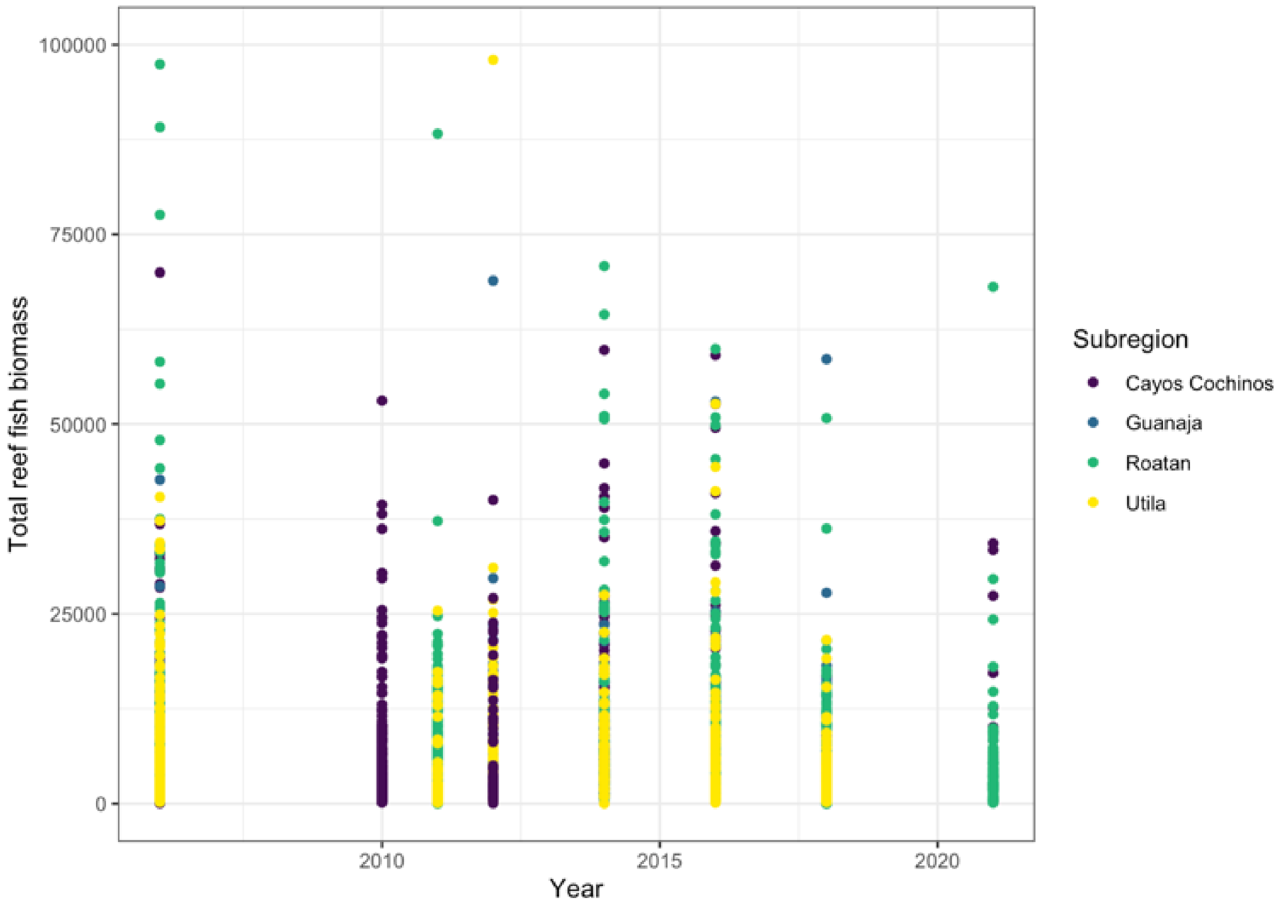
V. Residual plots for modelled fish declines

Appendix V: Residual plots for modelled fish declines including A: Total reef fish, B: Herbivorous reef fish, and C: Commercially valuable reef fish.

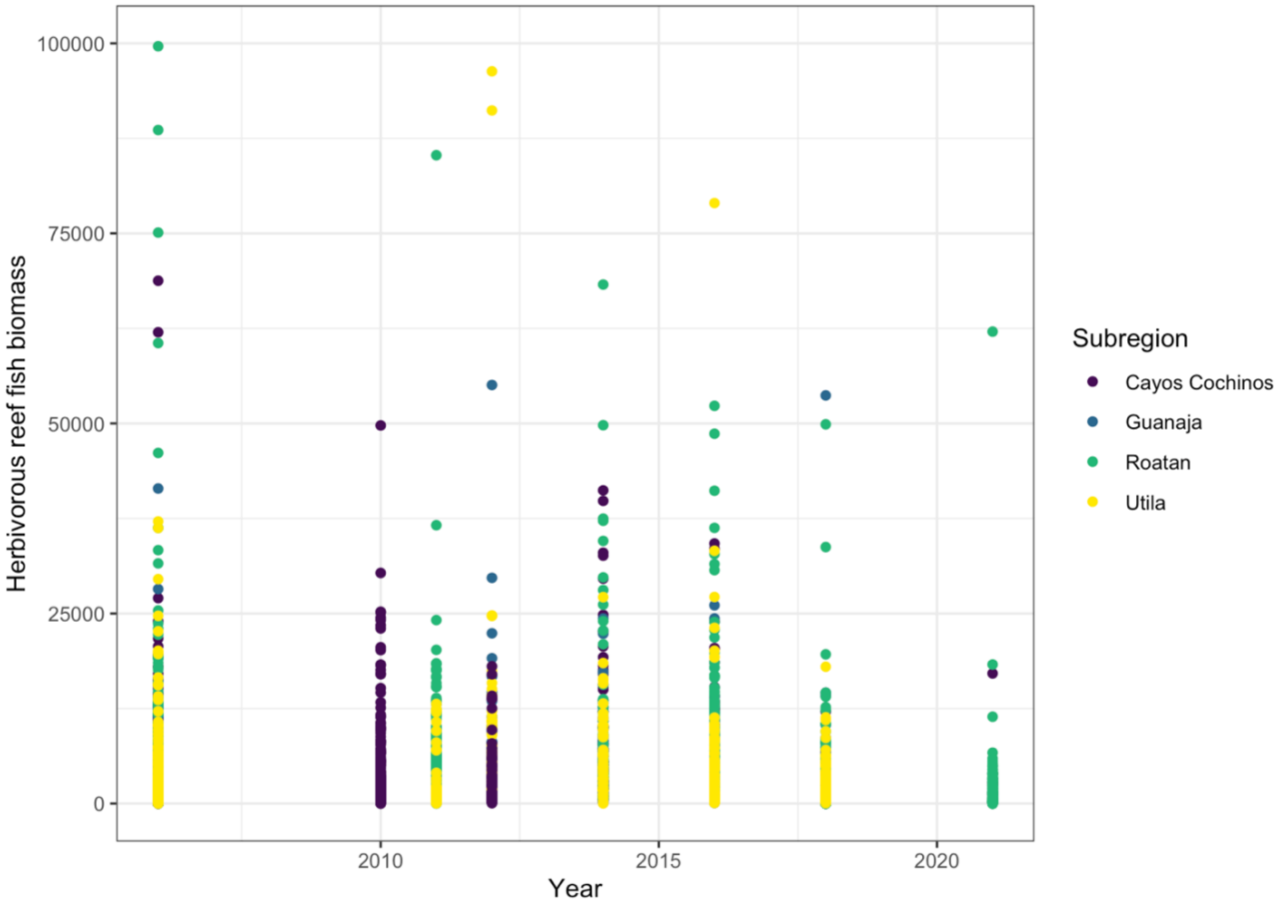


VI. Scatterplots of fish data

Appendix VI: Scatterplots of fish data including A: Total reef fish, B: Herbivorous reef fish, and C: Commercially valuable reef fish.

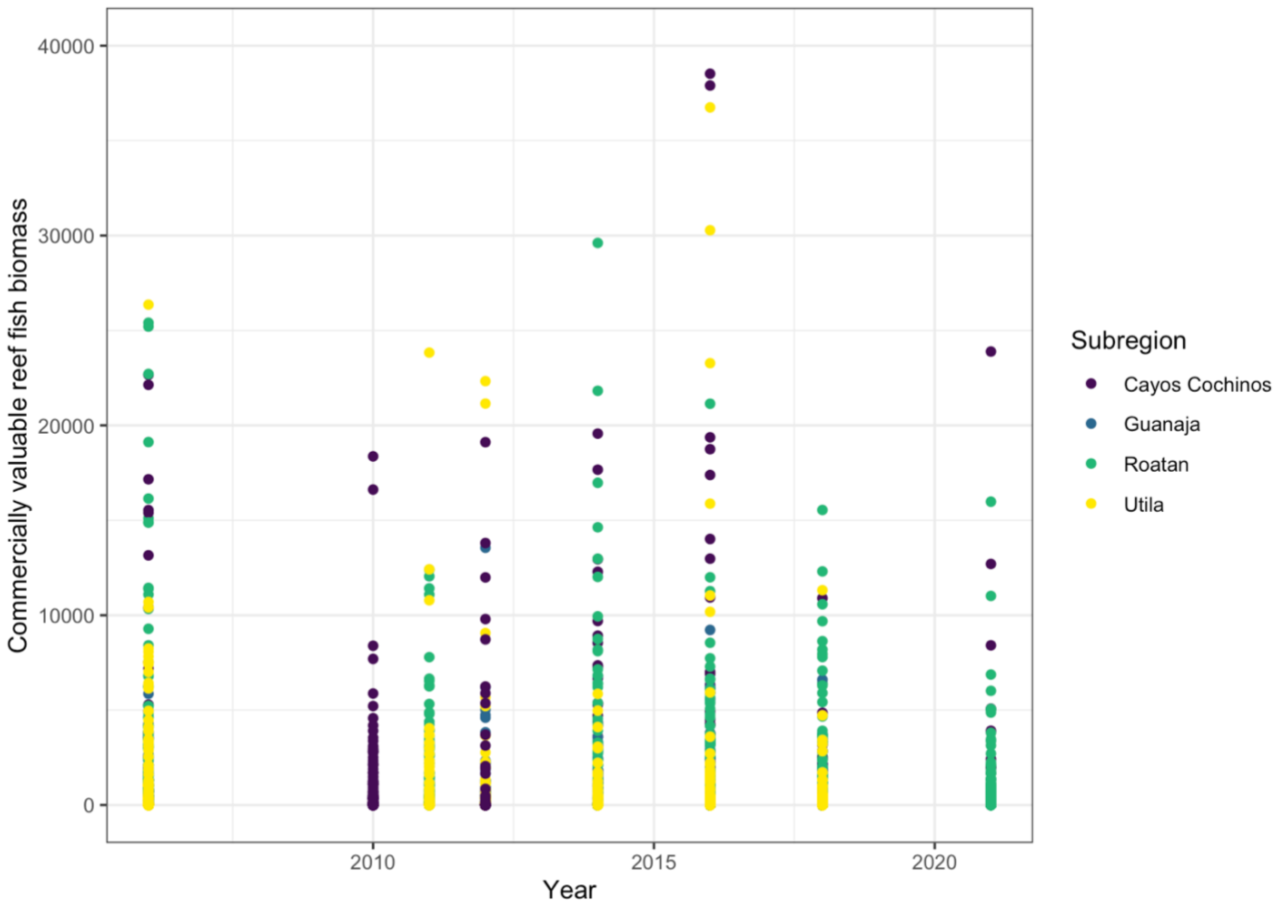


A



100000
75000
50000
25000
0
Herbivorous reef fish biomass
2010
2015
2020
Year
Subregion
Cayos Cochinos
Guanaja
Roatan
Utila

B


40000
30000
20000
10000
0
Commercially valuable reef fish biomass
2010
2015
2020
Year
Subregion
Cayos Cochinos
Guanaja
Roatan
Utila

C