Quantifying the state of the coral reef ecosystem in relation to biophysical benthic and pelagic indicators and biological drivers of change in the Saba National Marine Park, Dutch Caribbean

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Quantifying the state of the coral reef ecosystem in relation to biophysical benthic and pelagic indicators and biological drivers of change in the Saba National Marine Park, Dutch Caribbean

Kvantifiering av tillståndet för korallrevsekosystemet i relation till biofysiska bentiska och pelagiska indikatorer och biologiska påverkansfaktorer i Saba National Marine Park, Karibiska Nederländerna

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Abstract

Coral reefs are experiencing large scale degradation. Motivated by the need for regular data monitoring and for quantification of the state and change of benthic and pelagic organisms, the Global Coral Reef Monitoring Network protocol was executed on 18 dive sites in fished and unfished areas around the island of Saba in the Saba National Marine Park (SNMP) in the Dutch Caribbean from March to May 2019. Pictures of the benthos were taken and analysed with the Coral Point Count Excel extension software and fish biomass was calculated through the Bayesian length-weight-relationship. Although considerably below the Caribbean-wide average, coral cover around the island seems to be slowly recovering from past diseases and hurricane events. Coral species richness positively correlates with reef fish density and *Serranidae* species richness. As in other parts of the Caribbean, macroalgae in the SNMP are rapidly spreading and increasingly compete for space with habitat-providing gorgonians, sponges and other benthic organisms. In contrast to expectations, fish density and biomass continue to increase, even in zones where fishing is allowed. This might be explained by the higher availability of macroalgae that serve as food for various herbivorous fish species, which in turn are, amongst others, the prey of predatory fish and those higher up in the trophic cascade. However, with the exception of the commercially important fish family *Lutjanidae* all key fish species have declined in average size in recent years. Another finding is the increase of coral diseases. The results indicate the need for further species-specific research in order to identify the factors that are causing the degradation of the reefs in the SNMP. A better understanding of the interactions, ecological roles and functions of benthic and fish communities is therefore essential for the protection of reefs, that are of high value to Saba. The results of this study contribute to the adaptive management of the Saba Conservation Foundation that manages the SNMP.

Keywords: GCRMN, Reef Health Index, marine protected area, fish-benthos interaction, macroalgae, herbivory, trophic cascade, fishing, coral disease, Caribbean

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Abbreviations

AGRRA	Atlantic and Gulf Rapid Reef Assessment
CPCe	Coral Point Count with Excel extension
F	Fished zone
GCRMN	Global Coral Reef Monitoring Network
IPCC	Intergovernmental Panel on Climate Change
LWR	Length-Weight relationship
MPA	Marine Protected Area
RHI	Reef Health Index
SCF	Saba Conservation Foundation
SNMP	Saba National Marine Park
SocMon	Socio-economic variables of GCRMN
SST	Sea surface temperature
SLU	Swedish University of Agricultural Sciences
UF	Unfished zone

1. Introduction

1.1. Coral reefs

Coral reefs are known for their spectacular diversity. Because of their vibrant colours, their location in often pristine and clear waters and their richness, tropical coral reefs captivate almost everyone. Although they only make up around 0.01% of the marine environment, they provide a habitat for around one fourth of all known marine species (Gayle & Warner, 2018). Coral reefs can be thousands of years old and they can expand over several square kilometres as they are highly dynamic ecosystems (Spalding & Brown, 2015). Not only are they crucial to the world's biodiversity, coral reefs also provide essential ecosystem goods and services, on which at least 500 million people highly dependent on for protein, income and other needs as they support livelihoods, food security, recreation and other economic activities (Burke et al., 2011; Speers et al., 2016). Considering their direct benefits and wider ecosystem services the global value of coral reefs is estimated to be hundreds of billion dollars annually (Costanza et al., 2014; Hoegh-Guldberg, 2015; Rogers et al., 2015; Spalding et al., 2017).

Coral reefs around the world are experiencing large-scale degradation and are declining in condition globally, although more or less rapidly in different locations (Spalding & Brown, 2015). While a single coral head may take up to 20 years to cover 24 square kilometres, it may be irreversibly damaged in minutes (Manfrino, 2008). The main indirect and direct drivers as well as some example of declines can be seen in Figure 1, including anthropogenic factors such as overfishing, coastal development, pollution and climate change. According to the Special Report on Global Warming of 1.5°C of the Intergovernmental Panel on Climate Change (IPCC), coral reefs are expected to decline by 70-90% by the end of the century if we were to limit global warming to 1.5°C (Hoegh-Guldberg et al., 2018). IPCC claims that "almost all warm-water coral reefs are projected to suffer significant losses of area and local extinction" (IPCC, 2019, p.23).

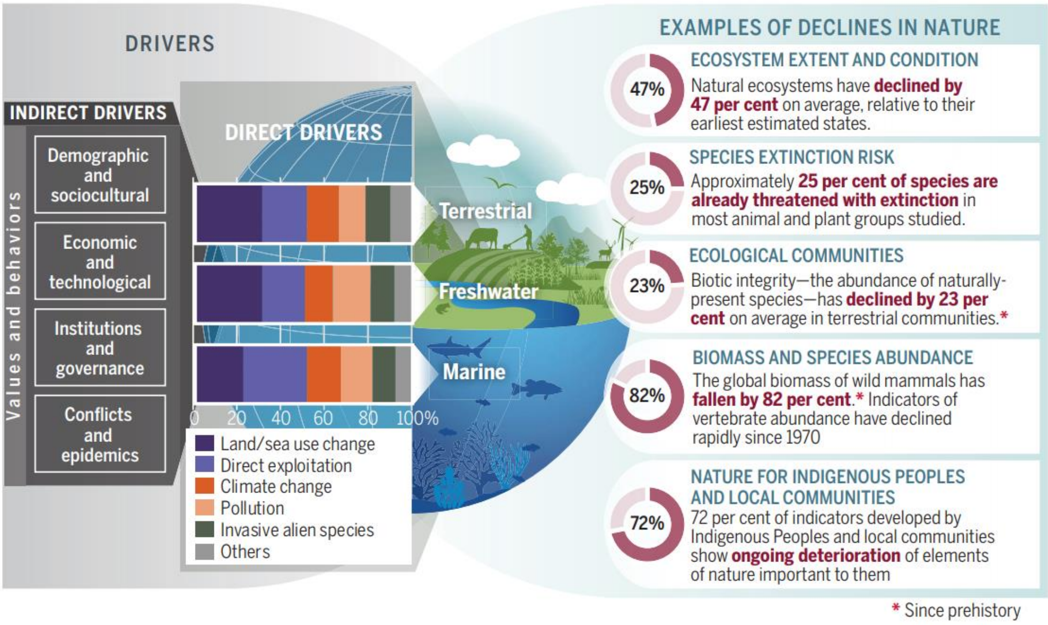


Figure 1. Indirect and direct drivers of change in nature and examples of its decline (Diaz et al., 2019).

Despite measures taken to minimize the negative impacts on coral reefs through the widespread development of marine protected areas (MPAs), the cumulative stress continues to threaten the existence of coral reefs (Gayle & Warner, 2018). Main drivers, which are mainly local and anthropogenic may be just as influential in the short-term as climate drivers in the long-term. Protecting marine life, stopping overfishing and stemming the plastic tide of pollution and the flow of fertilizers and chemicals that is suffocating fish and coral is therefore crucial to maintaining a healthy coral reef functioning ecosystem for as long as possible.

The establishment of MPAs is the foremost measure used for marine conservation, fisheries management and associated ecosystem services (McLeod et al., 2009; Molloy et al, 2009). Fish densities have been proven to increase by about 5% per year that a MPA is in place, meaning that the longer a MPA is established, the more effective it is in terms of fish populations (Molloy et al., 2009). In the Caribbean, MPAs have proven to lead to larger biomass of both herbivorous and carnivorous fish, and it was shown that there is a significant variation in macroalgae abundance between protected and unprotected sites (Mumby et al., 2006).

1.2. From coral- to macroalgae-dominated reefs

A rapid decline in hard coral cover within the Caribbean has occurred (Alvarez-Filip et al., 2009; Gardner et al, 2003; see Figure 2) and in this regard, the coral reefs in this geographic region are one of the most degraded in the world (Hughes, 1994).

Gayle and Warner (2018) indicate that the Caribbean may have lost more than 50% of its coral reef cover since 1970. Previously, habitats were dominated by reef-building corals, which were mostly from the *Acropora* and *Montastrea* genus (Cramer et al., 2017). Since the beginning of systematic reef monitoring in the 1970s, the amount of these reef-building coral species has declined by more than 80% on many Caribbean reefs from 1977 to 2001 (Gardner et al., 2003; Cramer et al., 2017). Statistics show that in 2012 the average coral cover for the wider Caribbean was 16.8%, whereas in 1970 coral cover was as high as 34.8% (Jackson et al., 2014). Today, coral cover has declined to a regional average of 13% (AGRRA, 2018) and reefs mostly consist of non-framework builders such as A*garicia*, *Porites* and sponges (Gardner et al., 2003). The non-framework builders show slower calcification rates and are therefore linked with overall declines in $CaCO_3$ production (Perry et al., 2015). These species are also slower growing, domed, plated, encrusted and highly susceptible to temperature shifts and storm damage (Knowlton, 2001). However, coral cover varies significantly within locations in the Caribbean (see graphs A and B in Figure 2). Coral species are not identical in resilience, which explains the significant variability in coral responses to stress and hence, differences in health.

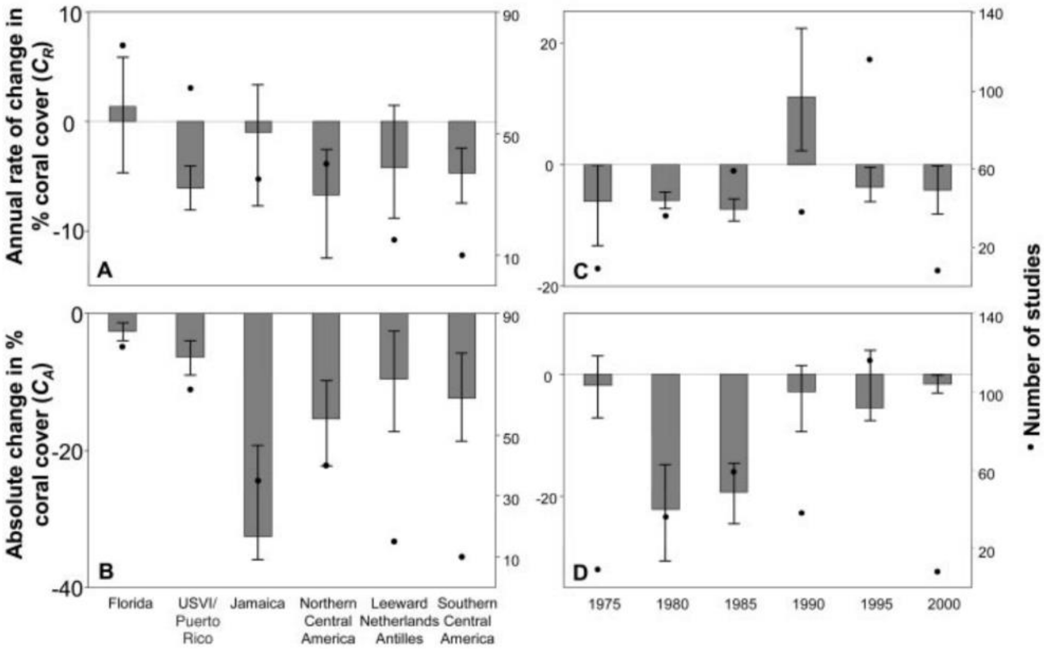


Figure 2. Coral cover change for subregions of the Caribbean for 5-year time periods from 1975 to 2000 (Gardner et al., 2003).

Nowadays, Caribbean coral reefs are dominated by macroalgae and have therefore been taken out of their naturally dynamic equilibrium and shifted towards an alternative state (McClanahan et al., 1999). Coverage of macroalgae increased from 7% to 23.6% between 1984 and 1998 (Jackson et al., 2014) and makes up around 40% of the forereef today (AGRRA, 2018). There is sufficient evidence that

Caribbean coral reefs have shifted away from a coral-dominated state towards an algal-dominated habitat over recent decades (Andersson et al., 2019; Cramer et al., 2017; Gardner et al., 2003; Mumby, 2009).

The disappearance of corals has been reported to affect fish density and richness negatively. Because of these ecological changes in the coral reef ecosystem and thus habitat destruction, reef fish numbers have been declining significantly since the 1990s (Paddack et al., 2009). In the Caribbean, loss rates between 1995 and 2007 were consistent with 2.7% and 6.0% per year. The loss occurs across several trophic groups as well as in both fished and unfinished species (ibid.).

1.3. Drivers of change

Assessing the main causes of this change has been challenging because of the synergistic nature of biological/natural, climate-related and anthropogenic stressors. Although there is scientific consensus that different factors are impacting the reefs negatively and simultaneously, “the relative importance of historical and local versus recent and regional or global anthropogenic causes of reef decline” is still controversial (Cramer et al., 2017, p.2). Gardner et al. (2003) claim that there is not yet convincing evidence of global stressors affecting the overall coral decline pattern at a Caribbean-wide scale, and rather refers to local factors originating both naturally and anthropogenically for the region.

Climate-related drivers include the increase in sea surface temperature (SST) and ocean acidification. Antuña-Marrero et al. (2016) calculated that SST rise in the Antilles in the Caribbean ranges between 1.39 and 2.21°C per century under the business-as-usual scenario. The ocean absorbs elevated levels of carbon dioxide which will culminate in the reduction of oxygen solubility in the water, the promotion of stratification of ocean layers leading to de-oxygenation and the dissolving of aragonite crystals formed at a lower pH. In some areas the pH level decreased with more than 40% (Andersson et al., 2019), which makes the Caribbean “one of the fastest changing chemical environments under ocean acidification” (p. 4) and increasingly less favourable for calcium carbonate production. Under a lower pH and aragonite saturation, the vulnerability of coral reef frameworks is enhanced as weakened CaCO3 structures are increasingly prone to be eroded by physical processes such as storms and wave action (Manzello et al., 2008; Tribollet et al., 2009; Wisshak et al., 2012). Simultaneously, hurricanes, which are projected to increase in frequency and intensity, cause mechanical damage to coral reefs (Eakin et al., 2010). They have been observed to damage coral tissue and to dislodge coral colonies (Wilkinson & Souter, 2008). On average, within the Caribbean coral cover is reduced by about 17% in the year following a hurricane (Gardner et al., 2005). A healthy coral has the means to heal again in a relatively short time (Meesters et al., 2019). However, corals are weakened after hurricane impact which could slow down recovery following other events, contributing to long-term ecosystem decline. The increase in SST and the following reactions have become a major threat to marine life and coral reef ecosystems around the world and pose increasing threats to the availability of Caribbean reefs to sustain themselves and recover from future stress events (Andersson et al., 2019).

Global climate change is projected to also lead to an increase of coral bleaching, which threatens the long-term integrity of coral reefs (Eakin et al., 2010). Hard coral species (e.g. *Orbicella faveolata*) have been found to skip a spawning season as a trade-off to replenishing lipid reserves that provide the coral host with energy in case they survive the stress period (Fisch et al., 2019). If coral colonies release less gamete bundles for reproduction, future generation are directly and indirectly impacted through lost opportunities for recombination, which further reduces their capability to adapt to increasing ocean temperatures and diseases (Dixon et al. 2015; Van Oppen et al. 2015). A decline in coral reproductive success has also been proven by Baird et al. (2009). The last severe bleaching event in the Caribbean in 2005 left 80% of all corals bleached, and 40% dead (Eakin et al., 2010; see Figure 3). More frequent and intense bleaching events “will undoubtedly have long-term consequences for Caribbean coral reefs as these have shown very slow rates of recovery to mortality from mass bleaching” (ibid., p.6; Baker et al., 2008). Hence, any additional bleaching event adds to the damage caused by past events, leading to a further decline of reefs.

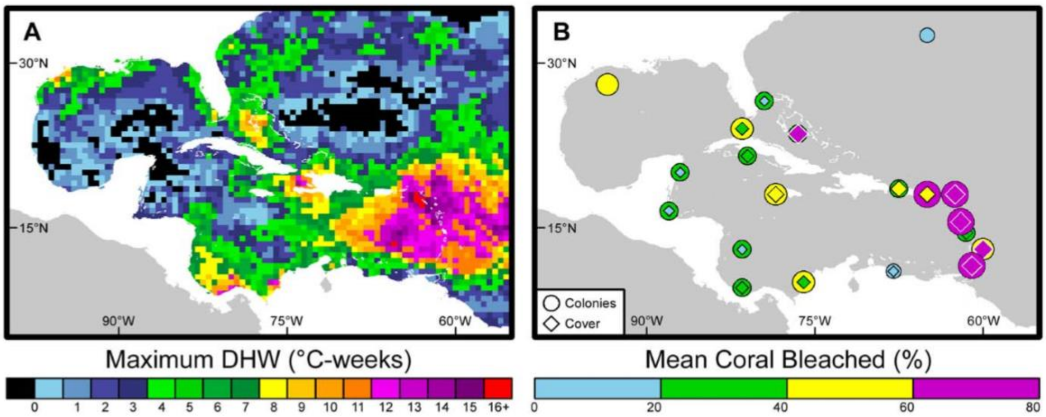


Figure 3. Thermal stress and bleaching during the 2005 Caribbean bleaching event (Eakin et al., 2010).

The following drivers of change are of biological nature. The appearance and intensification of coral disease and bleaching events have been linked to algal overgrowth that is also fuelled by the overexploitation of herbivorous fish amongst other factors. Diseases such as the white band disease from the 1970s killed *Acroporids*, which were major coral reef builders in the region (Aronson & Precht, 2001; Gladfelter, 1982; Kline & Vollmer, 2011). Since 2014, the stony coral tissue loss disease (SCTLD) has caused widespread loss of coral as it spread from Florida to other parts in the Caribbean, where it was first reported in 2018 (Alvarez-Filip et al., 2019). The sea urchin *Diadema antillarum*, which has undergone mass mortality in the early 1980s, is an important macroalgae grazer. Prior to its die-off the average *Diadema* density was 1-10 individuals m^{-2} (Lessios, 2005), by 2000 it had already been drastically reduced to 0.06 individuals m^{-2}, and more recent surveys indicate even lower numbers ($0.02m^{-2}$ +- 0.3 SD) (Newman et al., 2006). Its loss combined with a reduction in herbivorous fish population due to unsustainable fishing practices let fleshy algae to dominate the reef (Andersson et al., 2019). Turtles that also ingest algae are declining in numbers and sponges that provide critical structure to the reef habitat remain inadequately protected (Burke et al., 2011). Another natural driver of change is the appearance of invasive species such as in the Caribbean the lionfish (*Pterois volitans*) (Gracia et al., 2011). The presence of the lionfish has effects on a reef's biological productivity, habitat structure and species composition (ibid). Since the lionfish found an ecological niche and does not have any natural predators within the Caribbean, it is able to spread rapidly throughout the whole region. They feed on parrotfish and on other commercially important fish, and are thus of high concern for both coral reef health and fisheries (Green et al., 2012). The geographic and biological isolation of the Caribbean has the potential to magnify the vulnerability of Caribbean reefs to introduced pathogens and non-native species making them inherently fragile (Andersson et al., 2019; Jackson et al., 2014).

Alvarez-Filip et al. (2009) found that Caribbean reefs are flattening out, meaning architectural complexity is lost. This widespread breakdown of the reef matrix has consequences for its biodiversity, functioning and associated environmental impacts (Graham & Nash, 2013). Since many reef fish species are dependent on the rugosity of the reef to feed, recruit and hide (Alvarez-Filip et al.,2009), the decline in reef complexity results in a lack of settlement sites and refuges, which in turn affects recruitment numbers negatively (Mumby & Steneck, 2008). The lost structural complexity also affects predator-prey interactions since physical refuges allow prey to escape predation. Thus, a high availability of refuges increases the vulnerability of predators, especially when fishing pressure increases (Rogers, Blanchard, Newman et al., 2018). Small changes in the biomass of reef fish propagate through the food web and therefore determine overall productivity of fisheries (Rogers, Blanchard & Mumby, 2018). A coral reef food web model study (ibid.) showed that reef fisheries appear to be fairly robust in the initial stages of reef degradation due to increased resource availability (more available prey and higher turf production leads to higher growth rates in large-bodied fish), but decrease if a reef is dead. Birchenough (2017) also points to the decline of herbivorous fish biomass as well as to diseases, whose direct impacts on coral integrity have been underestimated.

Anthropogenic drivers include overfishing, coastal development, habitat destruction, pollution, the influx of fertilisers and pesticides from agriculture, habitat and other substances in run-off, oil spills and tourism. For example, human activities affect water quality in terms of nutrient provision, which then stimulates and supports the growth of macroalgae on reefs (Bowen, 2015).

The combined effects of climate change, the introduction of non-native species and anthropogenic impacts could exacerbate negative effects on Caribbean coral reefs in the future (Birchenough, 2017). All these factors have triggered ecological phase shifts, and coral-dominated reefs have given way to macroalgal dominance (Gardner et al., 2003; Mumby, 2009; Andersson et al., 2019). Differences in reef ecosystem health across different locations are due to varying degrees of these impacts (Gayle & Warner, 2018). Table 1 shows the events that affected the coral reef ecosystem on Saba since the 1970s.

Table 1. Timeline of events affecting the coral reef ecosystem in the Saba National Marine Park.

Date	*Event*	*Impact*	*Source*
Mid 1970s	White-band disease	Killed approx. 90% of the acroporid corals and exposed their branching skeletons	Aronson & Precht, 2001
1983-1984	Mass mortality of sea urchin *Diadema antillarum*	Region-wide disease-induced (unidentified pathogen)	Carpenter, 1990 Lessios et al., 1984; Hughes et al., 1985
1987-88	Mild bleaching event	Associated mortality	
1989	Hurricane Hugo (category 4)		cited in Hildebrand (2017)
1995	Hurricane Luis (Category 4)	Physical damage to corals, especially *Acropora palmata in shallow, high-surge areas*	Klomp & Kooistra (2003)
1995	Hurricane Marilyn (Category 2)		cited in Hildebrand (2017)
1996	Hurricane Bertha (Category 1)		cited in Hildebrand (2017)
1998	Coral bleaching event	Widespread coral bleaching event	McWilliams et al., 2005

1998	Hurricane Georges (category 2)	Physical damage to corals, especially *Acropora palmata in shallow, high-surge areas*	Klomp & Kooistra (2003)
1999	Hurricane Jose (Category 1)		cited in Hildebrand (2017)
1999	Hurricane Lenny (Category 4)	Physical damage to corals, especially *Acropora palmata in shallow, high-surge areas*	Klomp & Kooistra (2003)
1999	Diseases	Yellow band disease (YBD), White plague (WP), Black Band Disease (BBD)	Jackson et al. (2014)
2000	Hurricane Debby (Category 1)		cited in Hildebrand (2017)
2005	Coral bleaching event	Worst event on record at that time	NOAA (2010)
2008	Hurricane Omar (Category 4)		cited in Hildebrand (2017)
2010	Hurricane Earl (Category 3)		cited in Hildebrand (2017)
2010	First invasive lionfish detected on Saba		cited in Hildebrand (2017)
2010	Coral bleaching event		
2017	Hurricane Irma (category 5) & Maria (category 5)		DCNA (2017)
2019	Hurricane Dorian (category 5) & Jerry	The most powerful hurricane on record in the open Atlantic region	

1.4. The Global Coral Reef Monitoring Network (GCRMN) and the Reef Health Index (RHI)

All of the aforementioned factors have an effect on the health of coral reef ecosystems and cannot be decoupled from one another. The Global Coral Reef Monitoring Network (GCRMN) has acknowledged the value in monitoring temporal changes to the coral reef ecosystem (UNEP, 2016). GCRMN led by UN Environment is the world's premier coral reef data network and brings together different stakeholders to strengthen the best available scientific information and communication about the status of coral reef ecosystems. GCRMN tracks the impacts of climate change on coral reefs as well as the progress made towards internationally adopted targets including Sustainable Development Goal 14: Life below water (United Nations, n.d.). Their guidelines were established by the International Coral Reef Initiative (ICRI) in 1994. The main goals of GCRMN are to improve the understanding of coral reef status and trends, globally and regionally; to analyse and communicate coral reef biophysical, social and economic trends; to enable and facilitate greater utilization of coral reef data, including in research; and to build human and technical capacity (UNEP, 2016).

The GCRMN defined a set of data and data collection techniques to harmonize monitoring practices across the globe and for the Caribbean. The GCRMN-Caribbean guidelines for coral reef biophysical monitoring consist of six indicators:

(1) abundance and biomass of key reef fish taxa,

(2) relative cover of reef-building organisms (corals, coralline algae) and their dominant competitors,

(3) assessment of coral health,

(4) recruitment of reef-building corals,

(5) abundance of key macro-invertebrate species, and

(6) water quality (UNEP, 2016).

The Healthy Reefs Initiative (HRI) considers a coral reef ecosystem healthy if the population of both herbivorous and commercial fish as well as coral cover is high and macroalgae cover is low. The Reef Health Index (RHI) was developed by the Healthy Reef Initiative and is one of the first attempts to globally develop measurable ranking criteria to assess the health of a coral reef ecosystem. It has been established and is quite consistent within the Mesoamerican Reef in the Western Caribbean. It was also used for the GCRMN in Saba in the past years. The RHI includes the following four indicators:

1. Coral Cover = the amount of reef surface covered by live stony corals, contributing to its three-dimensional framework
2. Fleshy Macroalgal Cover = the proportion of reef covered by fleshy algae
3. Key Herbivorous Fish = biomass of important grazers on plants that could overgrow the reef
4. Key Commercial Fish = biomass of fish species commercially important to people

The RHI score ranges from critical (1) to very good (5; see Figure 9).

1.5. Biophysical indicators of a healthy coral reef ecosystem

Coral reef health requires an ecological balance between fish, corals and algae.

Critical fish species for maintaining ecosystem health are snappers (*Lutjanidae*), groupers (*Serranidae*), parrotfish (*Scaridae*), surgeonfish (*Acanthuridae*) and grunts (*Haemulidae*). These are principal food fish among Caribbean small-scale fisheries with still relatively intact numbers (UNEP, 2016). The herbivorous species – parrotfish and surgeonfish –graze on macroalgae and thus decrease its abundance. Herbivory has the ability to structure the benthos whereas the three other species, which are key carnivore fish groups on the reef, are crucial for predator control and for preventing the occurrence of trophic cascades (Van der Vlugt, 2016). Fish that also play an important role in fisheries are barracudas, grunts and parrotfish. With regard to ecosystem maintenance, damselfish and triggerfish are critical (UNEP, 2016). Invasive species such as the lionfish influence the health too, as do key macro-invertebrates such as sea urchins and sea cucumbers through their role of nutrient recycling.

The size of reef fish can be correlated with the complexity and status of the coral reef (Rogers, Blanchard & Mumby, 2018; see Figure 4). While a loss of branching corals, which indicates a worse reef condition, results in an increase in the average body size of both predators and herbivores, the size of herbivores declines significantly once all structure was lost. This suggests that non-complex habitats cannot support large-bodied herbivores (ibid.). Predatory fish size on the other hand increases on reefs with dead coral and little structural complexity because small-bodied fished decline in numbers, reflecting a resource shift from many small-bodied to fewer large-bodied reef fish. Healthier reefs also support the availability of shelters and variety in food, and thus are equal to an increase in diversity and abundance of species (Rogers et al., 2014).

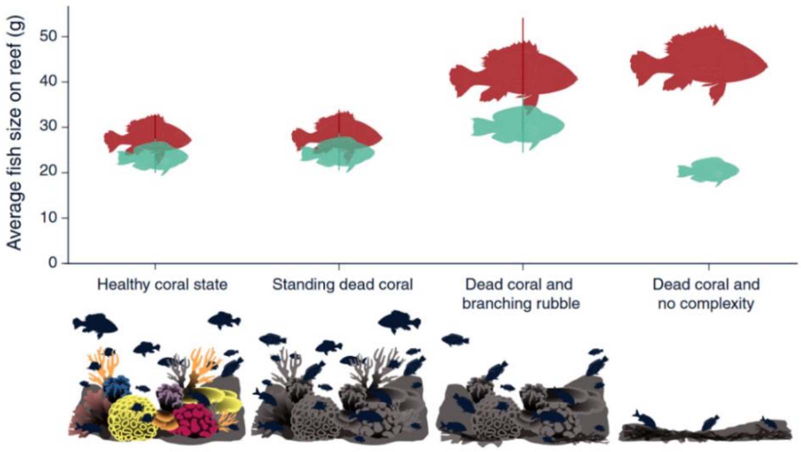


Figure 4. Reef degradation and average of predatory (red) and herbivorous (green) reef fish (Rogers, Blanchard & Mumby, 2018).

Benthic cover serves as an indicator as well. This includes stony and gorgonians as well as their most important competitors. Stony corals and some calcifying algae are the dominant taxa building the reef structure (UNEP, 2016). Gorgonians, or soft corals, act like a terrestrial forest with a canopy and thus provide critical habitat for associated organisms. They add soft physical structure to the benthic environment (Tsounis et al., 2020). Other benthic organisms that are attached to the bottom limit reef structure growth. These are turf, some macroalgae and some benthic invertebrates. The most abundant genera of macroalgae are *Dictyota* and *Lobophora* (Cardoso et al., 2009; Diaz-Pulido et al., 2011; Suchley and Alvarez-Filip, 2017). High macroalgae coverage indicates poor health as it negatively affects coral in all its life stages. Macroalgae can outcompete coral recruits by taking up the space a recruit can settle on (Venera-Ponton et al., 2011). Once the coral grows, macroalgae can overgrow it, which results in damage to the coral by separating a colony into smaller patches (Hughes & Tanner, 2000) and reduces growth of the coral reef system (Box & Mumby, 2007). Macroalgae also increase the prevalence of diseases (Birrell et al., 2008). Therefore, the lower the percentage of macroalgae and the higher the percentage of stony and reef-building corals the healthier an ecosystem is considered to be. While cyanobacteria are considered to be essential reef-builder assisters and nitrogen providers on the reef, they inhibit coral recruitment through occupying space. In addition, they can form pathogenic microbial consortia in association with other microbes that cause coral death (Charpy et al., 2012). Lower coral cover is further accompanied by lower coral reproduction rates. This is because less gametes are produced and in addition, these have to survive an increasing distance for fertilization. As a result, the coral reef becomes less genetically diverse and less stable and resilient (Knowlton, 2001). Additionally, the appearance of coral disease and the occurrence of coral bleaching negatively affects the health of the ecosystem (Cramer et al., 2012).

Lastly, water quality has proven to be a health indicator as well. Turbidity and subsequent reduction in light availability are not favourable for coral growth. Water quality in terms of nutrients and chemical characteristics may stimulate macroalgae growth and the expansion of coral diseases (Jackson et al., 2014).

1.6. Saba and the Saba National Marine Park (SNMP)

Saba (17'36'N, 63''15'W) belongs to the Windward islands of the Caribbean and as of 2010 it is the smallest special municipality of the Netherlands. It is the peak of an isolated volcanic island of the late Pleistocene to mid-Holocene origin (Westermann and Kiel, 1961). Saba is a relatively small island with a land area of 13km^2 and a coastal length of 16km (Jackson et al., 2014). The coastline is formed out of steep, rocky cliffs and because of rapid erosion development on the island human development is constraint to places higher up in altitude. As of June 2020

1,933 people live on Saba (CBS, 2020), spread over the three main villages that are connected by one street known as ‘The Road’. Coastal development on Saba is limited to a small harbour (Klomp & Kooistra, 2003), where the Marine park office, the dive operators Sea Saba and Saba Divers and a power plant are located.

Figure 5. The island of Saba.

In 1987 the Saba National Marine Park (SNMP) was established and is today known for its spectacular pinnacles rising from the ocean floor up to 20 metres above the surface. The Marine Park is managed and actively regulated by the non-governmental organisation Saba Conservation Foundation (SCF), aiming to preserve Saba’s natural and cultural heritage. The marine park has a size of 13km² encircling the entire island (DCNA, n.d. b). It encompasses the seabed and waters between the high-water mark down to a depth of 60 meters (Klomp & Kooistra, 2003; DCNA, n.d. a). A zoning system, which includes no-take fishing zones and zones meant for yachting, ensures the best possible compromise between different recreational, commercial and conservation uses of the marine park (SabaTourism, n.d.). 33% of the SNMP is a no-take zone, in which fishing and anchoring by larger recreational vessels is prohibited but scuba diving is permitted (cited in Menger, 2016). Permanent mooring buoys on selected sites eliminate anchor damage on corals. Furthermore, in 2015 the Yarari Marine Mammal and Shark Sanctuary was established, which comprises the waters around the Dutch Caribbean islands Bonaire, Saba and St. Eustatius.

Coral communities are found circumfusing the island within a reef area of 3.08km² (Debrot et al., 2018; see Figure 6). They settle on granite boulders, pinnacles and lava formations. Although every dive site has different unique features, the majority of the coral structures around Saba are classified as coral-encrusted boulders of volcanic origin. Walls close to the shore are covered with sponges of all sizes. The deep water seamounts attract pelagic fish and other creatures and frequently sharks pass by (Saba Conservation Foundation, n.d.). Saba is known for the pinnacles and boulders off the west coast (DCBD, 2018). Saba also has two small rocky islets, Green Island and Diamond Rock (ibid.).

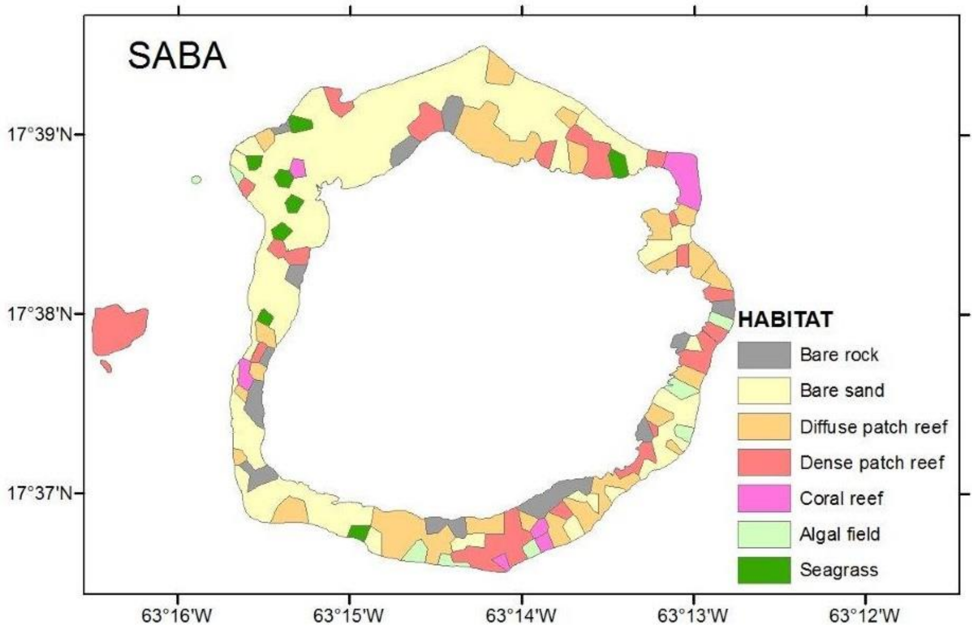


Figure 6. Habitat map of the SNMP (Kuramae & van Rouendal, 2013).

Only few studies have looked at the health of Saba's coral reef ecosystem since the early 1990s. Buchan (1998) executed CARICOMP from 1993-1998 and in 2003 and included corals, *Diadema antillarum* and macroalgae in his monitoring site at Ladder Labyrinth. In 1999, the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol examined the status of the corals around Saba and the other Dutch Islands of St. Eustatius and St. Maarten. Damage caused by Hurricane Lenny was evaluated by Klomp & Kooistra (2003). Other studies have assessed the impact of fishing on the surrounding reefs (Polunin & Roberts, 1993; Roberts et al., 1993; Roberts, 1995; Robert & Hawkins, 1995; Noble et al., 2013). The GCRMN was executed twice in Saba (by Van der Vlugt in 2015/2016, and Menger and Hildebrand in 2016). Additionally, in November 2016 Sandin and his expedition colleagues from the Scripps Institute of Oceanography and the WAITT Foundation assessed fish, macro key invertebrates and benthos along the Windward Caribbean Islands in a survey method similar to the GCRMN (Sandin et al., 2016).

1.7. Research aim and questions

This study was motivated by the need for regular data monitoring in the SNMP to better understand the interaction between biophysical indicators and the biological drivers of change of the coral reef ecosystem in the SNMP for adaptive management. Detecting key interactions between fish and benthic communities that may affect the coral reef ecosystem both negatively and positively and that are yet unknown in the SNMP, is crucial for a small island like Saba, where coastal development and anthropogenic influence is limited. The effect of fishing is being tested by distinguishing fished and unfished zones. Monitoring and keeping track of the changes of the condition of the coral reef allows to make more informed decisions to safeguard the ecosystem and to establish protection priorities, especially with regard to future changes in the climate. Few studies have looked at the drivers of change and indicators of coral reef health in the SNMP to assess the status but little research has been done on the interaction of these indicators. Therefore, this study assesses and quantifies these correlations to better understand the relationships between the biophysical indicators in the coral reef ecosystem around Saba. With the results, it has the potential to contribute to the management of the SNMP. The central research aim is to quantify the state of the coral reef ecosystem in the Saba National Marine Park in relation to biophysical indicators and biological drivers of change. In order to provide answers to the central research aim, a subset of more specific questions were developed:

SRQ1) Is there a significant difference in the state of the coral reef ecosystem and the individual biophysical indicators between fished and unfished zones?

SRQ2) Is there a significant relationship between fish density, biomass, species richness, size and benthic cover?

SRQ3) Is there a significant relationship between the occurrence of coral diseases and fish density, biomass, species richness, size and benthic cover?

The working hypotheses for the study were:

I. Sites in the unfished zone are in a better coral reef ecosystem state as assessed by the RHI than those in the fished zone.

II. Coral cover positively correlates with fish density, biomass, species richness and size.

III. Macroalgae cover negatively correlates with key predatory fish indicators but positively correlates with key herbivorous fish indicators. In locations with more grazers (herbivores) present, there is less macroalgae.

IV. Coral diseases and bleaching negatively affect fish density, biomass, species richness, size and benthic organisms.

V. There is a temporal difference of the indicators over the years.

2. Methodology

2.1. Study area and sites

The data were collected between March and May 2019 in the SNMP surrounding the Dutch Caribbean island of Saba (see Figure 7 and Table 2).

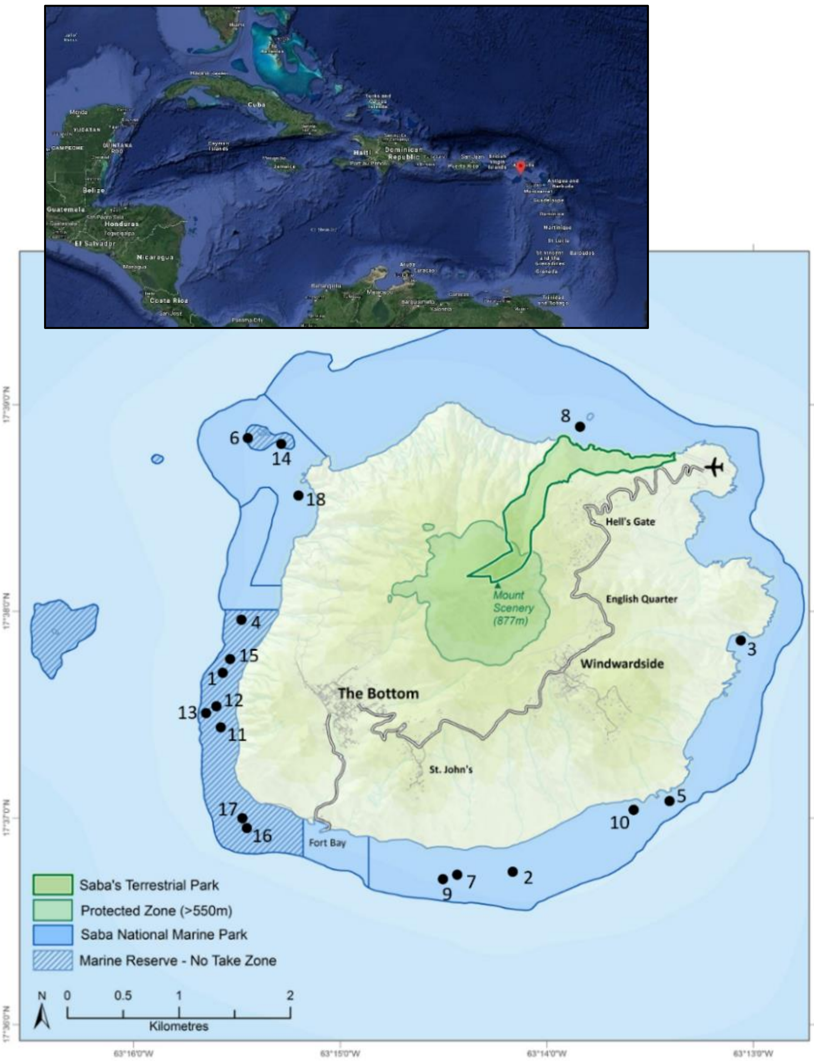


Figure 7. The location of Saba island within the Caribbean (top) and of the dive sites used for this study in the Saba Marine Park used for this study (modified from DCNA, n.d. b)

Table 2. Dive sites, coordinates and date of study.

Number	Dive site name	Latitude (°'N)	Longitude (°'W)	Study date
1	Babylon (BA)	17°37'42.66	63°15'34.50	24.04.2019
2	Big Rock Market (BRM)	17°36'45.06	63°14'10.44	08.05.2019
3	Core Gut (CG)	17°37'51.90	63°13'03.54	20.03.2019
4	Customs House (CH)	17°37'54.84	63°15'29.58	26.03.2019
5	David's Drop-off (DDO)	17°37'06.12	63°13'25.44	08.05.2019
6	Diamond Rock (DR)	17°38'49.80	63°15'24.00	02.05.2019
7	Giles Quarter Shallow (GSQ)	17°36'42.60	63°14'28.80	07.05.2019
8	Green Island (GI)	17°38'53.88	63°13'50.16	08.05.2019
9	Greer Gut (GG)	17°36'42.54	63°14'30.30	28.03.2019
10	Hole in the Corner (HIC)	17°37'03.72	63°13'34.92	30.04.2019
11	Hot Springs (HS)	17°37'28.68	63°15'34.50	24.04.2019
12	Ladder Labyrinth (LL)	17°37'34.44	63°15'36.24	02.05.2019
13	Ladder Labyrinth 2 (LL2)	17°37'33.60	63°15'37.80	07.05.2019
14	Man of War Shoals (MWS)	17°38'47.94	63°15'19.20	03.05.2019
15	Porites Point (PP)	17°37'45.54	63°15'31.98	26.03.2019
16	Tents Reef (TR)	17°36'58.80	63°15'30.60	12.03.2019
17	Tents Reef Deep (TRD)	17°36'59.34	63°15'30.60	27.03.2019
18	Torrens Point (TP)	17°38'35.88	63°15'11.94	13.03.2019

2.2. Data collection

This study uses the Global Coral Reef Monitoring Network (GCRMN) guidelines as a tool to investigate the research aim and the interaction of biophysical indicators and biological drivers of change. Due to the scope of this study, only biophysical variables of the GCRMN were considered, and not the socio-economic ones. The GCRMN guidelines were executed on 18 different dive sites that have previously been surveyed by other studies. The sites were surveyed in an order based on local weather conditions as well as on the logistical management and availability of the boat of SCF.

At each site the six GCMRN indicators (mentioned in 1.4) were assessed. For this, the hands of at least three people were necessary. The first diver counted the fish and then headed back to take photographs of the coral recruits and measure their size. The second diver stayed behind the first diver to not scare fish away but followed closely to lay out the transect line. The third diver went along the transect line to take pictures of the benthos. The necessary tools for this marine survey were a complete dive equipment, slates for fish counts and coral recruits, a photo quadrant (20x20cm), a t-bar (90x60cm), one camera for benthic assessment and one camera for the coral recruits, a measurement stick to measure height of turf, macroalgae and size of coral recruits, a Secchi Disk and a dive computer to track depth and temperature. Transect lines were placed haphazardly and after one another on sites. Additionally, the maximum depth of every study dive site was noted. The six indicators were executed as follows:

(1) The method of the Atlantic and Gulf Rapid Reef Assessment (AGRRA, 2018) was used to estimate the density of coral reef fish. Species of snappers (*Lutjanidae*), groupers (*Serranidae*), parrotfish (*Scaridae*), and surgeonfish (*Acanthuridae*) are considered key reef fish taxa and were thus at the core of the data collection. Nonetheless, all fish spotted were recorded to get a full picture of the fish assemblage. At each site, five transects of 30m length and 2m width were surveyed, adding up to 300m² surveyed on every dive site. Herein, all fish were counted and sorted regarding their size (categories: 0-5cm, 6-10cm, 11-20cm, 21-30cm, 31-40cm, 41-50cm and larger than 50cm). Data were later pooled to get an average of the density and size structure of all fish on each site. Taxonomic expertise was trained for several weeks before the actual GCRMN assessment.

(2) To assess the benthic environment the percentage of the reef bottom that is covered by stony corals, gorgonians, sponges, and various types of algae (such as turf algae, macroalgae and crustose coralline algae) was documented. The data were collected using the photo quadrant method. A one meter long t-bar was used to later allow observers to cut out photo quadrants with the size of 90 x 60 cm. Photographs were taken along the five transect lines (set up for (1)) at every other meter from approximately one meter above. This resulted in 15 pictures per transect and consequently, 75 pictures for every dive site. The images are archived in case of future-reanalysis or for other interests.

(3) Diseases in stony corals was recorded in order to describe the proportion of coral colonies that exhibit signs or pathologies of any disease. In order to do so, the proportion of images that contain a coral with a disease were taken as a measure. Pictures containing a coral with a disease were marked as "with disease" to get a proportional estimation of disease prevalence.

(4) The AGRRA methodology (AGRRA, 2018) was used to collect data to estimate the density of young corals contributing to the next generation of adult corals. For this, photo quadrants of 25 x 25cm were used to detect coral recruits. They are placed every two meter for five times in the first three transect lines (set up for (1)). Coral recruits that are 0.5-4cm big and

are visible to the diver in situ were counted and measured. The lower diameter number represents the possibility of a diver to spot the recruit, and the upper limit of 4cm was chosen as the maximum since this is considered to be the approximate size of transition from juvenile to adult. Many coral species begin to gain capacities typical of adult corals such as increased competitive ability and reproduction. If possible, the genus of the coral species was noted.

(5) Key macro-invertebrate species were counted on the pictures taken for the benthos (see (2)) to estimate the density of the ecologically and economically important species on the reef. These are the long-spined sea urchin (*Diadema antillarum*), other sea urchins, all sea cucumbers, lobsters and conch. While the long-spined sea urchin is an important herbivore on Caribbean reefs to control seagrass, the other species are considered vital fisheries targets in some locations.

(6) Data on the quality of the water were collected to estimate the concentration of particulates in the water column. Water quality was tested by estimating visibility by using the black-and-white Secchi disk, which is 20cm in diameter. Attached to a measured rope, the disk was lowered into the water until it was out of sight. However, due to the fact that the visibility sometimes was higher than the actual depth of the dive site, visibility needed to be estimated based on a horizontal measurement. While one diver held the end of the rope, another diver swam away with the Secchi Disk as far as to where the diver that stayed could not see the different colours of the Secchi Disk anymore. The length was noted in m.

2.3. Analysis

The data were analysed in several steps. First, an image analysis for benthos was conducted with CPCe. Then, fish biomass and the RHI were calculated and literature searched for data to indicate trends. Lastly, the data were statistically tested using the SPSS package.

2.3.1. Image analysis

In order to analyse the pictures taken with the GoPro, every single picture first needed to be white-balanced. This was done in Adobe Photoshop Lightroom. These edited images taken for the benthic survey were then post-processed and analysed with the software Coral Point Count with Excel extensions (CPCe version 4.1; Kohler & Grill, 2006; see Figure 8). CPCe is a visual program to determine coral and substrate coverage (ibid.). The random point count methodology has been used to estimate the statistics of the benthic community. After an image calibration was performed using the t-bar in the picture, a frame of 90 x 60 cm was retrieved and 25 points were randomly located within the frame. Every point was manually identified using species codes (see appendix 8.1). Standardized benthic categories include key species of corals and algae. While reef building corals were identified to species level, soft corals, sponges and macroalgae were identified to genus level. In order to monitor the presence of cyanobacteria, I added a respective taxon code to the code list in CPCe (see appendix 8.1). In addition, diseases and bleaching were noted as well. The observers practiced the identification for several weeks with an expert before applying it to this study.

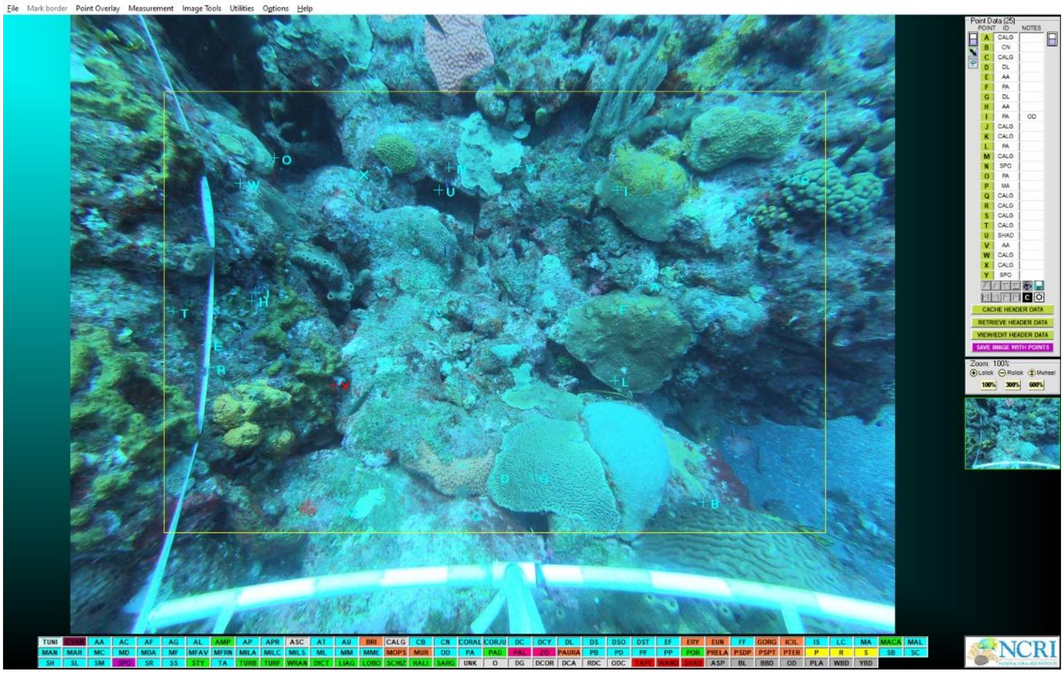


Figure 8. Example of CPCe software image analysis from Man of War Shoals transect 1.5.

2.3.2. Fish biomass analysis

Fish size is measured in body length. For fishery management and conservation purposes, information about the body weight to regulate fish catches as well as an estimation of the biomass is needed. Therefore, the Bayesian hierarchical approach was applied by combining prior probabilities with a likelihood function (Froese et al., 2014). The weight of each fish was calculated by the length-weight relationship (LWR). According to Bohnsack and Harper (1988), a regression line fits to the equation $\log(W) = \log(a) + b*\log(L)$. This is equivalent to $W = a*Lb$. W equals the weight of the fish in gram, L the length in mm, and *a* and *b* are the species-specific parameters (ibid.). *b* indicates isometric growth in body proportions, and *a* describes body shape and condition, if for both *b* is approximately 3 (Froese, 2006). The constants (parameters *a* and *b*) were derived from Fishbase, where LWR parameters have been compiled for thousands of species (Froese & Pauly, 2016) and can be found in appendix 8.2. For every dive site, biomass and density were calculated for the five key families: *Scaridae*, *Acanthuridae*, *Haemulidae*, *Lutjanidae* and *Serranidae*. To do so, mean sizes of the respective reef fish were calculated for every dive site.

2.3.3. Species richness

To calculate species richness, the number of different species was calculated. For benthic coverage, the Shannon-Wiener Index of diversity was calculated per site.

2.3.4. The Reef Health Index (RHI)

The RHI considers four indicators namely the cover of coral and macroalgae as well as biomass of key herbivorous (parrotfish and surgeonfish) and key commercial fish (snappers and groupers; see Figure 9). By averaging values for each indicator, the mean was calculated for each dive site. In order to get the mean RHI for the whole SNMP, the scores for the 18 dive sites were averaged and ranked according to the index.

Reef Health Index (RHI)

Reef Health Index Indicators	Very Good (5)	Good (4)	Fair (3)	Poor (2)	Critical (1)
Coral Cover (%)	≥40	20.0-39.9	10.0-19.9	5.0-9.9	<5
Fleshy Macroalgal Cover (%)	0-0.9	1.0-5.0	5.1-12.0	12.1-25	>25.0
Key Herbivorous Fish (g/100m^2) *(only parrotfish and surgeonfish)*	≥3480	2880-3479	1920-2879	960-1919	<960
Key Commercial Fish (g/100m^2) *(only snappers and groupers)*	≥1680	1260-1679	840-1259	420-839	<420

Figure 9. Reef Health Index ranking (Healthy Reefs, 2015)

2.3.5. Temporal changes

To examine temporal change of the indicators, descriptive data from past studies were assembled and compared. This was done via literature study.

2.3.6. Statistical analysis

The statistical analysis was performed with the statistic program IBM SPSS Statistics version 26. For all tests, a 95% confidence interval was used. 95%

confidence limits were used as it is a generally accepted method to avoid Bonferroni corrections in inflated type I errors.

For the statistical analysis the data were first transformed. The variables were transformed with the natural logarithm to adjust for normal distribution. If normality still was not significant (based on the outcome of Shapiro-Wilk test for normality and Levene's test for equal variance), the variable was instead transformed using the square root function. The variables that were square root transformed were: 'Zoanthids Cover', 'Tunicate Cover', 'Cyanobacteria Cover', 'SandRubblePave', 'Species Richness Lutjanidae', Species Richness Haemulidae', 'Density Lutjanidae', 'Density Haemulidae', 'Biomass Lutjanidae' and 'Biomass Haemulidae'.

SRQ1: The data first were transformed. Means and 95% confidence intervals were calculated for every fish and benthos variable. Where visual significant differences between unfished and fished areas were detected, t-tests were performed to assess statistical significance.

SRQ2 and 3: First, Spearman rho correlations were calculated to assess whether there is a positive or negative correlation and if so, whether the correlation is weak, medium or strong. This initial calculation indicated which relationships are worth exploring. A visual analysis of the residual vs fitted value plots indicated the need to transform the data. Linear regressions were conducted between every fish indicator with every benthos indicator. When significant a fitted line gave the R^2 value. Visual scatterplots indicate whether the relationship between the two variables is positive or negative.

2.4. Limitations

The monitoring method of GCRMN is advised to be executed on 20 dive sites to have more statistical power to compare different locations with one another. However, due to logistics and time it was only possible to execute GCRMN on 18 different dive sites, that are, however, spread around the island. To counteract the effect of spill overs, not only neighbouring sites have been chosen, but sites on all sides of the island as well as zones within the MPA.

The missing data for fish and benthos on one site each happened because of an accident where the camera got flooded. Using the Secchi disk horizontally is not advised as light conditions will vary strongly underwater and looking down from the surface. Furthermore, the GCRMN data collection involved several divers. Personal differences in skills, knowledge and effort during the data collection and handling could affect the accuracy and consistency of the data collected. Since the study was executed in a natural environment with moving fish, it can be assumed that the size of moving schools of fish could have been either under- or overestimated. Fish density, species richness and size need thus be viewed with an appreciation of this natural dynamism.

The quality of the pictures taken for both benthos and coral recruits differed a lot and influenced the accuracy of the analysis. Some of the benthos pictures taken with a GoPRo were blurry, which made the identification to coral species level challenging and in some cases, images could not be taken for the analysis. The wide lense of the GoPro affects the ratio of the picture and the frame. It should additionally be considered, that due to the 2D nature of a picture/frame only the upper part of the coral reef can be identified. Another factor to consider is that after the CPCe image analysis, the .cv files were downloaded in a way that the data were immediately grouped per dive site instead of per transect. Hence, comparisons between different dive sites are not possible. Prior training of the researchers is also a factor that influences the accuracy of the analyses of the data. Data on benthos were collected through images, which are less prone to user bias, and allows discussion during post-procession to error check across observers.

There is a trade-off between the time spent/effort made for the data collection in the field and the amount of fish individuals that was recorded. Overall, one would expect higher number of densities if more time is available. To avoid this issue, the RHI provides standardized times to be spend on every transect. However, in some cases time did not allow to look more in depth for macro-invertebrates, that may have been hidden underneath or within the reef structure. In the case of macro-invertebrates, they were seen on the reefs during dives not used for this study. However, at the time of the data collection not one individual was recorded in the analysed transects. It can therefore not be said that there were no macro-invertebrates in the SNMP at all. They were excluded from the analysis because of the low numbers recorded.

Another point that needs to be considered is the fish biomass analysis: The following mean sizes for the categories (0-5, 6-10, 11-20, 21-30, 31-40, 41-50, >50cm) were used for the analysis: 2.5, 8, 15.5, 25.5, 36.5, 46.5, 50cm, respectively. The last category must be taken with caution as fish in this size category may have been significantly larger than the assumed and taken average of 50cm. Except three yellowtail snapper and one yellowfin grouper, no key fish larger than 50cm has been counted.

The reason why no interaction between different indicators of benthos itself has been assessed in this study is due to the fact, that percentage cover cannot exceed 100%. When macroalgae cover increases, the space that remains for other benthic organisms must decline and may therefore lead to trivial results.

3. Results

Data on fish and benthos were recorded on each of the 18 sites in the SNMP. Information on the different dive sites and their environmental data can be found in Table 3. Due to logistical challenges there are no benthos data for Tents Reef Deep, and no fish data for Diamond Rock.

3.1. Dive site information

Table 3. Dive site information (UF=Unfished zone, F=Fished zonen, n.d.=no data).

Site	Zone	Max. depth (in m)	Temp (in °C)	Visibility (in m)
BA	UF	11.55	26	30
BRM	F	10.57	26	n.d.
CG	F	11.90	26	20
CH	UF	28.50	26	20
DDO	F	12.47	26	n.d.
DR	UF	20.10	26	30
GQS	F	6.20	26	n.d.
GI	F	11.58	26	n.d.
GG	F	15.74	26	n.d.
HIC	F	8.50	26	n.d.
HS	UF	7.91	26	20
LL	UF	9.80	26	n.d.
LL 2	UF	13.86	26	20
MWS	UF	16.52	26	n.d.
PP	UF	12.70	26	13
TR	UF	7.50	26	25
TRD	UF	16.48	26	n.d.
TP	F	9.20	26	50

3.2. Reef fish

In total, 17685 reef fish individuals of 83 different species on 17 different sites were counted during the data collection. Figure 10 shows the total number of all counted reef fish species and species richness per site (300m²). A complete list with the total count per species per site can be found in appendix 8.3.

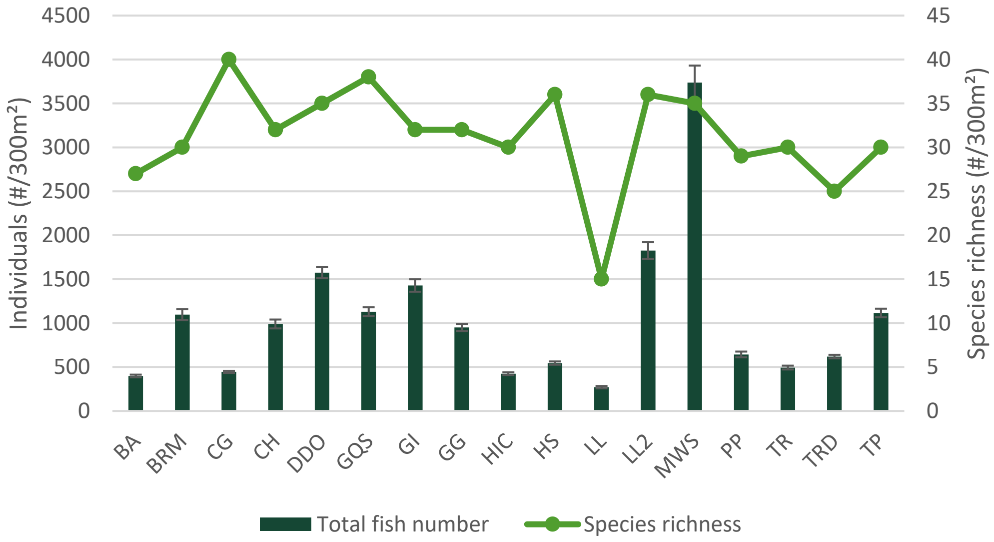


Figure 10. Total number of all reef fish individuals (#/300m²) with standard deviation bars and species richness per site.

Density and biomass of the five key fish families parrotfish (*Scaridae*), surgeonfish (*Acanthuridae*), grunts (*Haemulidae*), snappers (*Lutjanidae*) and groupers (*Serranidae*) were recorded per site (see Figure 11). There was variability between the sites. The sites GQS, BRM and TRD were the most abundant in terms of key reef fish density. The three sites with the highest biomass were MWS, GG and GQS.

Additionally, mean body size of key families was recorded and is also shown in Figure 11. Body sizes of herbivores are smaller than those of the commercial fish grunts. While the mean body size of the two herbivores parrotfish and surgeonfish is about the same, it varies within the commercial fish with snappers being almost twice as large on average than groupers.

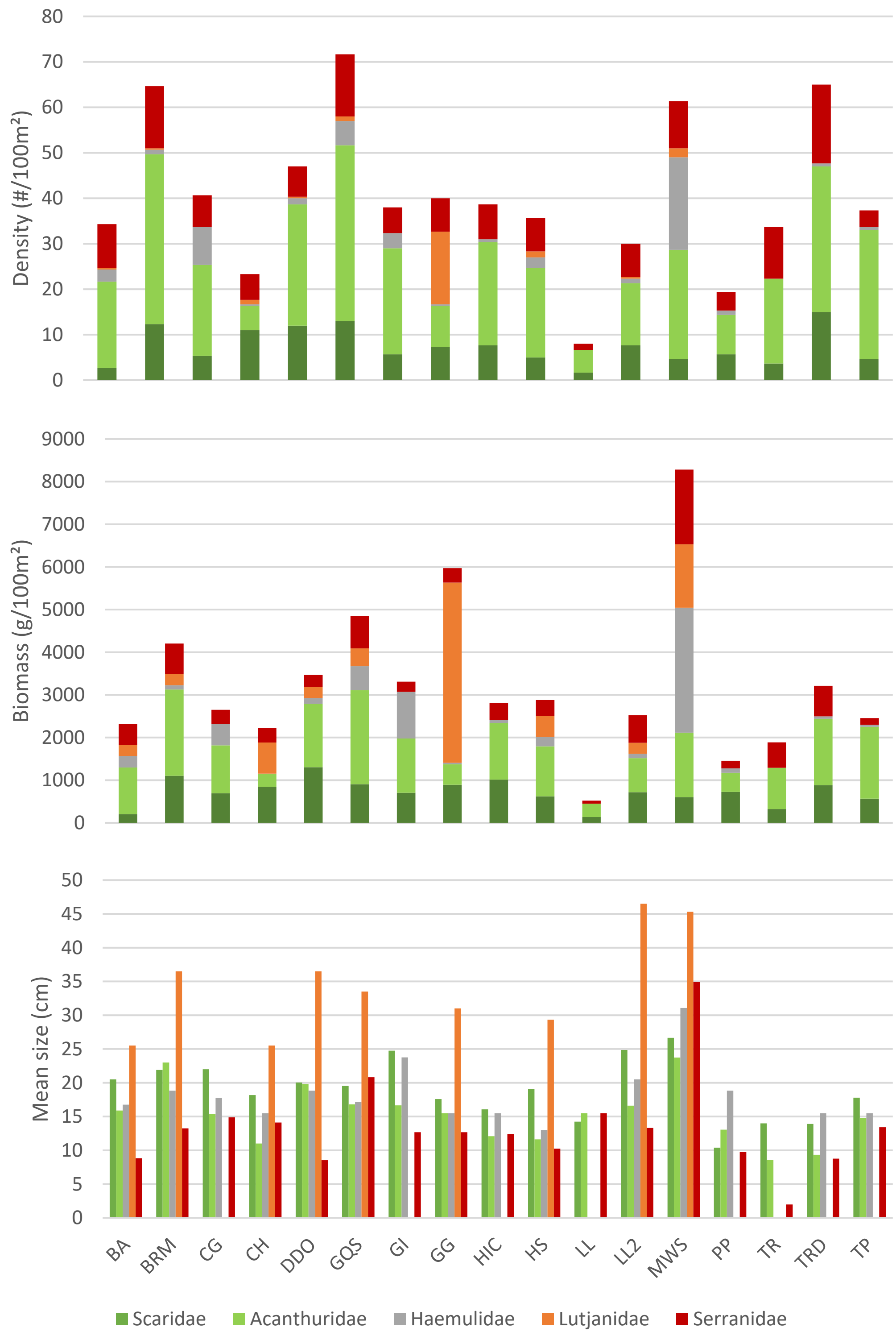


Figure 11. Density (#/100m²), biomass (g/100m²) and mean size (cm) of key fish species per site.

3.3. Benthos

For the benthos, 1260 frames were analysed which resulted in 31497 points. Excluding tape, wand and shadow 31369 points were used for the analysis.

3.3.1. Benthic cover

Data revealed the presence of hard corals, gorgonians, macroalgae, turf, coralline algae, cyanobacteria, tunicates, zoanthids, sponges and abiotic cover such as sand and rubble. Mean percentages per species and site can be seen in appendix 8.4. The codes for the abbreviations can be found in appendix 8.1. 32 different species of hard corals were counted. Figure 12 shows benthic cover averages in the SNMP.

The majority of benthos coverage is comprised of 30.52% macroalgae (95% confidence limits: 21.48, 43.38) and 27.87% turf (21.70, 35.78). Hard coral cover accounts for 7.74% (6.47, 9.26) and gorgonian cover 2.52% (1.54, 4.13). The rest is made up of sponges (4.06%; 2.65, 6.2), coralline algae (3.85%; 2.39, 6.21), cyanobacteria (1.22%; 0.83, 1.51), tunicates (0.80%; 0.64, 0.93) and zoanthids (0.66%; 0.40, 0.84). 1.37% (1.11, 1.59) is bare substrate such as sand or rubble. Figure 13 indicates the benthic cover composition per site.

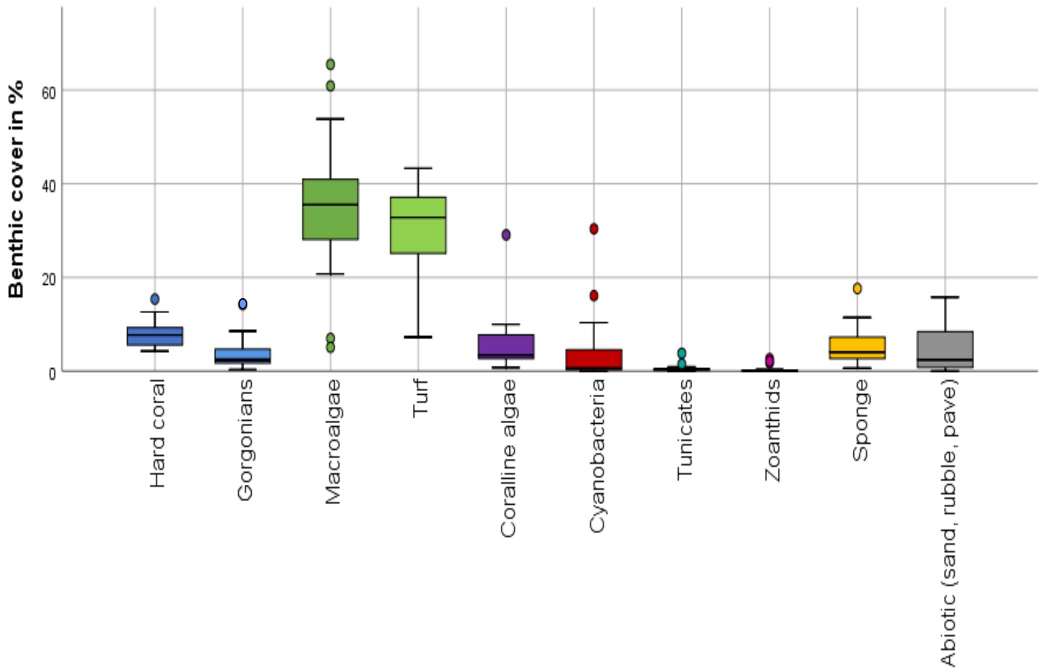


Figure 12. Boxplot showing Benthic cover in % in the SNMP. Hard coral: Q1 = 5.6, Median = 7.7, Q3 = 9.7; Gorgonians: Q1 = 1.6, Median = 2.4, Q3 = 5; Macroalgae: Q1 = 27.9, Median = 35.5, Q3 = 45.5; Turf: Q1 =24.8 , Median = 32.8, Q3 = 39; Coralline Algae: Q1 = 2.5, Median = 3.4, Q3 = 8; Cyanobacteria: Q1 = 0.3, Median = 0.6, Q3 = 6.9; Tunicate: Q1 = 0.1, Median = 0.3, Q3 = 0.6; Zoanthids: Q1 = 0, Median = 0.1, Q3 = 0.3; Sponge: Q1 = 2.5, Median = 4, Q3 = 7.2; Abiotic (Sand, rubble, pave): Q1 = 0.7, Median = 2.4, Q3 = 8.7.

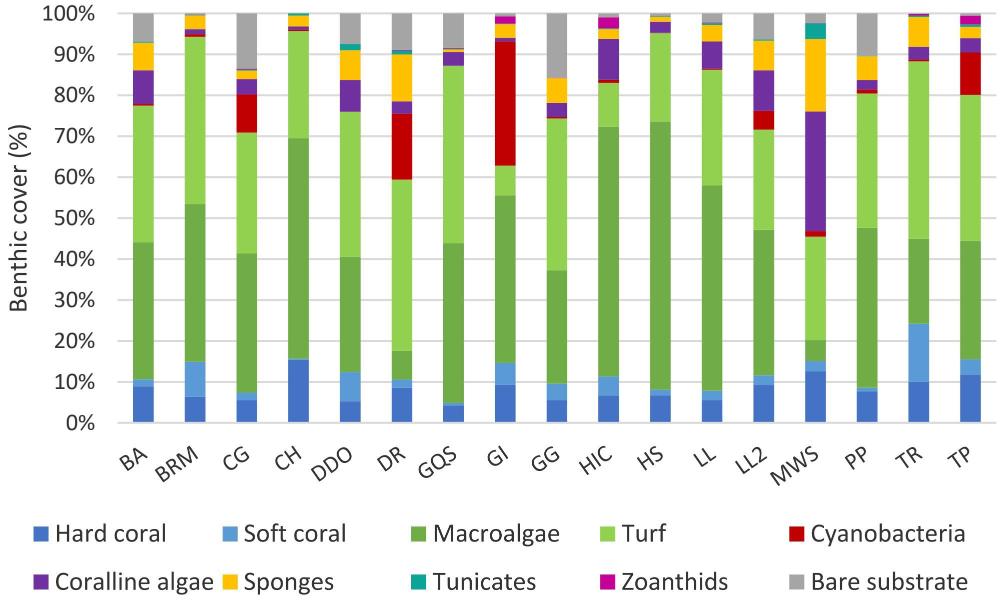


Figure 13. Benthic cover composition (%) per site in the SNMP.

3.3.2. Species richness per site

The calculated Shannon-Wiener Index shows the taxon diversity of benthic cover per site (see Figure 14). The index increases as taxon richness and the evenness of the community increases. MWS followed by DR is the most benthic diverse site in the SNMP.

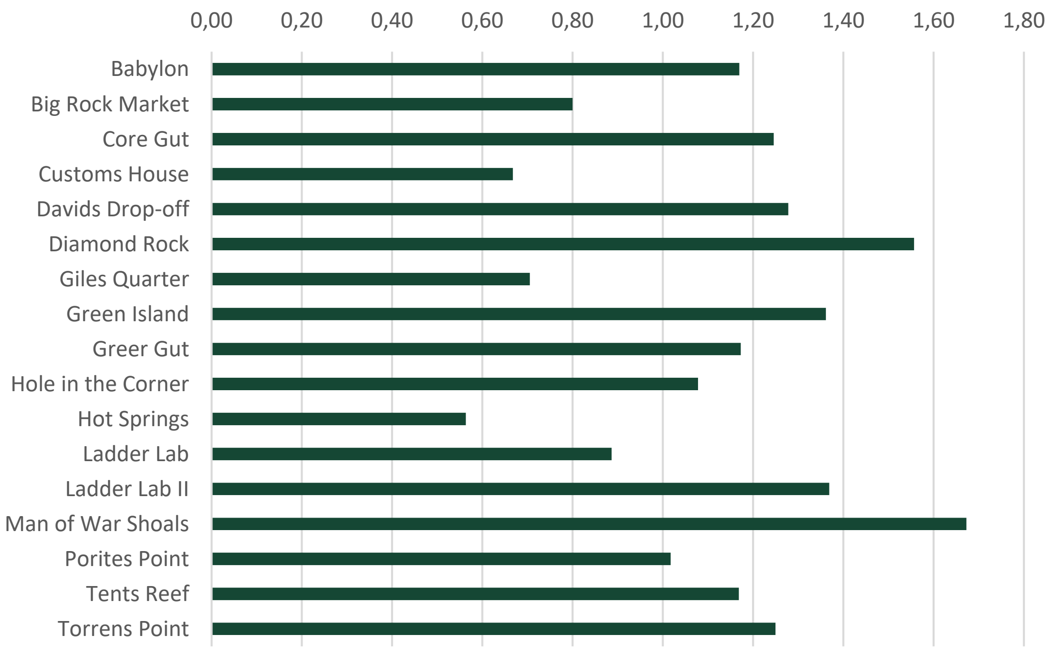


Figure 14. Shannon-Wiener Index of diversity (taxon) for benthic cover.

3.3.3. Coral disease and bleaching

9% of the analyzed pictures contained diseases (see Appendix 8.5, Table 16). The most affected sites were Green Island, Man of War Shoals and Torrens Point with each16 images showing coral disease, whereas David's Drop-off and Hot Springs did not show any signs of disease.

Coral bleaching was recorded on 0.01% of all pictures on 17 different sites. The site with the most images with coral bleaching is Diamond Rock, followed by Green Island and Torrens Point.

3.3.4. Coral recruits

Coral recruits were counted and measured on 17 out of the 18 dive sites, excluding Tents Reef Deep. Every photoquadrant (25cm x 25cm) had an area of 625cm². In total, 196 coral recruits were recorded in 255 photoquadrants which is equal to an area of almost 16m² (see Appendix 8.6, Table 17). The mean amount of coral recruits was 11.53 ± 4.56 individuals/dive site. Per m², the number of coral recruits ranges from 22.40 (David's Drop-off) to 3.2 (Ladder Labyrinth 2). On average, 12.30 ± 4.72 SD coral recruit individuals can be found per m².

Figure 15. Porites astreoides coral juvenile.

Eight species of coral recruits were found. By far the most abundant recruits were *Siderastrea radians (SR)*. *Porites astreoides (PA)* comes second with half the counts. Notable is the high number of unidentified species. In total, 22% of the recruits were unable to identification.

3.3.5. Key macro-invertebrates

On the 1260 analysed benthos pictures, not a single key macro-invertebrate species (the long-spined sea urchin (*Diadema antillarum*), other sea urchins, all sea cucumbers, lobsters and conch) was counted. Therefore this indicator was removed from analyses.

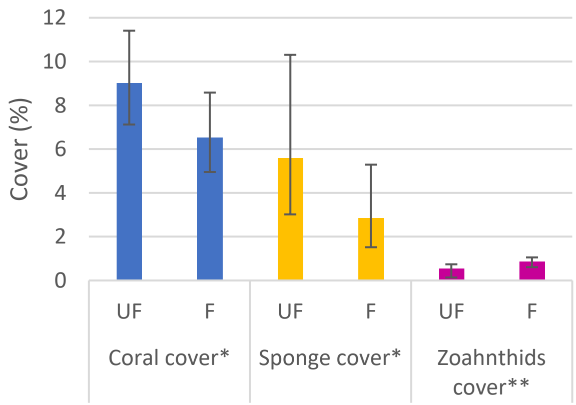
3.3.6. Water quality

Regarding the visibility 9 out of 17 data were retrieved. The average visibility was 25.3 ± 10.7m. The lowest recorded visibility was 13m, whereas the highest was 50m. Due to the low number of observations, this indicator was removed from analyses.

3.4. Unfished/fished sites

The calculation of 95% confidence limits and execution of independent t-tests show that some indicators significantly differ between the unfished and fished site (see Figure 16) but not the overall RHI. The number of hard corals and sponges is higher in the unfished zone, whereas zoanthid cover is higher in the fished zone. The key herbivores *Scaridae* and *Acanthuridae* are more abundant and have a higher biomass in the fished zone. The density of all key fish without *Haemulidae* is also higher in the fished zone.

A full list with backtransformed means, standard deviations, standard error and 95% confidence limits for all indicators as well as additionally the results of the t-tests for the indicators with a significance below 0.1 can be found in Table 18 in appendix 8.7.



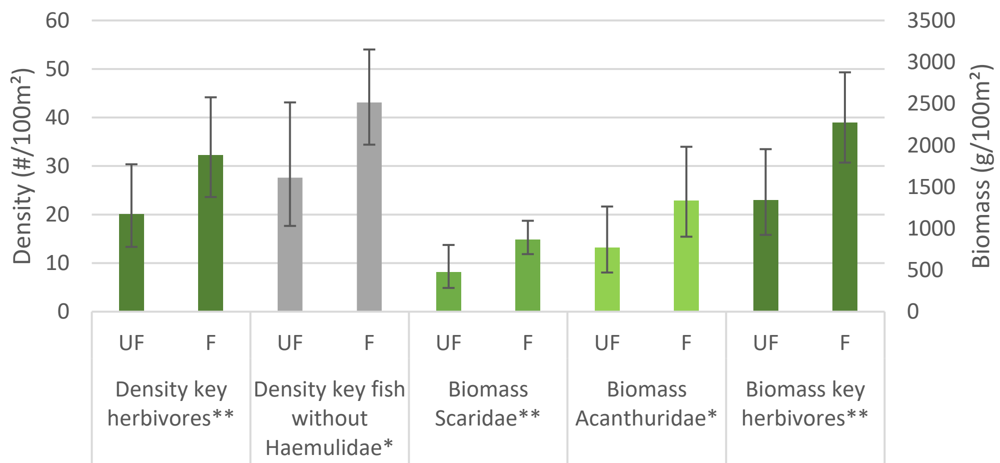


*Figure 16. Diagrams showing the backtransformed means and 95% confidence limits (for values see appendix 8.7) for benthic cover (top) and fish density (left bottom) and biomass (right bottom). ** indicates a significant difference (p<0.05) and * indicates a suspicious difference (0.05<p<0.1).*

3.5. Correlation of fish and benthic cover

There are a number of positive and negative relationships that stand out. Selected correlations are visualised in Figure 17 but statistical results of all correlations can be found in appendix 8.7. The number of *Acanthuridae* species increases as gorgonian cover goes up (the same for density but groupers become smaller. With more coral cover, the number of coral species goes up as well, which in turn positively correlates with fish density (all fish), and species richness and mean size of groupers but decreases if there is a higher percentage of bare substrate. There are also indications of negative relationships, for example between species richness of groupers and commercial fish, and mean size of groupers with gorgonian cover. While parrotfish species richness goes down when sponge coverage increases, mean size of grunts increases. The increase of macroalgae, however, only has negative relationships with the fish community. Density of fish declines when more macroalgae is present, and so does the biomass of groupers, grunts, commercial fish and key fish as well as the mean size of key herbivores, especially that of surgeonfish. The presence of both cyanobacteria and zoanthids is negatively correlated with the abundance, number of species and biomass of snappers. The mean size of *Lutjanidae*, however, increases if coralline algae cover goes up while grunts grow in size when coverage of tunicates increases.

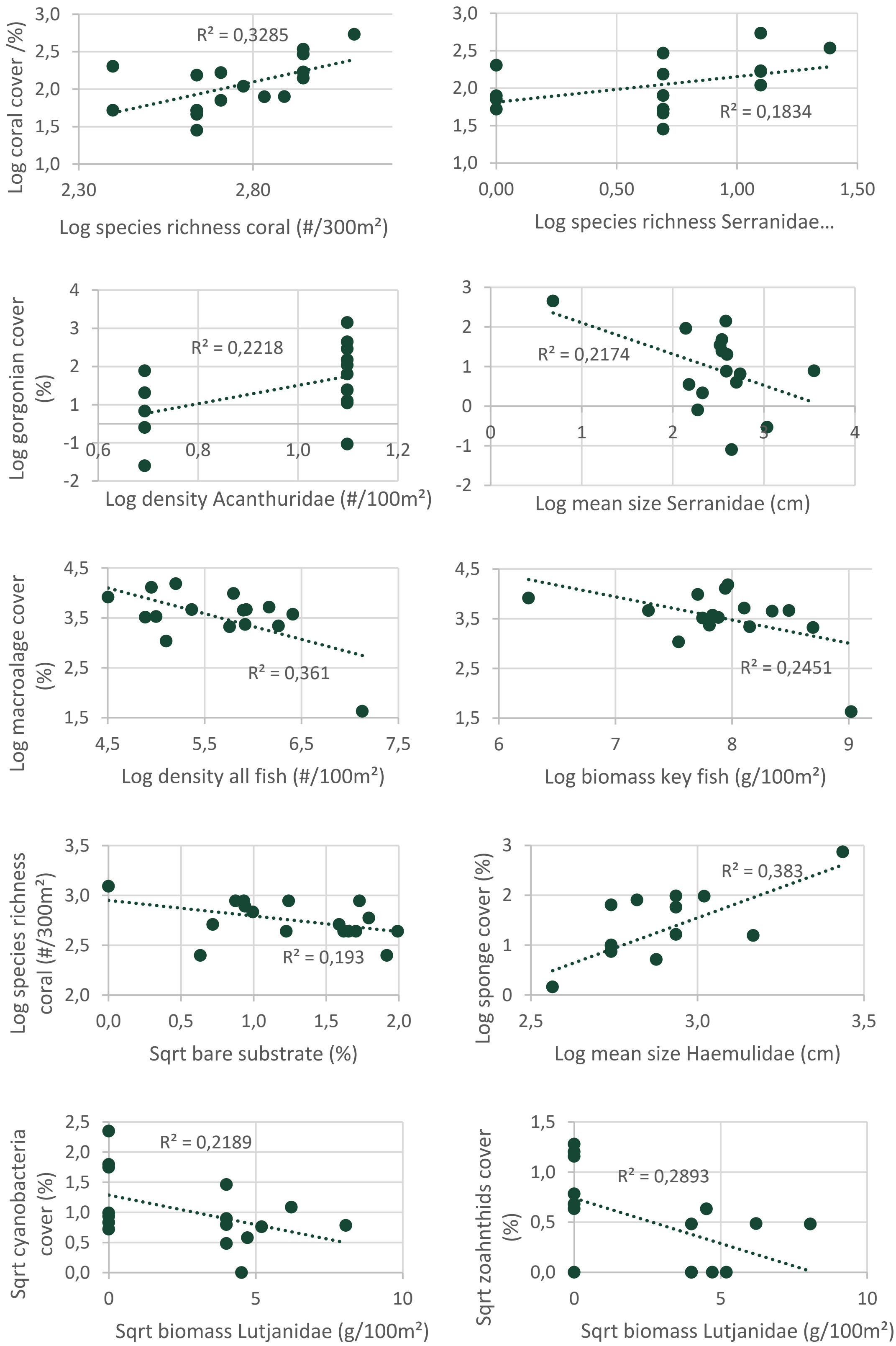


Figure 17. Scatterplot showing selected relationships between fish and benthos. Note the log scale.

3.6. Disease and coral bleaching interaction

Coral bleaching negatively correlates with species richness of parrotfish, in biomass of groupers and in mean size of snappers. Coral diseases, however, positively correlate with the mean size of grunts (see Figure 18).

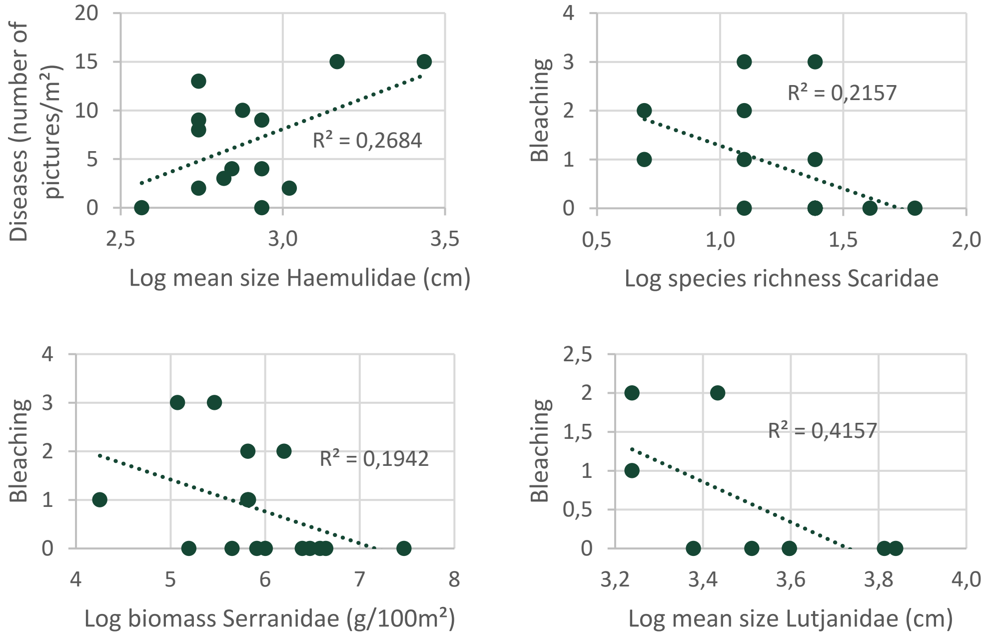


Figure 18. Scatterplots showing the relationship between coral diseases and bleaching and fish communities. Note the log scale.

3.7. Status of the coral reef (RHI)

In order to establish a broad overview of the status of the reefs around Saba, the RHI was assessed. RHI 5 means "very good" (dark green), 4 "good" (light green), 3 "fair" (yellow), 2 "poor" (orange) and 1 "critical" (red). The RHI score was calculated for each of the four indicator for every site. A mean score was calculated for both unfished and fished zone as well as for the SNMP in total (Table 4).

The total RHI score for the SNMP is "poor". Coral cover and commercial fish score poor, whereas macroalgae scores critical and herbivorous fish just fair. There is much variability between the indicators themselves and the different sites, especially within the fished zone. The unfished sites on the contrary are all poor. Notable is the high variation in commercial fish, as some sites score very good while others are critical.

Table 4. RHI score table (dark green=very good (RHI score 5), light green=good (4), yellow=fair (3), orange=poor (2), red=critical (1)).

	Coral cover		*Macroalgae cover*		*Key herbivorous fish*		*Key commercial fish*		***RHI 2019***
	%	RHI	%	RHI	g/100m²	RHI	g/100m²	RHI	
BA (UF)	8.90	2	33.49	1	1295.56	2	749.54	2	**1.75**
BRM (F)	6.36	2	38.50	1	3125.49	4	977.20	3	**2.50**
CG (F)	5.58	2	33.94	1	1815.62	2	335.55	1	**1.50**
CH (UF)	15.37	3	53.83	1	1141.87	2	1069.48	3	**2.25**
DDO (F)	5.29	2	28.12	1	2789.11	3	541.08	2	**2**
DR (UF)	8.56	2	6.99	3					**2.50**
GQS (F)	4.27	1	39.03	1	3113.85	4	1181.34	3	**2.25**
GI (F)	9.30	2	40.92	1	1975.80	3	236.14	1	**1.75**
GG (F)	5.55	2	27.66	1	1374.94	2	4562.57	5	**2.5**
HIC (F)	6.67	2	60.88	1	2343.24	3	404.22	1	**1.75**
HS (UF)	6.70	2	65.46	1	1794.21	2	865.02	3	**2**
LL (UF)	5.58	2	50.11	1	450.46	1	70.30	1	**1.25**
LL2 (UF)	9.22	2	35.50	1	1515.34	2	904.40	3	**2**
MWS (UF)	12.60	3	5.09	3	2113.41	3	3238.47	5	**3.50**
PP (UF)	7.68	2	39.04	1	1173.86	2	180.15	1	**1.50**
TR (UF)	10.03	3	20.75	2	1288.88	2	597.54	2	**2.25**
TRD (UF)					2438.76	3	719.20	2	**2.50**
TP (F)	11.79	3	28.98	1	2252.25	3	159.80	1	**2**
Fished	6.86	2	37.23	1	2347.53	3	1050.64	2.13	**2.03**
Unfished	9.41	2.33	34.43	1.56	1468.58	2.11	930.99	2.44	**2.15**
MEAN	**8.21**	**2.18**	**35.75**	**1.29**	**1882.21**	**2.53**	**987.29**	**2.29**	**2.10**

3.8. Temporal change

In order to look for temporal changes in the biophysical indicators and to look for trend indication, the data of this study were compared to GCRMN data from previous studies. To put the data into a regional context, data from other regions within the Caribbean where available were used for comparison.

3.8.1. RHI

Table 5 shows the change in total RHI in the Saba National Marine Park (SNMP) from 2015 and 2016 to 2019. The overall RHI has declined from 2015 to 2019. The RHI for coral cover and commercial fish remain in a poor state, whereas the state of macroalgae has declined drastically to critical. Herbivores were high in abundance in 2016, and aligned back to 2015 levels in 2019. Their state is fair. Notable is that the state of the unfished sites declined more than the state of the fished sites. Both are in a poor state. Out of the 18 sites, only three sites (Big Rock Market (BRM), Greer Gut (GG) and Man of War Shoals (MWS)) have improved in total RHI score. The other 15 sites have worsened in state or remained similar.

3.8.2. Biophysical indicators

Temporal changes in the biophysical indicators are shown in Figure 19.

Fish biomass and density numbers have increased since first data was recorded in 1991 with a high in 1999. Fish seem to follow an upward trend with density of key fish increasing by almost tenfold from 1991 to 2019. Notable is the difference in biomass and density between herbivorous and commercial fish, with herbivore fish numbers and biomass much higher and larger than those of commerical fish. While herbivore fish generally are more abundant and have a higher biomass in the fished zone, commercial fish have higher values in the unfished zone.

Since data monitoring began in 1991 coral cover increased to 68% in 1994. While coral cover was relatively stable in the unfished zone during this time, it changed a lot in the fished zone. From 1994 onwards coral cover has declined and more than half of the coral cover in the fished zone was lost. Coral cover reached its minimum coverage recorded in 2015 with just 11%. Since then, coral cover has been slightly increasing with higher coverage in the unfished than in the fished zone.

Macroalgae cover in the Caribbean has been increasing since the first data recorded in 1970. In the Caribbean, macroalgae coverage stabilizes at around 30% until 2015, when macroalgae cover started to increase drastically in Saba. Macroalgae in the SNMP has increased by more than four times to 66% since it was first quantified in 2015.

Table 5. Trend of RHI indicators (dark green=very good (RHI score 5), light green=good (4), yellow=fair (3), orange=poor (2), red=critical (1)).

	RHI Coral cover			*RHI Macroalgae cover*			*RHI Herbivorous fish*			*RHI commercial fish*			*Total*		
	2015	2016	2019	2015	2016	2019	2015	2016	2019	2015	2016	2019	2015	2016	2019
BA (UF)	2	2	2	3	2	1	2	4	2	1	2	2	2	2.50	1.75
BRM (F)	1	1	2	3	1	1	2	5	4	1	1	3	1.75	2	2.50
CG (F)	1	2	2	2	1	1	4	2	2	4	2	1	2.75	1.75	1.50
CH (UF)	2	3	3	2	1	1	1	4	2	5	1	3	2.50	2.25	2.25
DDO (F)	2	2	2	2	1	1	3	5	3	1	3	2	2	2.75	2
DR (UF)	2	3	2	3	3	3	1	4		5	5		2.75	3.75	2.50
GQS (F)	1	1	1	2	2	1	4	3	4	2	2	3	2.25	2	2.25
GI (F)	2	1	2	3	2	1	3	5	3	1	1	1	2.25	2.25	1.75
GG (F)	1	1	2	2	1	1	2	3	2	1	4	5	1.50	2.25	2.50
HIC (F)	2	2	2	2	1	1	5	5	3	1	2	1	2.50	2.50	1.75
HS (UF)	1	1	2	4	4	1	2	3	2	1	2	3	2	2.50	2
LL (UF)	2	2	2	2	2	1	2	4	1	1	1	1	1.75	2.25	1.25
LL2 (UF)	2	2	2	2	1	1	3	5	2	2	2	3	2.25	2.50	2
MWS (UF)	2	2	3	4	3	3	1	5	3	5	5	5	3	3.75	3.5
PP (UF)	1	1	2	1	1	1	3	3	2	1	1	1	1.50	1.50	1.50
TR (UF)	2	3	3	4	5	2	4	5	2	3	2	2	3.25	3.75	2.25
TRD (UF)	2	1		4	4		2	2	3	5	1	2	3.25	2	2.50
TP (F)	1	2	3	2	2	1	2	5	3	1	2	1	1.50	2.75	2
Fished	1.38	1.50	2	2.25	1.38	1	3.13	4.13	3	1.50	2.13	2.13	2.06	2.28	2.03
Unfished	1.80	2	2.33	2.90	2.60	1.56	2.10	3.90	2.11	2.90	2.20	2.44	2.43	2.68	2.11
MEAN	**1.61**	**1.78**	**2.18**	**2.61**	**2.06**	**1.29**	**2.56**	**4**	**2.53**	**2.28**	**2.17**	**2.29**	**2.26**	**2.50**	**2.10**

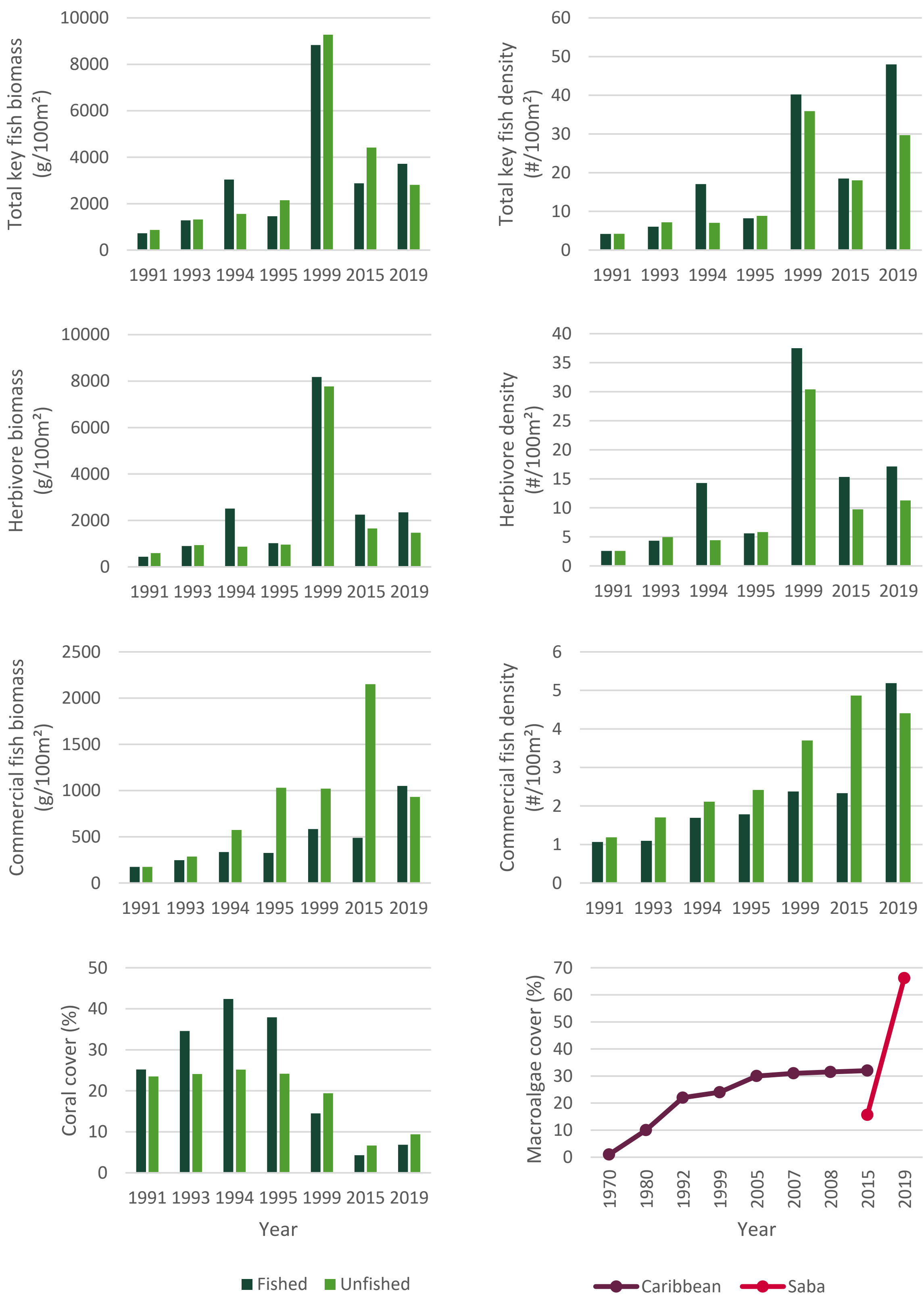


Figure 19. Temporal change in RHI indicators by zone and by region (for macroalgae). Data for years prior to 2015 sourced from Polunin & Roberts (1993), Roberts (1995), Roberts & Hawkins (1995) and Klomp & Kooistra (2003). Macroalgae on Saba includes macroalgae and turf cover.

When looking at the five different key fish families separately (see Figure 20), it is evident that biomass and density of the herbivores (parrotfish and surgeonfish) are higher than those of the commercial fish (snappers and groupers). The peak in abundance and biomass in 1999 can mostly be attributed to the increase in *Acanthuridae*. While in the early 1990's the main herbivore fish group were *Scaridae*, by the end of the decade the trend reversed and surgeonfish numbers are now higher. Striking is also the increase of groupers. While the density was relatively stable with 2.2 to 4.8 individuals per 100m² until 2015, the abundance increased in 2019 by almost fourfold. Grouper biomass, however, has not increased to such an extent. In fact, biomass has actually decreased since 2015. Grouper density and biomass follow a steady upward trend.

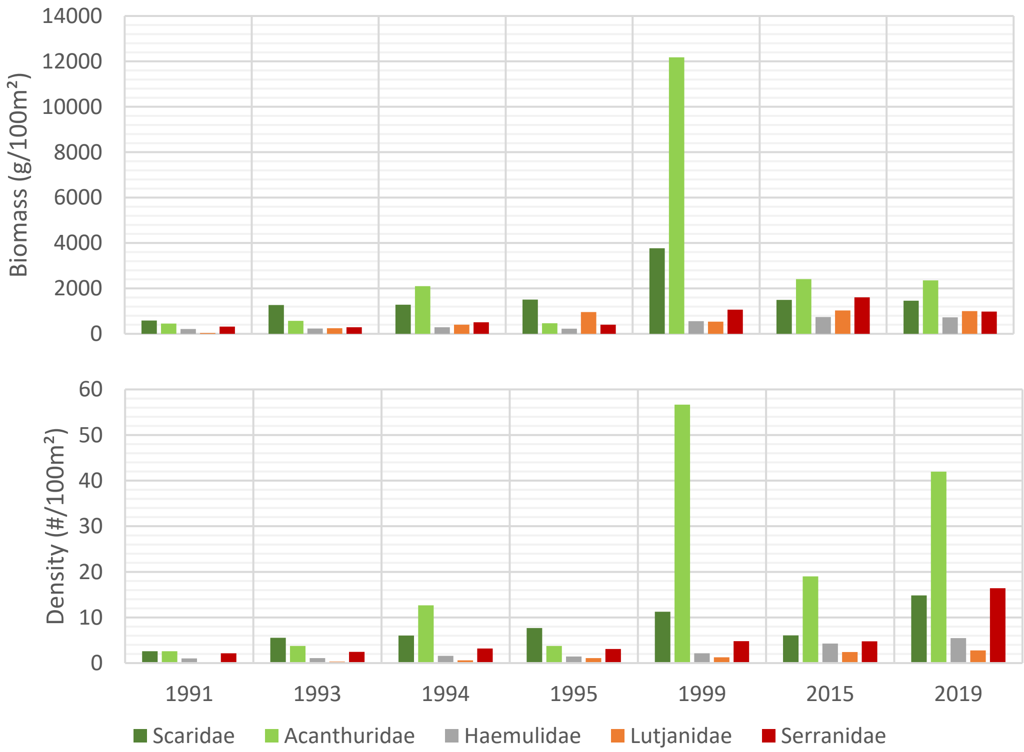


Figure 20. Temporal change in fish biomass (g/100m²) and density (#/100m²) by key fish family from 1991 to 2019.

Biomass also temporally varies within the SNMP (see Figure 21). Biomass differs greatly at different dive sites in terms of numbers and whether biomass increases or decreases. On some sites biomass declined from 2015 to 2019, whereas in others it increased.

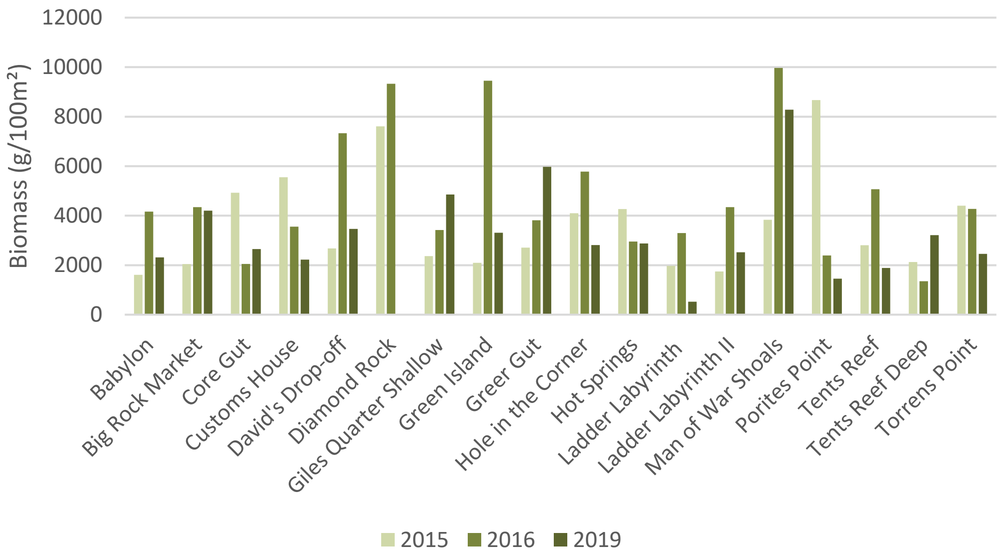


Figure 21. Total biomass of all key species in 2015, 2016 and 2019 per site. 2016 unlike 2015 and 2019 does not include Haemulidae.

Temporal changes are also visible in the mean size of fish (see Figure 22). From 2015 to 2019, four of the five key fish families declined in size. Only *Lutjanidae* fish have grown larger in this timeframe. Significant is the decrease in every data year in mean size of *Serranidae* that have gotten smaller by more than half (from 24.6cm (21.76, 27.89) to 18.9cm (16.84, 21.29) in 2016 to 11.7cm (8.73, 15.71) in 2019) as well as the decrease in mean size of *Scaridae* from 2015 (23.9 (21.52, 26.45)) to 2019 (18.41(16.22, 20.88)). Mean sizes of every key family in each of the three year can be found in Appendix 8.9.1, (Table 20).

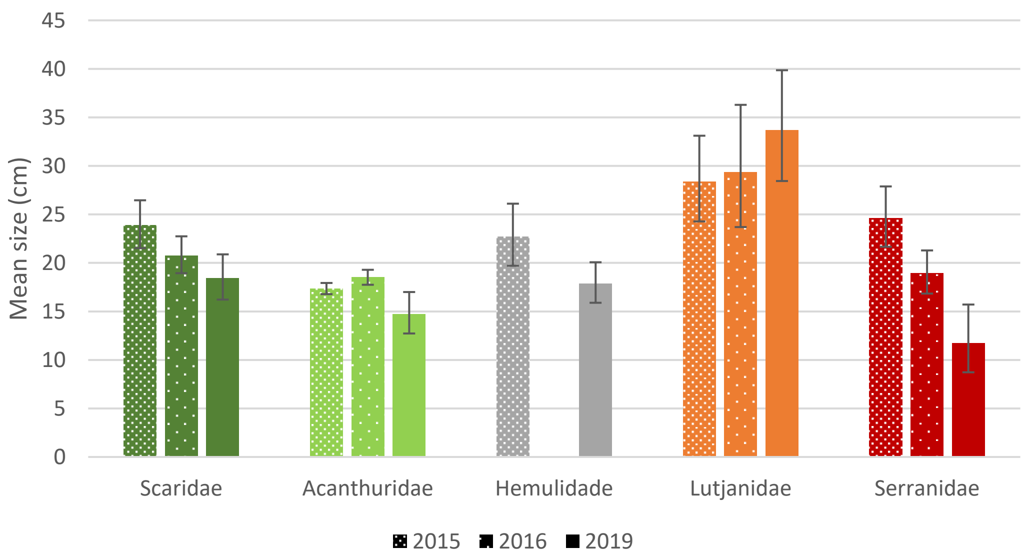


Figure 22. Mean size (cm) per key fish family and year with 95% confidence limits.

When looking at benthic change since the first GCRMN assessment in 2015 per site, it is visible that benthic cover has changed over time (see Figure 23). The data can be found in appendix 8.9.3.

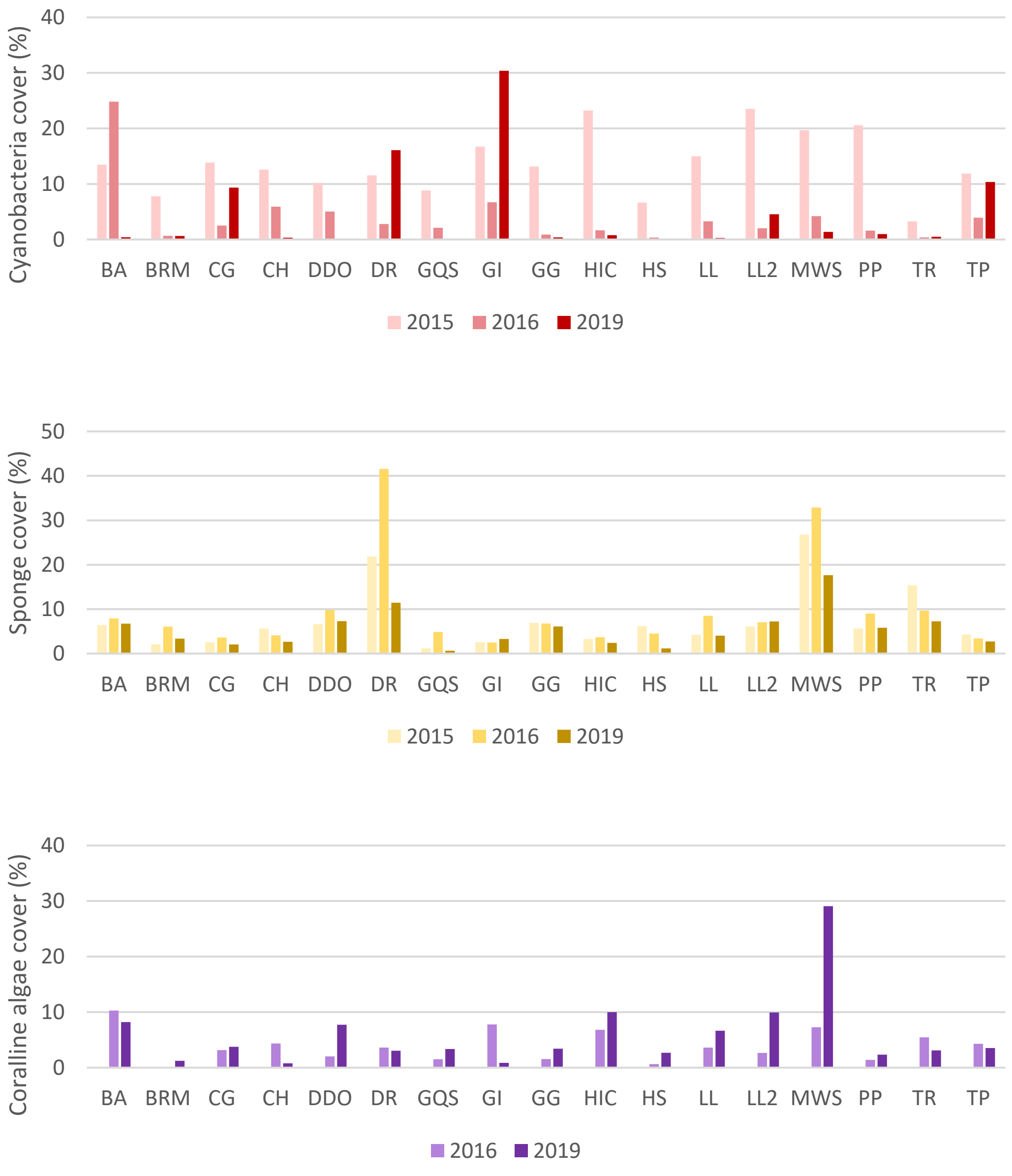


Figure 23. Temporal change (2015, 2016 and 2019) for benthic coverage by benthic group per site (in %).

4. Discussion

The aim of the study was to quantify the interaction between the biophysical indicators and biological drivers of change of the coral reef ecosystem in the SNMP. The main indicators of the RHI are related to fish and benthos, and the calculation of the individual and the overall RHI is used as a tool for this analysis.

4.1. Unfished/fished sites

The hypothesis that sites in the unfished zone are in a better ecosystem state than those in the fished site cannot be confirmed as the difference is not significant. Despite being non signficant, the RHI score in the unfished zone was slightly higher, suggesting the importance of having marine protected areas with no fishing zone.

Nonetheless the overall status, few significant differences between individual biophysical indicators and the unfished/fished zone were found. Coral and sponge cover were higher in the unfished zone, and zoanthid cover was higher in the fished zone. The establishment of the SNMP in 1987 seems to be beneficial for the hard corals as their cover has shown to be higher in unfished zones just ten years after the establishment. Macroalgae cover seems to be higher and more diverse in the fished zone, although no significant difference was found. This may indicate that fishing can have indirect negative effects on the reef through trophic cascades. Commercial fishing is, however, low in the SNMP (Hawkins & Roberts, 2004), suggesting that other factors might be influencing the amount of benthic cover.

All fish indicators (density, biomass, species richness and size) with a $p<0.1$ were that of herbivores (and one of all key species). They were all higher in the fished zone. Higher biomass of all key species in the fished sites can be explained by more and larger individuals. Van Looijengoed (2013) claims that the low fishing pressure on Saba may be the reason that not more fish indicators were higher in the unfished zone, in partcular with regard to fish abundance. Fish biomass and density were actually expected to be higher in zones, where fishing is not allowed, especially with regard to commercial fish species. The only indicator that was found to be slightly higher in the unfished sites is that of all reef fish. This could be explained by the higher numbers of coral cover in the no-take zone. Many of the reef fish that are not key fish are dependent on live coral cover to hide, and feed. A higher live coral as well as sponge cover percentage is correlated with increasing numbers in fish abundance and biomass (Seemann et al., 2018), as confirmed by the density of all reef fish indicator in this study.

Despite that, the number of key fish was higher in the fished sites, which aligns with the study by Friedlander and DeMartini (2002), who found that fished areas are often dominated by herbivores. The fished sites have a significantly higher amount of biomass than the unfished sites. Herbivores thus seem to thrive more on sites in the fished zone. A potential reason for this can be fishery induced predation releasure. Fish of commercial importance, which are predatory fish, are not able to predate as much since they are predated on themselves. Although fishing is very limited in the SNMP, studies on artisanal and recreational fishing have shown to already be sufficient to alter the reef fish assemblage (Mangi & Roberts, 2006). Additionally, the results show larger average sizes of key fish species in fished areas, which can be directly attributed to the higher abundance and more species rich occurence of macroalgae in the fished zone, on which the herbivores feed. The finding that there are more, larger but less diverse commercial fish in the fished area (see Figure 16 and appendix 8.7) fits to this as not all of them feed on macroalagae. It also shows that fisheries target selected species. In the SNMP, the most targeted fish species are *Lutjanidae* and *Serranidae* (Hawkins & Roberts, 2004). Thus, predatory species are affected differently by the zonation, whereas the higher but not significant species diversity of herbivores in the fished zone (see appendix 8.7) indicates a more balanced assemblage of *Scaridae* and *Acanthuridae*.

4.2. Status and interaction of fish and benthos

There are several indications of relationships between fish and benthos.

4.2.1. Hard corals

Coral cover seems to have slightly improved in recent years, although the difference is not significant and levels are very low. Lester et al (2020) argue that corals and fish may experience asymmetrical effects of different and various stressors and argue that while climate change may impact corals, fishing may be the main driver for fisheries communities. Caribbean stony corals have suffered from two coral bleaching events in 2005 and 2015 following an El Nino. Notwithstanding the impacts of global warming, ocean acidification and increased herbivory, the build up of corals in the SNMP suggests recovery. This may also be one of the reasons why fish numbers and biomass are generally increasing. Stony corals support reef fish that are dependent on the coral as habitat and food (Seemann et al., 2018). Coral cover itself is additionally often linked with habitat complexity. Rugosity was not measured in this study. It can, however, be assumed that it is has not changed a lot since the last assessment in 2016 because most of Saba's reef are no true carbonate reefs, but rather rocky formations that provide the structure for corals to grow on (Polunin & Roberts, 1993).

The results of this study also show that an increase in coral cover, which supports an increase in coral species richness. This in turn positively correlates with fish density (all fish), grouper species richness and grouper mean size, but negatively correlates with a higher percentage of bare substrate. The positive relationship between corals and groupers can be explained in that corals serve as important habitat for the prey of groupers.

Contradicting in itself is the finding that both coral and macroalgae cover increase simultaneously. As competitors over space, one would expect that either one of these decreases if the other one increases. Macroalgae have been found to benefit from benthic community changes as they grow faster than stony corals and benefit from missing groups of herbivores (Roff & Mumby, 2012).

4.2.2. Gorgonians

Gorgonians are increasing in numbers (from an average of 2.41% ± 2.1SD in 2015 to 3.73% ±3.53SD in 2019) on Saba which is in line with studies from other parts in the Caribbean (Lenz et al., 2015; Ruzicka et al., 2013; Tsounis & Edmunds, 2017). Gorgonians have been found to be able to thrive in changing environmental conditions and thus, they will play a growing role in providing habitat structure when climate change threatens the existence of hard coral species and structural complexity in shallow reef environments. Nonetheless, several sea fans have been found to be diseased with the fungal pathogen *Aspergillosis*, which may lead to partial tissue loss or even localized mass mortality of gorgonians. Studies on the functional roles of gorgonians have only started to emerge in the last decade, leaving a lot of room for further research.

This study showed that *Acanthuridae* seem to prefer sites with a higher abundance of gorgonians, whereas they seem to avoid places with hard corals that in turn also attract groupers. The reason why groupers and commercial fish species richness are negatively correlated with an increase in gorgonian could be that the subsequent increase in habitat structure enables prey of groupers and snappers to make use of it and thus making it harder for them to find their prey. The question why in particular groupers are negatively affected by the presence of gorgonians, remains unclear.

4.2.3. Macroalgae and turf

As expected, macroalgae affect the coral reef ecosystem and the fish communities negatively. Macroalgae have drastically increased and together with turf they now make up more than 65% of benthic coverage, which is higher than the average Caribbean percentage of 40% (AGRRA, 2018). *Dictyota* makes up the majority of macroalgae cover. As a fleshy brown algae, this species presents one of the last colonising algae if space has opened up on the reef (Adey & Vassar, 1975, Hughes et al., 1987, Steneck & Dethier, 1994). This shows that the successional development of algae is in an advanced stage in the SNMP. Simultaneously, turf (fast growing filamentous green and blue algae) coverage is as high as for *Dictyota* (see appendix 8.4) and indicates that there is also a high amount of early algal settler (ibid.) that can foster higher rates of algal growth. The high turf coverage combined with the mass mortality of the sea urchin *Diadema antillarum* in the 1980s may explain the high macroalgae cover compared to other parts of the world such as the Indo-Pacific (Roff & Mumby, 2012).

The correlation results demonstrate that the occurrence of macroalgae particularly impacts commercial and predatory fish species, such as groupers and grunts. A reason that their density and biomass numbers decline when more macroalgae are present can be that macroalgae are competing for space with corals and other benthic organisms and overgrow it (Hughes & Tanner, 2000). Thus, with an increasing cover of macroalgae, reef fish that would otherwise live in the coral structures, decline in numbers and can therefore not act as prey for the bigger predatory fish.

On the other hand, the increasing density and biomass of herbivores over the past decades indicate that they may benefit from the increase of macroalgae as more food is available. A study on key macroalgal consumers in the Caribbean (Dell et al., 2020) showed that *Acanthurus coeruleus* (blue tang), *Sparisoma aurofrenatum* (redband parrotfish) and the chub *Kyphosus* consume around 44g, 50g and 100g of macroalgae per day, respectively. *A. coeruleus* has been found in very high numbers relative to other species on the reefs in the SNMP (see appendix 8.2), which shows that they may indeed profit from macroalgae growth. The high and increasing amount of herbivore density further leads to the presumption that the SNMP is not heavily fished, which has also been proven by Hawkins and Roberts (2004). In other Caribbean areas with high fishing pressure, grazing competitors and prey of fish, namely sea urchins, have become dominant (Hay, 1984; McClanahan, 1995; Watson & Ormond, 1994). Although sea urchins and other macro-invertebrates have not been recorded, they were present in the SNMP (personal observation) but the low number seems to support this statement of low fishing pressure. Furthermore and contradictory to what would be expected, key herbivores (in particular surgeonfish) are significantly smaller when more macroalgae are present.

While the high amount of macroalgae may support a high number of herbivorous fish individuals, fish do not reach the size they used to get. It may indicate that the fleshy algae act as a place for juvenile fish. However, because of the complex interactions of abiotic and biotic drivers of change, the identification of the reason for the smaller fish size is challenging and cannot be derived from this study.

4.2.4. Coralline algae

The recent increase in the primary producer crustose coralline algae (CCA) indicates positive change for the coral reef ecosystem. CCA has been found to directly promote coral recruitment with and without the participation of their associated microbial films that contain bacteria (Morse et al., 1994; Negri et al., 2001; Sneed et al., 2014). However, in this study the contrary was found as there is an indication that coral recruitment is negatively correlated with CCA. That less corals are able to settle may indicate that CCA could be affected by the peyssonnelid algal crusts (PAC) which has been aggressively spreading and affecting shallow water CCA in the Caribbean since 2010 (Eckrich et al., 2011) as they grow over vacant space, corals, and sponges (Eckrich & Engel, 2013). This point would not explain though, and rather go against the finding that more diverse coral recruits are settling on CCA. Hence, other factors seem to also have an influence on the cover of cyanobacteria. Nonetheless, coralline algae are positively related to the mean size of *Lutjanidae*. A study in Kenya (O'Leary & McClanahan, 2010) has shown that *Lutjanidae* are not likely to affect CCA cover, leading to the assumption that a higher cover of CCA must have positive consequences for snappers. A possible explanation may be the increase of reef material through calcification by coralline algae (Harrington et al., 2004), which supports build-up of reef habitat structure and thus, the life of the prey of *Lutjanidae*.

4.2.5. Other benthic organisms

Like gorgonians, sponges are critical habitat-forming reef organisms and therefore have the ability to counteract some effects of reef degredatation (Seeman et al., 2018). In recent years the cover of sponges has decreased, probably due to less space being available as macroalgae have increased significantly. Although not significant, sponge cover seems to posivitely correlate with the mean size of grunts. Sponges have developed specific defense mechanism that target particular consumers, which may indirectly affect predatory fish families such as grunts (Wulff, 2020). The negative relationship found between species richnes of *Scaridae* and sponges is inconsistent with the results of other studies that show that sponges positively correlate with a diversity of associated species (ibid.).

Cyanobacteria cover has slightly increased from 3.7% in 2016 (Hildebrand, 2016) to 4.5% although coverage was extremely high in 2015 (13.1%), which could be traced back to different researchers executing GCRMN. It is very unlikely that cover of cyanobaceria changes so rapidly in just a few years. As in 2016, no significant difference of cyanobacteria cover between the unfished and fished zone was found although coverage seems to be higher in the unfished zone. Positive is the relationship between visibility and cyanobacteria cover (Hildebrand, 2016). As they are photosynthetic organisms, meaning that their growth is dependent on the availability of light. The growth of cyanobacteria cover is further stimulated by an increase of sea surface temperatures as well as by nutrient enrichment through enhanced erosion and more frequent and intense hurricanes (Charpy et al., 2012; Eakin et al., 2010; Jackson et al., 2014). This can culminate in toxic cyanobacteria blooms, which may explain the finding that cyanobacteria are negatively correlated with indicators of *Lutjanidae* as its species richness, density and biomass are decreasing with increasing cover of cyanobacteria. These toxic changes are affecting crustacean species (Regueiras et al., 2018), which represent one of the main preys of snappers.

Zoanthids have a similar correlation as cyanobacteria, namely a negative relationship with species richness, density and biomass of *Lutjanidae*, but the reason for this remains unclear. That grunts benefit from an increase in tunicates is due to their widespread diet that has been found to also include tunicates among others (Babrowicz, 2015).

4.2.6. Mean size of key fish

Obvious is the harsh decline in the size of reef fish. In the case of *Serranidae* mean size even halved in four years from 2015 to 2019. Here, it must be considered that most of the groupers that were recorded are small groupers (coney, graysby, red hind, rock hind, barret hamlet, barlequin bass; see appendix 8.3.2) and only one yellowfin grouper, which is much larger, was spotted. The yellowfin grouper is a commonly fished species, which does indicate that more protection measures should be taken for this species. Since the other commercially important fish species Lutjanidae does increase in size, it could be assumed that groupers are fished more specifically and the community is less able to regenerate.

The mean size of herbivores in the SNMP is 17.2cm, whereas the three other key fish combined have a mean size of 23.1, which is not significantly larger. Referring back to figure 4 on the effect of reef degradatation on fish size, it is notable that the difference in size between herbivores and predators increases the more dead a reef is considered to be. The measured mean sizes are below the average for even a healthy coral reef, which points to a degraded state of the coral reef ecosystem in the SNMP (Rogers, Blanachat & Mumby, 2018). Due to the volcanic structure of the coral reefs around Saba, however, which is not likely to change considerably in a short period of time, this does not seem to explain the decline in mean size. The mean size indicator goes against the other pelagic indicators of fish density and biomass, which are increasing. Therefore, more specific research needs to be conducted to find what causes this decline.

These results also illustrate the need to conduct more species-specific research by disentangling the role of individual fish species. It is necessary for critical species to be identified and protected (Dell et al., 2020). Studies have so far focused on parrotfish as the main herbivore on Caribbean reefs, while other taxa such as *Kyphosus* have received far less attention (Duran et al., 2019) even though this genus can form 25% of the herbivorous fish biomass in the Caribbean (Paddack et al., 2006; Hernández-Landa et al., 2015).

4.3. Coral disease and bleaching

The prevalence of coral diseases has increased in recent years. Whereas the percentage of pictures that contain diseased corals was 2.5% in 2015 (Van der Vlugt, 2016), 9% of the corals showed signs of diseases in 2019. On the neighbouring Dutch island St. Eustatius 5% of the benthic photoquadrants contained corals with diseases in 2015 (de Graaf et al., 2015). That coral diseases appear more often could be because of the lowered resilience of the coral reef ecosystem in the Caribbean. This is due to the loss of fast-growing and reef-building corals such as corals of the *Acropora* family (Roff & Mumby, 2012) that only make up 0.01% of benthic cover in the SNMP (see appendix 8.4, Table 14). This study showed that the most common coral species around Saba is the non-framework builder *Porites Astreoides* with 2.9%. Interestingly, the occurence of coral disease was only positively correlated with one factor: Grunts are increasing in size when more corals are diseased. Grunts are predatory fish and the reason they grow in size is contradictory to current literature that show that coral disease negatively affects the health of the coral reef ecosystem (Birchenough, 2017; Cramer et al., 2012). The death of corals after a disease and subsequent loss of structural complexity therefore indirectly affects the predatory fish by minimizing habitat for its prey.

As hypothesized, coral bleaching negatively impacts fish communities (see Figure 18). Negative correlations have been found between coral bleaching with species richness, biomass and mean size of parrotfish, groupers and snappers, respectively. When a coral bleaches, it expells its symbiotic and photosynthetic algae living inside the coral tissue. If this stress continues, the coral dies. There was no significant correlation between coral bleaching and benthic cover, therefore no conclusion can be drawn on any interactions with benthos. However, it is known that coral bleaching can lead to coral death and be destructive for the whole coral reef ecosystem (Cramer et al., 2012).

4.4. RHI as an assessment tool

In this study, the RHI has been used as an absolute tool to better understand the drivers of changes in the coral reef ecosystem as well as their relationships. The indicators used in this tool, namely coral and macroalgae cover and density and biomass of key herbivores and key commercial fish are weighted the same for the calculation of the status of the reef. This is done for convenience to be able to compare the data across space and time. However, the implications of this should be discussed and local circumstances considered. The RHI is rather suited for temporal comparisons and less for comparisons in space. If the RHI is conducted and measured in regular time intervals, changes to the ecosystem can be detected and potentially a trend can be established. If the RHI is nonetheless taken for spatial comparisons between sites or locations, the factor of natural dynamism needs to be accounted for. On some locations, specific indicators or drivers of change are more important than others and the results of a localized study may not necessarily scale up to an entire region. Currently, there is no way to account for this in the RHI.

Another point is that even if there is no change in RHI, there may be in fact change of the overall status of the coral reef ecosystem. As an example, the RHI does not take into account the complexity of the reef (rugosity). The importance of reef structure has long been found to be beneficial for coral reef ecosystems (Alvarez-Filip et al., 2009). The data collection and analysis should be adjusted accordingly. With the CPCe software it is not possible to distinguish between the 3D reef structure as two-dimensional pictures were used for the analysis. A (randomly allocated) point is only available for the upper part of the reef. It should be discussed to make the inclusion of environmental variables such as depth, temperature, rugosity, oxygen solubility, nitrate and phosphate concentrations manadatory in the GCRMN analysis.

4.5. Further research

There is potential for fostering further research to better understand the dynamics within the coral reef ecosystem in the SNMP in order to make more informed decisions on how to protect it. This study is only looking at biophysical indicators and biological drivers of change, and does not include socio-economic variables, that have an impact on the ecosystem as well. GCMRN has recognized the importance of also addressing socio-economic variables (called SocMon) to get a full picture of all drivers influencing the coral reef ecosystem. It would therefore be recommended to include SocMon in the next assessment on the status of the coral reef in the SNMP.

Future studies shall aim to research the effect the distance from anchorage sites and the distance from coastal development has on the coral reefs. When laying the RHI results on a map of the SNMP (see Figure 24), it seems that there could be a geographical advantage or disadvantage of some sites. Sites in the south of the SNMP as well as around Diamond Rock are in a better state than those in other areas of the SNMP, and sizes in the no-take zone seem to have a much higher variability. Notable is the worse condition of the reef on the western side of the SNMP, which is the location of many scuba dive sites. These sites are frequently used for tourism purposes. An investigation of the impact of recreational scuba diving on the coral reef ecosystem around Saba can be helpful in determining its impact, and whether regulations need to be adjusted. Also, due to the strong swell event in 2017/2018 coming from St. Eustatius, sand was transported from St. Eustatius to Saba and Tents Reef (dive site number 16) is now accessible from land (personal observation). Since it is in foot reach from the harbour, people use the opportunity to snorkel and free dive from land.

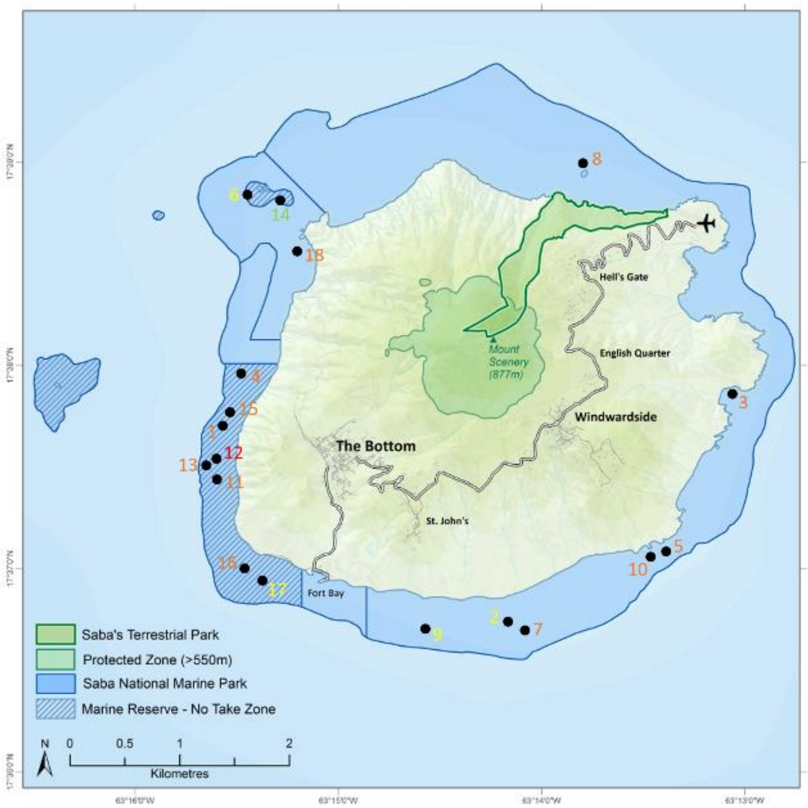


Figure 24. Map of the SNMP visualising the different total RHI score for every dive site.

Another question that has not been addressed in this study but is of high relevance relates to the environmental impact erosion and wastewater sewage have on the coral reefs around Saba. With hurricanes forecasted to increase in numbers and intensity due to global warming, more sediments are expected to enter the water of the SNMP. Surface run-off and land erosion occur during rain events and affect the water quality (Dekker et al., 2014). With more sediments in the water, visibility worsens and less light reaches the benthos, and the impacts of this need to be assessed. Erosion is further intensified through overgrazing by the uncontrolled increasing amount of free-roaming goats on the island. A recommendation to SCF is to create an open dialogue space between the responsible people on Saba and SCF to reach a common agreement on how to manage these goats that feed on terrestrial vegetation.

Lastly, it would be of high interest to conduct new research on fishery around Saba. Collecting data on the number, type and size of fish as well as their market value gives an indication of the pressure that fishing is exacerbating on the fish in the SNMP. As overfishing represents a potential threat, monitoring its impact on the coral reef ecosystem shall be considered.

5. Conclusion

The status of the coral reef ecosystem as judged by the RHI in the Saba National Marine Park is further decreasing. While not significant there is some indication that sites in the no-fishing zone are in a slightly better state than those in zones, where fishing is allowed. This points to the importance of establishing MPAs. Although coral cover has slightly increased over the past years, levels remain low and below the average of the Caribbean. Macroalgae and turf seem to rapidly grow and are dominating the reefs in the SNMP. Unlike other parts in the Caribbean, fish numbers in the SNMP are continuing to increase, and commercial fish density and thus biomass seems to recover in the fished zones, where herbivory fish thrive in abundance and larger and more and different species are found. The finding that there is less species diversity of commercial fish although density, biomass and size remains high in the fished zone indicates targeted fishing despite exacerbating low pressure.

Biophysical indicators of fish and benthic communities have found to interact in many diverse ways. While coral cover is positively correlated with coral species richness and groupers, macroalgae only has negative correlations with fish communities in regard to biomass, density and mean size. With the exception of the commercially important snapper, all other key fish groups have declined in size from 2015 to 2019, which may result in a trophic cascade effect on predators. Nonetheless, herbivory may benefit from the increasing number of macroalgae to feed, while with increasing abundance of macroalgae the herbivorous species that remove the algae may be increasingly important in promoting reef health. Coralline algae and sponges seem to impact the coral reef ecosystem in a positive way by providing habitat for coral recruits to settle on, and by adding structural complexity to the reef. On the other hand, an increase in cyanobacteria and the occurrence of zoanthids have negative effects on the predatory fish species *Lutjanidae*.

More corals colonies are diseased than in recent years, which can possibly have widespread consequences for the whole coral reef ecosystem. Coral bleaching has been found in low numbers. It negatively impacts species richness, biomass and mean size of different fish species.

With regard to the declining status of the coral reef ecosystem and projected changes in climate that drive biological drivers of change, continuous monitoring of the biophysical indicators is important. The need to better understand the interactions within and ecological roles and functions of organisms groups as well as species-specific characteristics of the coral reef ecosystem is crucial to identify the factors causing the degradation. Overall, a combination of biological, anthropogenic and climate-related drivers of change seems to impact Saba's reef. This study assessed the relationship between different biophysical indicators and biological drivers of change in more detail, put a number on it and is therefore contributing to the future management of the SNMP by providing indications of crucial correlations between fish and pelagic communities for adaptive management.

6. References

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8. Appendix

8.1. Benthic code names for CPCe analysis

Table 6. Categories and subcategories of benthic coverage of the CPCe analysis.

Categories	Subcategories	*Code*	*Common name*	*Type*
Stony coral	*Acropora palmata*	AP	elkhorn coral	branching and pillar coral
	Agaricia agaricites	AA	lettuce coral	leaf, plate & sheet coral
	Agaricia fragilis	AF	fragile saucer coral	leaf, plate & sheet coral
	Agaricia lamarcki	AL	whitestar sheet coral	leaf, plate & sheet coral
	Colpophyllia natans	CN	boulder brain coral	brain coral
	Dendrogyra cylindrus	DCY	pillar coral	branching and pillar coral
	Dichocoenia stokesi	DSO	ellipitical star coral	encrusting, mound & boulder coral
	Diploria clivosa	DC	knobby brain coral	brain coral
	Diploria labyrinthiformis	DL	grooved brain coral	brain coral
	Diploria strigosa	DS	symmetrical brain coral	brain coral
	Eusmilia fastigiata	EF	smooth flower coral	cup & flower coral
	Favia fragum	FF	golfball coral	encrusting, mound & boulder coral
	Madracis decactis	MD	ten-ray star coral	encrusting, mound & boulder coral
	Manicina areolata	MAR	rose coral	brain coral
	Meandrina meandrites	MME	maze coral	brain coral

	Millipora alcicornis	MILA	branching fire coral	fire coral
	Millipora complanata	MILC	blade fire coral	fire coral
	Montastraea annularis	MA	lobed star coral	encrusting, mound & boulder coral
	Montastraea cavernosa	MC	great star coral	encrusting, mound & boulder coral
	Montastrea faveolata	MFAV	mountainous star coral	encrusting, mound & boulder coral
	Montastrea franksi	MFRN	boulder star coral	encrusting, mound & boulder coral
	Mycetophyllia ferox	MF	rough cactus coral	fleshy coral
	Porites astreoides	PA	mustard hill coral	encrusting, mound & boulder coral
	Porites branneri	PB	blue crust coral	encrusting, mound & boulder coral
	Porites divaricata	PD	thin finger coral	branching and pillar coral
	Porites furcata	PF	branching finger coral	branching and pillar coral
	Porites porites	PP	clubtip finger coral	branching and pillar coral
	Scolymia lacera	SL	Atlantic mushroom coral	cup & flower coral
	Siderastrea radians	SR	lesser starlet coral	encrusting, mound & boulder coral
	Siderastrea siderea	SS	massive starlet coral	encrusting, mound & boulder coral
	Solenastrea bournoni	SB	smooth star coral	encrusting, mound & boulder coral
	Solenastrea hyades	SH	knobby star coral	encrusting, mound & boulder coral
Gorgonian	*Gorgonian*	GORG	octocorals	gorgonians
Macroalgae	*Amphiroa tribulus & rigida*	AMP	flat/y-twig algae	red algae
	Dictyota spp.	DICT	y-branched algae	brown algae
	Halimeda (different species)	HALI	leaf algae	green algae
	Liagora albicans	LIAG		red algae
	Lobophora variegata	LOBO	encrusting fan-leaf alga	brown algae

	Macroalgae	MACA	general	
	Padina sanctae-crucis	PAD	white scroll alga	brown algae
	Sargassum	SARG	sargassum seaweed	seagrass
	Stypopodium zonale	STY	leafy flat-blade alga	brown algae
	Turbinaria turbinata & tricostata	TURB	(blistered) saucer leaf alga	brown algae
	Turf	TURF		
	Wrangelia penicillata	WRANG	pink bush algae	red algae
Coralline algae	*Coralline algae*	CCA	crustose coralline algae	red algae
Cyanobacteria	*Cyanobacteria*	CYAN		
	Schizothrix	SCHIZ		
Tunicate	*Tunicate*	TUNI		
Sponge	*Sponge*	SPO		
Zoanthids	*Zoanthid*	ZO		
Bare substrate	*Rubble*	R		
	Sand	S		

8.2. Fish species-specific *a* and *b* parameters for LWR and biomass calculation

Table 7. Species-specific a and b parameter derived from FishBase for the LWR calculation as well as the key group to which they belong.

Family	*Common name*	*a*	*b*	*group*
Scaridae	Greenblotch parrotfish	0,0121	3,0280	herbivores
	Midnight parrotfish	0,0185	3,0600	herbivores
	Princess parrotfish	0,0135	3,0000	herbivores
	Rainbow parrotfish	0,0155	3,0630	herbivores
	Redband parrotfish	0,0123	3,1300	herbivores

	Redtail parrotfish	0,0129	3,1000	herbivores
	Stoplight parrotfish	0,0170	3,0600	herbivores
	Striped parrotfish	0,0158	3,0400	herbivores
	Yellowtail parrotfish	0,0093	3,0400	herbivores
Acanthuridae	Blue Tang	0,0257	2,9000	herbivores
	Doctorfish	0,0204	2,9200	herbivores
	Ocean surgeonfish	0,0348	2,6890	herbivores
Haemulidae	Black margate	0,0195	3,0500	commercial
	Caesar grunt	0,0404	2,7400	commercial
	Cottonwick	0,0200	2,9900	commercial
	French grunt	0,0148	3,0200	commercial
	Smallmouth grunt	0,0166	3,0400	commercial
	Spanish grunt	0,0209	3,0300	commercial
	Tomtate	0,0138	3,0000	commercial
	White grunt	0,0170	2,9900	commercial
Lutjanidae	Dog snapper	0,0182	2,9900	commercial
	Mahogany snapper	0,0170	2,9600	commercial
	Schoolmaster	0,0141	2,9800	commercial
	Yellowtail snapper	0,0148	2,9500	commercial
Serranidae	Coney	0,0162	3,0100	commercial
	Graysby	0,0110	3,1100	commercial
	Red hind	0,0141	3,0500	commercial
	Rock hind	0,0174	3,1100	commercial
	Barret hamlet	0,0178	3,0800	commercial
	Yellowfin grouper	0,0095	3,1400	commercial
	Harlequin bass	0,0145	3,0480	commercial

8.3. Reef fish

8.3.1. Fish in the SNMP

Table 8. Collected fish species, their characteristics and abundance in the SNMP

Family	Genus	Species	Common Name	#/5100 m²	Trophic group
Acanthuridae	*Acanthurus*	chirurgus	Doctorfish	100	herbivorous
Acanthuridae	*Acanthurus*	coeruleus	Blue tang	515	herbivorous
Acanthuridae	*Acanthurus*	tractus	Ocean surgeonfish	461	herbivorous
Aulostomidae	*Aulostomus*	maculatus	Trumpetfish	17	piscivorous
Balistidae	*Balistes*	vetula	Queen triggerfish	2	Invertebrate feeder
Balistidae	*Melichthys*	niger	Black durgon	265	herbivorous
Carangidae	*Caranx*	ruber	Bar jack	234	piscivorous
Carangidae	*Seriola*	rivoliana	Almaco jack	2	piscivorous
Carcharhinidae	Carcharhinus	perezii	Caribbean reef shark	3	apex predator
Chaetodontidae	*Chaetodon*	capistratus	Foureye butterflyfish	69	invertebrate feeder
Chaetodontidae	*Chaetodon*	ocellatus	Spotfin butterflyfish	43	invertebrate feeder
Chaetodontidae	*Chaetodon*	striatus	Banded butterflyfish	2	invertebrate feeder
Chaetodontidae	*Prognathodes*	aculeatus	Longsnout butterflyfish	4	invertebrate feeder
Cheloniidae	Chelonia	mydas	Green turtle	5	herbivorous
Diodontidae	*Diodon*	hystrix	Porcupinefish	2	invertebrate feeder
Epinephelidae	Mycteroperca	venenosa	Yellowfin grouper	1	piscivorous
Ginglymostomoatidae	Ginglymostoma	cirratum	Nurse shark	2	piscivorous
Gobiidae	Elacatinus	evelynae	Sharknose goby	317	
Grammatidae	Gramma	dejongi	Fairy basslet	2	invertebrate feeder
Haemulidae	*Anisotremus*	surinamensis	Black margate	13	omnivorous
Haemulidae	*Haemulon*	aurolineatum	Tomtate	66	omnivorous
Haemulidae	*Haemulon*	carbonarium	Caesar grunt	2	invertebrate feeder
Haemulidae	*Haemulon*	chrysargyreum	Smallmouth grunt	7	planktivorous
Haemulidae	*Haemulon*	flavolineatum	French grunt	46	invertebrate feeder
Haemulidae	*Haemulon*	macrostomum	Spanish grunt	10	invertebrate feeder
Haemulidae	*Haemulon*	melanurum	Cottonwick	2	omnivorous

Haemulidae	*Haemulon*	plumierii	White grunt	105	invertebrate feeder
Holocentridae	*Holocentrus*	adscensionis	Squirrelfish	11	invertebrate feeder
Kyphosidae	*Kyphosus*	vaigiensis	Brassy chub	34	omnivorous
Labridae	*Bodianus*	rufus	Spanish hogfish	410	invertebrate feeder
Labridae	*Clepticus*	parrae	Creole wrasse	7	herbivorous
Labridae	*Halichoeres*	bivittatus	Slippery dick	3047	invertebrate feeder
Labridae	*Halichoeres*	garnoti	Yellowhead wrasse	5	invertebrate feeder
Labridae	*Halichoeres*	radiatus	Puddingwife	2	invertebrate feeder
Labridae	*Lachnolaimus*	maximus	Hogfish	859	invertebrate feeder
Labridae	*Thalassoma*	bifasciatum	Bluehead wrasse	8	herbivorous
Lutjanidae	*Lutjanus*	apodus	Schoolmaster	2	piscivorous
Lutjanidae	*Lutjanus*	jocu	Dog snapper	51	piscivorous
Lutjanidae	*Lutjanus*	mahogoni	Mahogany snapper	7	piscivorous
Lutjanidae	*Ocyurus*	chrysurus	Yellowtail snapper	1	piscivorous
Monocanthidae	*Aluterus*	scriptus	Scrawled filefish	25	Herbivorous
Monocanthidae	*Cantherhines*	macrocerus	Whitespotted filefish	1	invertebrate feeder
Monocanthidae	*Cantherhines*	pullus	Orangespotted filefish	191	omnivorous
Mullidae	*Mulloidichthys*	martinicus	Yellow goatfish	8	invertebrate feeder
Mullidae	*Pseudopeneus*	maculatus	Spotted goatfish	1	piscivorous
Muranaenidae	Gymnothorax	miliaris	Goldentail moray	1	piscivorous
Muranaenidae	Gymnothorax	moringa	Spotted moray	3	piscivorous
Muranaenidae	*Gymnothorax*	saxicola	Honeycomb moray	6	piscivorous
Ostraciidae	Acanthostracion	polygonius	Honeycomb cowfish	1	invertebrate feeder
Ostraciidae	*Lactophrys*	bicaudalis	Spotted trunkfish	47	omnivorous
Ostraciidae	*Lactophrys*	triqueter	Smooth trunkfish	4	invertebrate feeder
Palinuridae	Panulirus	argus	Caribbean spiny lobster	12	omnivorous
Pomacanthidae	*Holacanthus*	ciliaris	Queen angelfish	27	omnivorous
Pomacanthidae	*Holacanthus*	tricolor	Rock beauty	3	omnivorous
Pomacanthidae	*Pomacanthus*	arcuatus	Gray angelfish	4	omnivorous
Pomacanthidae	*Pomacanthus*	paru	French angelfish	335	omnivorous
Pomacentridae	*Abudefduf*	saxatilis	Sergeant major	3298	omnivorous
Pomacentridae	*Chromis*	cyanea	Blue chromis	3078	herbivorous
Pomacentridae	*Chromis*	multilineata	Brown chromis	87	herbivorous
Pomacentridae	*Microspathodon*	chrysurus	Yellowtail damselfish	70	herbivorous
Pomacentridae	*Stegastes*	adustus	Dusky damselfish	3078	herbivorous

Pomacentridae	*Stegastes*	partitus	Bicolor damselfish	4	omnivorous
Pomacentridae	*Stegastes*	planifrons	Threespot damselfish	7	omnivorous
Scaridae	*Scarus*	coelestinus	Midnight parrotfish	2	herbivorous
Scaridae	*Scarus*	guacamaia	Rainbow parrotfish	28	herbivorous
Scaridae	*Scarus*	iseri	Striped parrotfish	170	herbivorous
Scaridae	*Scarus*	taeniopterus	Princess parrotfish	1	herbivorous
Scaridae	*Sparisoma*	atomarium	Greenblotch parrotfish	100	herbivorous
Scaridae	*Sparisoma*	aurofrenatum	Redband parrotfish	31	herbivorous
Scaridae	*Sparisoma*	chrysopterum	Redtail parrotfish	3	herbivorous
Scaridae	*Sparisoma*	rubripinne	Yellowtail parrotfish	40	herbivorous
Scaridae	*Sparisoma*	viride	Stoplight parrotfish	2	herbivorous
Scombridae	Thunnus	atlanticus	Blackfin tuna	1	piscivorous
Scorpaenidae	*Pterois*	volitans	Lionfish	5	piscivorous
Serranidae	*Cephalopholis*	cruentata	Graysby	357	piscivorous
Serranidae	*Cephalopholis*	fulva	Coney	5	piscivorous
Serranidae	Cephalopholis	polleni	Harlequin hind	11	piscivorous
Serranidae	*Epinephelus*	adscensionis	Rock hind	3	piscivorous
Serranidae	*Epinephelus*	guttatus	Red hind	39	invertebrate feeder
Serranidae	Hypoplectrus	puella	Barred hamlet	11	invertebrate feeder
Serranidae	*Serranus*	tigrinus	Harlequin bass	21	invertebrate feeder
Sphyraenidae	*Sphyraena*	barracuda	Great barracuda	1	apex predator
Tetraodontidae	*Canthigaster*	rostrata	Sharpnose pufferfish	100	invertebrate feeder
Tetraodontidae	*Sphoeroides*	spengleri	Bandtail pufferfish	515	invertebrate feeder

8.3.2. Mean size of every key fish species by site

Table 9. Mean size (cm) of Scaridae (parrotfish) by site.

	Greenblotch	*Midnight*	*Princess*	*Rainbow*	*Redband*	*Redtail*	*Stoplight*	*Striped*	*Yellowtail*
BA	-	-	20.50	-	20.50	-	-	-	-
BRM	-	-	18.56	-	20.50	12.04	36.50	-	-
CG	-	-	14	-	22.64	-	25.83	25.50	-
CH	-	-	11.17	-	17.85	-	-	25.50	-
DDO	-	-	16.09	-	19.42	16.75	27.90	-	-
GQS	-	-	18.88	-	15.50	18	25.50	20.50	18.83
GI	-	-	13.63	-	23.70	25.50	36.17	-	-
GG	-	-	16.93	-	13.63	-	22.17	-	-
HIC	-	-	15.08	-	15.50	15.50	18.20	-	-
HS	-	11.75	16.70	-	16.13	-	25.50	25.50	-
LL	-	-	15.50	-	13	-	-	-	-
LL2	-	-	23.50	-	23.90	26	26	-	-
MWS	-	-	19.94	-	20.50	-	39.50	-	-
PP	2.50	-	15	-	16.13	-	8	-	-
TR	-	-	8	14.43	8	-	25.50	-	-
TRD	-	-	6.86	-	14	-	29.17	5.63	-
TP	-	-	16.7	-	16.21	-	20.50	-	-
Mean	***2.50***	***11.75***	***16.14***	***14.43***	***17.66***	***15.70***	***26.08***	***8.82***	***18.83***

Table 10. Mean size (cm) of Acanthuridae (surgeonfish) by site.

	Blue Tang	*Doctorfish*	*Ocean surgeonfish*
BA	14.67	17.50	15.50
BRM	18.03	36.50	14.46
CG	15.20	15.50	15.50
CH	11.75	-	10.25
DDO	16.59	25.50	17.36
GQS	16.08	18	16.33
GI	17.17	15.50	17.32
GG	15.50	-	16
HIC	14.04	10.50	11.75
HS	11.09	-	12.17
LL	15.50	-	15.50
LL2	15.50	17.72	16.61
MWS	20.40	31	19.79
PP	11.75	-	14.375
TR	9.15	80	8.60
TRD	10.75	9.03	8.25
TP	15.19	15.5	13.6
Mean	***15.38***	***13.18***	***14.50***

Table 11. Mean size (cm) of Lutjanidae (snapper) by site.

	Dog	*Mahogany*	*Schoolmaster*	*Yellowtail*
BA	-	-	25.50	-
BRM	-	-	36.50	-
CG	-	-	-	-
CH	-	-	-	25.50
DDO	-	-	36.50	-
GQS	-	20.50	46.50	-
GI	-	-	-	-
GG	36.50	25.50	-	-
HIC	-	-	-	-
HS	-	22.17	36.50	-
LL	-	-	-	-
LL2	-	-	46.50	-
MWS	-	-	41.50	49.13
PP	-	-	-	-
TR	-	-	-	-
TRD	-	-	-	-
TP	-	-	-	-
Mean	***36.50***	***25.18***	***38.88***	***39***

Table 12. Mean size (cm) of Serranidae (grouper) by site.

	Coney	Graysby	Red hind	Rock hind	Barret hamlet	Yellowfin	Harlequin bass
BA	9.67	-	-	-	-	-	8
BRM	13.24	-	-	-	-	-	-
CG	18	-	-	-	-	-	11.75
CH	18.83	-	15.50	-	8	-	-
DDO	14.56	-	-	-	-	-	2.50
GQS	16.14	-	25.50	-	-	-	-
GI	14.56	15.50	-	-	-	-	8
GG	22.87	-	-	-	-	-	2.50
HIC	12.43	-	-	-	-	-	-
HS	12.50	-	-	-	-	-	8
LL	15.50	-	-	-	-	-	-
LL2	16.44	-	-	15.50	-	-	8
MWS	22.40	-	31	36.17	-	50	-
PP	18.70	-	-	-	8	-	2.50
TR	1.99	-	-	-	-	-	-
TRD	8.59	-	13.63	-	-	-	4.12
TP	18.83	-	-	-	-	-	8
Mean	***14.69***	***15.50***	***19.45***	***27.90***	***8***	***50***	***5.37***

Table 13. Mean size (cm) of Haemulidae (grunts) by site.

	Black margate	Caesar	Cottonwick	French	Smallmouth	Spanish	Tomtate	White
BA	-	-	-	16.75	-	-	-	-
BRM	-	-	-	18.83	-	-	-	-
CG	-	-	15.50	16.75	25.50	-	15.50	15.50
CH	-	-	-	-	-	-	15.50	-
DDO	-	15.50	-	22.17	-	-	-	-
GQS	-	19.25	-	16.75	15.50	-	-	-
GI	46.50	15.50	-	17.50	15.50	-	-	-
GG	-	-	-	15.50	-	-	-	-
HIC	-	-	-	-	15.50	-	-	-
HS	-	15.5	-	15.50	-	-	8	-
LL	-	-	-	-	-	-	-	-
LL2	-	15.5	-	25.50	-	-	-	-
MWS	46.50	25.5	-	21.21	-	-	-	-
PP	-	-	-	18.83	-	-	-	-
TR	-	-	-	-	-	-	-	-
TRD	-	-	-	-	-	15.50	-	-
TP	-	-	-	-	15.50	-	15.50	-
Mean	***46.50***	***17.79***	***15.50***	***18.66***	***17.50***	***15.50***	***13.63***	***15.50***

8.4. Benthic coverage

Table 14. Mean percentage of benthic cover per type by species (for taxon codes see appendix 8.1).

SITE	BA	BRM	CG	CH	DDO	DR	GQS	GI	GG	HIC	HS	LL	LL II	MWS	PP	TR	TP	**MEAN**
Hard coral	**8.90**	**6.36**	**5.58**	**15.37**	**5.29**	**8.56**	**4.27**	**9.30**	**5.55**	**6.67**	**6.70**	**5.58**	**9.22**	**12.60**	**7.68**	**10.03**	**11.79**	**8.22**
AP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.11	**0.01**
AA	0.06	0.05	0.54	0.55	0.11	0.43	0.05	0.16	0.05	0.11	0.11	0.16	0.21	1.99	0.32	0	0.59	**0.32**
AF	0	0	0	0.06	0.05	0	0	0	0	0	0	0	0	0.22	0	0	0	**0.02**
AL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	**0**
CN	0	0.32	0	0.17	0.11	0.16	0	0	0.32	0.05	0	0.11	0.05	0.33	0.16	0.21	0.16	**0.13**
DCY	0.23	0	0	0	0.11	0.11	0	0	0	0.05	0.11	0.05	0	0	0.21	0	0	**0.05**
DSO	0	0	0	0	0	0	0	0.05	0.16	0	0	0	0	0.06	0.05	0.05	0.11	**0.03**
DC	0	0.11	0	0.11	0	0.27	0.05	0.05	0	0	0.17	0.05	0	0.06	0	0	0.21	**0.06**
DL	0.23	0.27	0.16	0.61	0	0.05	0	0.49	0	0.05	0.28	0.11	0.16	0.44	0.11	0.05	0.11	**0.18**
DS	0.40	0.37	0.27	0.17	0.76	0.81	0.11	0.97	0.53	0.98	0.67	0.80	0.43	0.88	0.59	1.07	0.91	**0.63**
EF	0	0	0	0.11	0	0	0	0	0	0	0	0	0.05	0	0.05	0	0	**0.01**
FF	0	0	0	0	0	0	0	0	0.05	0.05	0	0	0	0.06	0	0	0	**0.01**
MD	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0.06	0	0	0	**0.01**
MAR	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0.11	0.05	0	0	**0.01**
MME	0	0.05	0	0.22	0.11	0.76	0	0.16	0	0	0.06	0	0.27	0	0.16	0.05	0	**0.11**

MILA	0.40	1.34	0.43	0	0.59	0	0.05	0.59	0.48	0.43	0	0.05	0.21	0.22	0.16	1.07	0.32	**0.37**
MILC	0.46	0.11	0.80	0.06	0.22	0.05	1.17	0.22	0	0.16	0.33	0.16	0	1.93	0	4.96	2.13	**0.75**
MA	0.11	0	0	0.17	0	0.54	0.27	0.32	0.11	0.27	0.11	0	0.05	0.44	0.05	0.05	0.05	**0.15**
MC	0.57	0.16	0.16	0.67	0.59	2.98	0	1.46	0.21	0.33	0.50	0.43	0.48	1.49	0.27	0.69	0.32	**0.67**
MFAV	0.63	1.12	0.16	3.83	0.11	0.33	0.80	1.78	0.91	0.92	1.28	1.02	1.77	0.72	1.49	0	1.87	**1.10**
MFRN	0.29	0	0	1.61	0.11	0.11	0.16	0.11	0	0	0.11	0.05	1.55	0	0	0	0	**0.24**
MF	0	0	0	0	0	0.05	0	0	0	0.05	0	0	0	0	0	0	0	**0.01**
PA	4.94	0.53	1.45	5.05	1.67	1.03	0.32	1.41	0.91	1.90	1.45	2.20	3.38	2.54	3.04	1.01	2.77	**2.09**
PB	0	0	0	0.11	0	0.05	0.16	0	0.05	0.27	0	0.05	0	0	0	0	0	**0.04**
PD	0	0	0.11	0	0	0	0.05	0.54	0	0	0	0	0	0	0	0	0.11	**0.05**
PF	0	0	0	0.22	0	0.05	0	0	0	0.05	0.06	0	0	0	0	0	0.16	**0.03**
PP	0.06	0.16	0.27	0.50	0	0.05	0.05	0.16	0	0.11	0.45	0	0.21	0.72	0	0	0.43	**0.19**
SL	0	0	0	0.06	0	0	0	0	0.05	0	0	0	0	0	0	0	0	**0.01**
SR	0.06	0.05	0	0.06	0	0.05	0	0.05	0	0	0.06	0	0	0.06	0	0	0	**0.02**
SS	0.46	1.66	1.23	0.44	0.59	0.65	0.64	0.65	1.33	0.87	0.84	0.32	0.27	0	0.53	0.80	1.33	**0.74**
SB	0	0	0	0.5	0.16	0	0.37	0.05	0.37	0	0.06	0	0.11	0.28	0.43	0	0	**0.14**
SH	0	0	0	0	0	0	0	0.05	0	0	0.06	0	0	0	0	0	0.05	**0.01**
Gorgonians	**1.72**	**8.56**	**1.82**	**0.33**	**7.12**	**2.01**	**0.59**	**5.35**	**4.00**	**4.67**	**1.40**	**2.25**	**2.41**	**2.43**	**0.91**	**14.19**	**3.68**	**3.73**
Macroalgae	**33.49**	**38.50**	**33.94**	**53.83**	**28.12**	**6.99**	**39.03**	**40.92**	**27.66**	**60.88**	**65.46**	**50.11**	**35.50**	**5.09**	**39.04**	**20.75**	**28.98**	**35.78**
AMP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.59	**0.03**
DICT	29.98	27.59	33.40	23.09	27.90	6.88	37.05	40.11	21.94	58.93	65.46	49.62	26.49	4.53	18.67	20.64	26.79	**30.53**
HALI	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0.06	0	0	0	**0.01**

LIAG	0.17	0	0.54	0.11	0.11	0	0	0.32	0	0	0	0	0	0	0.16	0.05	1.60	**0.18**
LOBO	3.33	3.21	0	30.63	0.11	0.05	0	0.16	5.23	0.05	0	0.48	9.01	0	20.16	0	0	**4.26**
MACA	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	**0**
PAD	0	0	0	0	0	0	0.16	0	0.11	0	0	0	0	0	0.05	0	0	**0.02**
SARG	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	**0**
STY	0	0.11	0	0	0	0	0.05	0.32	0.37	0	0	0	0	0	0	0	0	**0.05**
TURB	0	7.59	0	0	0	0	1.66	0	0	1.90	0	0	0	0.28	0	0.05	0	**0.68**
WRAN	0	0	0	0	0	0	0	0	0	0	0	0	0	0.22	0	0	0	**0.01**
Turf	**33.31**	**40.86**	**29.54**	**26.14**	**35.40**	**41.84**	**43.25**	**7.24**	**37.11**	**10.74**	**21.60**	**28.22**	**24.45**	**25.15**	**32.80**	**43.31**	**35.65**	**30.39**
Coralline algae	**8.21**	**1.23**	**3.75**	**0.78**	**7.72**	**3.04**	**3.36**	**0.86**	**3.42**	**9.98**	**2.68**	**6.65**	**9.92**	**29.08**	**2.35**	**3.09**	**3.52**	**5.86**
Cyanobacteria	**0.40**	**0.64**	**9.33**	**0.33**	**0.05**	**16.10**	**0**	**30.38**	**0.37**	**0.76**	**0.11**	**0.27**	**4.56**	**1.38**	**0.96**	**0.48**	**10.35**	**4.50**
CYAN	0.40	0.64	9.33	0.33	0	16.10	0	30.38	0.37	0.76	0.11	0.27	4.56	1.38	0.96	0.48	10.35	**4.50**
SCHIZO	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Tunicates	**0.29**	**0.16**	**0.27**	**0.55**	**1.51**	**0.92**	**0.21**	**0.11**	**0**	**0.22**	**0.11**	**0.43**	**0.27**	**3.81**	**0.11**	**0.37**	**0.64**	**0.59**
Zoanthids	**0**	**0.05**	**0.21**	**0**	**0**	**0.16**	**0.16**	**1.78**	**0.05**	**2.66**	**0**	**0.16**	**0**	**0.06**	**0**	**0.37**	**2.08**	**0.46**
Sponges	**6.72**	**3.37**	**2.04**	**2.66**	**7.29**	**11.44**	**0.64**	**3.30**	**6.09**	**2.39**	**1.17**	**4.02**	**7.24**	**17.63**	**5.81**	**7.25**	**2.72**	**5.40**
Bare substrate	**6.89**	**0.27**	**13.51**	**0**	**7.5**	**8.94**	**8.44**	**0.76**	**15.75**	**0.98**	**0.78**	**2.25**	**6.38**	**2.38**	**10.35**	**0.16**	**0.59**	**5.05**
S	6.49	0.16	13.19	0	6.75	6.94	8.44	0.7	14.84	0.49	0.78	2.2	6.38	1.6	9.92	0.16	0.59	**4.68**

R	0.40	0.11	0.32	0	0.76	2.01	0	0.05	0.91	0.49	0	0.05	0	0.77	0.43	0	0	**0.37**

Table 15. 95% Confidence limits for benthic coverage.

	Backtransformed mean	lower	upper
Hard coral	7.74	6.47	9.26
Gorgonians	2.52	1.54	4.13
Macroalgae	30.52	21.48	43.38
Turf	27.87	21.70	35.78
Cyanobacteria	1.22	0.83	1.51
Coralline algae	3.85	2.39	6.21
Tunicates	0.80	0.64	0.93
Zoanthids	0.66	0.40	0.84
Sponges	4.06	2.65	6.20
Bare substrate	1.37	1.11	1.59

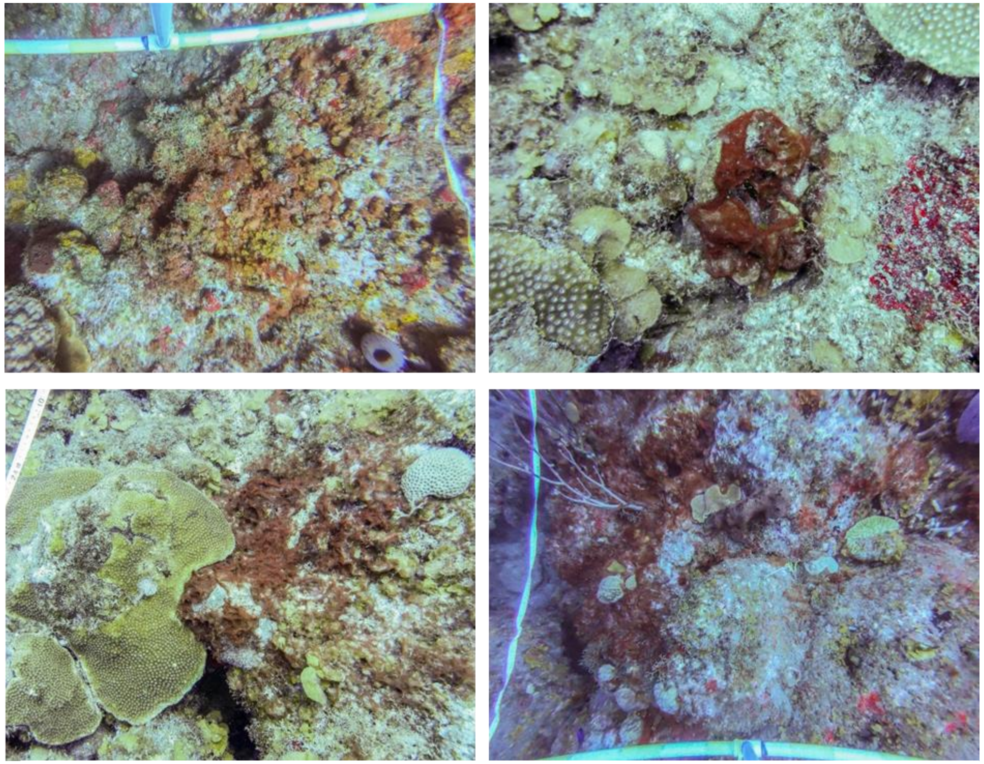

Figure 25. Examples of cyanobacteria.

8.5. Coral disease & bleaching

Table 16. Total percentage of images that contain coral diseases and bleaching (in %) per site.

	Coral disease	Coral bleaching
Babylon	4.30	0.03
Big Rock Market	12	0
Core Gut	13.30	0.01
Customs House	11	0.01
David’s Drop-off	0	0
Diamond Rock	4.10	0.07
Giles Quarter Shallow	5.30	0
Green Island	20.30	0.04
Greer Gut	12	0.03
Hole in the Corner	2.70	0
Hot Springs	0	0
Ladder Labyrinth	1.30	0.01
Ladder Labyrinth 2	2.70	0
Man of War Shoals	20.50	0
Porites Point	5.30	0
Tents Reef	17.30	0
Torrens Point	17.30	0.04
Mean	**9**	**0.01**

8.6. Coral recruits

Table 17. Counts, sum and mean percentage of coral recruits (# of individuals/0.94m²) per species and dive site (see appendix 8.1 for coral codes)

	AA	FF	MCAV	MILC	PA	PP	SS	SR	unidentified	**Total**	**Mean percentage**
BA	0	0	0	0	2	1	0	6	0	**9**	**4.59**
BRM	0	0	0	0	5	0	7	0	4	**16**	**8.16**
CG	0	1	2	0	1	0	2	2	0	**8**	**4.08**
CH	2	0	0	1	3	0	0	5	5	**16**	**8.16**
DDO	0	0	0	0	3	0	5	1	12	**21**	**10.71**
DR	1	0	0	0	2	0	3	3	2	**11**	**5.61**
GQS	0	0	0	0	0	1	0	18	1	**20**	**10.20**
GI	0	0	0	0	1	3	1	0	7	**12**	**6.12**
GG	0	0	0	0	1	0	0	5	5	**11**	**5.61**
HIC	4	0	0	0	2	1	0	0	2	**9**	**4.59**
HS	1	0	0	0	1	3	0	5	0	**10**	**5.10**
LL	2	0	0	0	0	2	3	5	0	**12**	**6.12**
LL2	0	0	0	0	1	0	0	1	1	**3**	**1.53**
MWS	3	0	1	1	3	1	1	0	2	**12**	**6.12**
PP	1	0	0	0	1	0	0	4	1	**7**	**3.57**
TR	0	0	0	0	4	0	1	3	1	**9**	**4.59**
TP	2	0	0	0	0	5	1	2	0	**10**	**5.10**
Total	**16**	**1**	**3**	**2**	**30**	**17**	**24**	**60**	**43**	**196**	
Mean percentage	**8.16**	**0.51**	**1.53**	**1.02**	**15.31**	**8.67**	**12.24**	**30.61**	**21.94**		

8.7. Unfished/Fished sites

Table 18. Mean, standard deviation, standard error, 95% confidence limits, backtransformed mean as well as lower and upper 95% confidence borders for all benthic indicators by zone.

		N	Mean	SD	SE	95CI	BTF mean	lower	upper
LogCoralRecruits	UF	9	2.21	0.47	0.16	0.36	9.11	6.32	13.12
	F	8	2.53	0.36	0.13	0.30	12.60	9.30	17.07
LogSpeciesRichnessCoralRecruits	UF	9	1.44	0.26	0.09	0.20	4.21	3.43	5.15
	F	8	1.31	0.19	0.07	0.16	3.70	3.16	4.33
LogCoralCover	UF	9	2.20	0.31	0.10	0.24	9.01	7.12	11.41
	F	8	1.88	0.33	0.12	0.27	6.52	4.96	8.58
LogGorgCover	UF	9	0.62	0.99	0.33	0.76	1.86	0.87	3.99
	F	8	1.26	0.86	0.30	0.72	3.53	1.72	7.25
LogSpongeCover	UF	9	1.72	0.80	0.27	0.61	5.58	3.02	10.31
	F	8	1.04	0.75	0.26	0.62	2.83	1.52	5.29
SqrtZoahnthidsCover	UF	9	0.28	0.34	0.11	0.26	0.53	1.02	1.72
	F	8	0.74	0.44	0.16	0.37	0.86	1.44	3.03
SqrtTunicateCover	UF	9	0.83	0.25	0.08	0.19	0.91	0.80	1.01
	F	8	0.66	0.32	0.11	0.27	0.81	0.63	0.96
LogMacroalgaeCover	UF	9	3.27	0.91	0.30	0.70	26.28	13.09	52.75
	F	8	3.59	0.26	0.09	0.22	36.05	28.95	44.90
LogTurfCover	UF	9	3.40	0.24	0.08	0.19	29.93	24.84	36.06
	F	8	3.25	0.68	0.24	0.57	25.69	14.57	45.31

SqrtCyanobacteriaCover	UF	9	1.02	0.45	0.15	0.34	1.01	0.83	1.17
	F	8	1.12	0.78	0.27	0.65	1.06	0.69	1.33
LogCorallineAlgaeCover	UF	9	1.50	1.04	0.35	0.80	4.48	2.01	9.97
	F	8	1.18	0.82	0.29	0.69	3.25	1.63	6.46
SqrtSandRubblePaveCover	UF	9	1.20	0.59	0.20	0.45	1.09	0.86	1.28
	F	8	1.35	0.52	0.18	0.43	1.16	0.96	1.33
LogSpeciesRichnessCoral	UF	9	2.78	0.21	0.07	0.16	16.12	13.73	18.92
	F	8	2.72	0.18	0.06	0.15	15.14	13.01	17.62
LogSpeciesRichnessMacroalgae	UF	9	0.95	0.44	0.15	0.33	2.59	1.85	3.62
	F	8	1.24	0.32	0.11	0.27	3.47	2.65	4.54
LogHeightMacroalgae	UF	9	1.36	0.27	0.09	0.21	3.89	3.16	4.78
	F	8	1.24	0.33	0.12	0.28	3.44	2.60	4.54
LogSpeciesRichnessScaridae	UF	9	1.19	0.33	0.11	0.25	3.30	2.57	4.24
	F	8	1.37	0.22	0.08	0.18	3.93	3.28	4.70
LogSpeciesRichnessAcanthuridae	UF	9	0.92	0.22	0.07	0.17	2.50	2.12	2.96
	F	8	1.05	0.14	0.05	0.12	2.85	2.53	3.22
SqrtSpeciesRichnessLutjanidae	UF	9	0.60	0.57	0.19	0.44	0.77	0.40	1.02
	F	8	0.55	0.59	0.21	0.49	0.74	0.23	1.02
LogSpeciesRichnessSerranidae	UF	9	0.80	0.50	0.17	0.39	2.22	1.51	3.26
	F	8	0.57	0.38	0.13	0.32	1.77	1.29	2.42
SqrtSpeciesRichnessHaemulidae	UF	9	0.87	0.51	0.17	0.39	0.93	0.69	1.12
	F	8	1.20	0.20	0.07	0.16	1.10	1.02	1.17
LogSpeciesRichnessKeyHerbivores	UF	9	1.78	0.20	0.07	0.16	5.91	5.06	6.90
	F	8	1.92	0.17	0.06	0.14	6.81	5.92	7.84
LogSpeciesRichnessKeyCommercial	UF	9	1.03	0.62	0.21	0.48	2.80	1.73	4.52
	F	8	0.88	0.46	0.16	0.39	2.41	1.64	3.55
LogSpeciesRichnessKeyFishwithoutHaemulidae	UF	9	2.19	0.26	0.09	0.20	8.98	7.34	10.97

	F	8	2.24	0.15	0.05	0.13	9.39	8.26	10.68
LogSpeciesRichnessAllFish	UF	9	3.35	0.27	0.09	0.21	28.63	23.21	35.31
	F	8	3.50	0.11	0.04	0.10	33.24	30.22	36.56
LogDensityScaridae	UF	9	1.65	0.68	0.23	0.52	5.19	3.07	8.77
	F	8	2.07	0.41	0.14	0.34	7.89	5.61	11.09
LogDensityAcanthuridae	UF	9	0.92	0.22	0.07	0.17	2.50	2.12	2.96
	F	8	1.05	0.14	0.05	0.12	2.85	2.53	3.22
SqrtDensityLutjanidae	UF	9	0.53	0.52	0.17	0.40	0.73	0.36	0.97
	F	8	0.57	0.72	0.25	0.60	0.75	#ZAHL!	1.08
LogDensitySerranidae	UF	9	1.92	0.74	0.25	0.57	6.82	3.86	12.07
	F	8	2.02	0.43	0.15	0.36	7.51	5.22	10.80
SqrtDensityHaemulidae	UF	9	0.92	0.65	0.22	0.50	0.96	0.65	1.19
	F	8	1.15	0.33	0.12	0.28	1.07	0.93	1.20
LogDensityKeyHerbivores	UF	9	3.00	0.53	0.18	0.41	20.13	13.35	30.37
	F	8	3.48	0.37	0.13	0.31	32.30	23.62	44.17
LogDensityKeyCommercial	UF	9	1.99	0.76	0.25	0.58	7.28	4.07	13.04
	F	8	2.18	0.60	0.21	0.50	8.86	5.37	14.62
LogDensityKeyFishwithoutHaemulidae	UF	9	3.32	0.58	0.19	0.45	27.60	17.67	43.11
	F	8	3.76	0.27	0.10	0.23	43.11	34.41	54.02
LogDensityKeyFish	UF	9	3.39	0.63	0.21	0.48	29.67	18.28	48.13
	F	8	3.83	0.26	0.09	0.21	45.83	37.03	56.73
LogDensityAllFish	UF	9	5.53	0.81	0.27	0.62	251.03	134.78	467.54
	F	8	5.74	0.50	0.18	0.41	309.90	204.73	469.11
LogBiomassScaridae	UF	9	6.17	0.67	0.22	0.52	478.19	285.14	801.92
	F	8	6.77	0.27	0.10	0.23	869.14	691.44	1092.50
LogBiomassAcanthuridae	UF	9	6.65	0.64	0.21	0.49	771.07	470.52	1263.59
	F	8	7.20	0.47	0.17	0.39	1336.09	900.81	1981.69

SqrtBiomassLutjanidae	UF	9	2.68	2.63	0.88	2.02	1.64	0.81	2.17
	F	8	2.57	3.03	1.07	2.54	1.60	0.19	2.26
LogBiomassSerranidae	UF	9	6.03	0.91	0.30	0.70	416.18	206.38	839.24
	F	8	5.88	0.53	0.19	0.44	357.81	229.52	557.81
SqrtBiomassHaemulidae	UF	9	2.91	2.24	0.75	1.72	1.71	1.09	2.15
	F	8	3.73	1.23	0.43	1.03	1.93	1.64	2.18
LogBiomassKeyHerbivores	UF	9	7.20	0.49	0.16	0.37	1342.41	922.70	1953.03
	F	8	7.73	0.28	0.10	0.24	2269.92	1791.17	2876.63
LogBiomassKeyCommercial	UF	9	6.41	1.10	0.37	0.84	605.20	260.60	1405.47
	F	8	6.38	1.07	0.38	0.89	588.45	241.33	1434.90
LogTotalBiomassKeyFishwithoutHaemulidae	UF	9	7.63	0.64	0.21	0.49	2056.76	1258.59	3361.13
	F	8	8.07	0.37	0.13	0.31	3201.10	2357.83	4345.97
LogTotalBiomassKeyFish	UF	9	7.72	0.73	0.24	0.56	2242.97	1280.65	3928.40
	F	8	8.18	0.31	0.11	0.26	3551.05	2739.96	4602.25
LogMeanSizeScaridae	UF	9	2.85	0.31	0.10	0.23	17.25	13.64	21.81
	F	8	2.99	0.14	0.05	0.12	19.81	17.61	22.29
LogMeanSizeAcanthuridae	UF	9	2.59	0.32	0.11	0.25	13.30	10.40	17.01
	F	8	2.80	0.20	0.07	0.16	16.47	13.98	19.40
LogMeanSizeLutjanidae	UF	9	3.50	0.30	0.13	0.37	33.18	22.85	48.19
	F	8	3.54	0.08	0.04	0.13	34.30	30.11	39.07
LogMeanSizeSerranidae	UF	9	2.35	0.76	0.25	0.58	10.52	5.89	18.80
	F	8	2.58	0.25	0.09	0.21	13.23	10.76	16.26
LogMeanSizeHaemulidae	UF	9	2.89	0.28	0.11	0.26	18.07	13.91	23.48
	F	8	2.87	0.15	0.05	0.12	17.70	15.66	20.02
LogMeanSizeKeyHerbivores	UF	9	2.73	0.28	0.09	0.21	15.38	12.42	19.05
	F	8	2.90	0.15	0.05	0.12	18.20	16.08	20.59
LogMeanSizeKeyCommercial	UF	9	2.64	0.88	0.29	0.67	14.06	7.17	27.55

	F	8	2.88	0.32	0.11	0.27	17.86	13.62	23.41
LogMeanSizeKeyFishwithoutHaemulidae	UF	9	2.76	0.43	0.14	0.33	15.87	11.37	22.15
	F	8	2.92	0.19	0.07	0.16	18.59	15.85	21.80
LogMeanSizeKeyFish	UF	9	2.78	0.40	0.13	0.31	16.12	11.87	21.89
	F	8	2.92	0.17	0.06	0.14	18.49	16.09	21.27

8.8. Interaction fish, benthos and coral disease and bleaching

Table 19. Significant (p<0.05) and suspicious (p<0.1) interactions between fish and benthos. For all is df=1.

	Hard coral	**Coral species richness**	**Gorgonian**	**Macroalgae**	**Coralline algae**	**Sponges**	**Tunicates**	**Cyanobacteria**	**Zoanthids**	**Coral disease**	**Coral bleaching**
Coral cover		F=7.34, p=0.02									
Bare substrate		F=3.59, p=0.08									
Species richness *Scaridae*						F=4.88, p=0.04					F=3.85, p=0.07
Species richness *Acanthuridae*			F=3.99, p=0.07								
Species richness *Lutjanidae*								F=5.62, p=0.03	F=8.56, p=0.01		
Species Richness *Serranidae*	F=3.14, p=0.10	F=4.19, p=0.06	F=4.70, p=0.05								
Species richness key commercial			F=4.30, p=0.06								
Density *Acanthuridae*			F=3.99, p=0.07								
Density *Lutjanidae*								F=3.90, p=0.07	F=4.22, p=0.06		
Density all fish		F=3.01, p=1.05		F=7.91, p=0.01							

Biomass *Haemulidae*				F=3.06, p=0.10							
Biomass *Lutjanidae*								F=3.92, p=0.07	F=5.70, p=0.03		
Biomass *Serranidae*				F=6.04, p=0.03							F=3.37, p=0.09
Biomass key commercial fish				F=3.23, p=0.09							
Biomass key fish				F=4.55, p=0.05							
Mean size *Acanthuridae*				F=3.16, p=0.10							
Mean size *Haemulidae*				F=16.90, p=0.001		F=7.45, p=0.02	F=4.39, p=0.06			F=4.40, p=0.06	
Mean size *Lutjanidae*				F=0.13, p=0.10	F=3.83, p=0.09						F=4.98, , p=0.06
Mean size *Serranidae*		F=3.88, p=0.07	F=3.89, p=0.07								
Mean size key herbivores				F=2.97, p=0.11							

8.9. Temporal analysis

8.9.1. Temporal change of key fish mean size

Table 20. Backtransformed means and 95% upper and lower confidence intervals of mean size of key fish families for 2015, 2016 and 2019 (n.d. = no data).

	Year	Mean	lower	upper
Scaridae	2015	23.86	21.52	26.45
	2016	20.76	18.94	22.74
	2019	18.41	16.22	20.88
Acanthuridae	2015	17.35	16.78	17.94
	2016	18.50	17.75	19.29
	2019	14.71	12.73	17.00
Haemulidae	2015	22.68	19.71	26.11
	2016	n.d.	n.d.	n.d.
	2019	17.86	15.89	20.07
Lutjanidae	2015	28.35	24.28	33.11
	2016	29.32	23.69	36.29
	2019	33.67	28.44	39.86
Serranidae	2015	24.58	21.67	27.89
	2016	18.93	16.84	21.29
	2019	11.71	8.73	15.71

8.9.2. Benthic indicators per site by year

Table 21. Mean percentages of benthic indicators per site by year (2015, 2016 and 2019) (n.d.= no data).

Site	Year	Hard coral	Gorgonians	Macroalgae	Turf	Cyanobacteria	Coralline algae	Sponges
BA	2015	6.52	2.91	15.94	n.d.	13.49	n.d.	6.42
	2016	9.87	1.51	23.45	7.39	24.83	10.27	7.90
	2019	8.90	1.72	33.49	33.31	0.40	8.21	6.72
BRM	2015	2.52	4.28	10.83	n.d.	7.78	n.d.	2.07
	2016	4.75	10.65	41.33	0.45	0.67	0.11	6.05
	2019	6.36	8.56	38.50	40.86	0.64	1.23	3.37
CG	2015	3.70	0.61	21.57	n.d.	13.86	n.d.	2.54
	2016	5.57	1.38	35.55	2.33	2.50	3.15	3.60

	2019	5.58	1.82	33.94	29.54	9.33	3.75	2.04
CH	2015	7.86	0.17	21.51	n.d.	12.57	n.d.	5.63
	2016	12.33	1.54	44.91	0.79	5.89	4.36	4.09
	2019	15.37	0.33	53.83	26.14	0.33	0.78	2.66
DDO	2015	5.87	6.69	21.82	n.d.	10.20	n.d.	6.62
	2016	6.35	11.20	34.03	1.62	5.03	2.02	9.78
	2019	5.29	7.12	28.12	35.40	0.05	7.72	7.29
DR	2015	6.89	2.06	7.05	n.d.	11.55	n.d.	21.83
	2016	14.87	1.36	5.96	0.57	2.80	3.61	41.56
	2019	8.56	2.01	6.99	41.84	16.10	3.04	11.44
GQS	2015	2.03	0.77	25.05	n.d.	8.83	n.d.	1.15
	2016	3.77	4.83	20.92	1.39	2.11	1.50	4.84
	2019	4.27	0.59	39.03	43.25	0.00	3.36	0.64
GI	2015	6.45	6.50	12.82	n.d.	16.70	n.d.	2.53
	2016	2.82	2.86	16.14	8.08	6.71	7.77	2.46
	2019	9.30	5.35	40.92	7.24	30.38	0.86	3.30
GG	2015	2.91	2.08	21.89	n.d.	13.14	n.d.	6.90
	2016	3.59	1.27	27.01	0.55	0.89	1.54	6.78
	2019	5.55	4.00	27.66	37.11	0.37	3.42	6.09
HIC	2015	6.75	0.62	14.92	n.d.	23.23	n.d.	3.30
	2016	7.29	1.92	38.47	3.72	1.64	6.81	3.69
	2019	6.67	4.67	60.88	10.74	0.76	9.98	2.39
HS	2015	2.50	1.16	16.09	n.d.	6.64	n.d.	6.16
	2016	4.26	1.11	3.14	1.12	0.34	0.62	4.50
	2019	6.70	1.40	65.46	21.60	0.11	2.68	1.17
LL	2015	5.77	1.56	18.66	n.d.	14.97	n.d.	4.21
	2016	5.52	2.65	16.47	4.33	3.26	3.61	8.51
	2019	5.58	2.25	50.11	28.22	0.27	6.65	4.02
LL2	2015	6.48	1.23	24.72	n.d.	23.51	n.d.	6.08
	2016	7.14	0.96	30.43	1.90	2.03	2.64	7.04
	2019	9.22	2.41	35.50	24.45	4.56	9.92	7.24
MWS	2015	8.30	1.02	6.31	n.d.	19.70	n.d.	26.79
	2016	9.95	2.72	6.13	6.19	4.22	7.28	32.88
	2019	12.60	2.43	5.09	25.15	1.38	29.08	17.63
PP	2015	4.65	0.69	29.07	n.d.	20.57	n.d.	5.63
	2016	4.71	0.84	25.15	3.01	1.61	1.39	8.99
	2019	7.68	0.91	39.04	32.80	0.96	2.35	5.81

TR	2015	7.69	5.25	6.73	n.d.	3.27	n.d.	15.38
	2016	13.23	12.15	0.50	11.80	0.39	5.45	9.68
	2019	10.03	14.19	20.75	43.31	0.48	3.09	7.25
TP	2015	4.34	3.39	5.35	n.d.	11.88	n.d.	4.30
	2016	5.37	1.96	18.05	20.31	3.93	4.29	3.38
	2019	11.79	3.68	28.98	35.65	10.35	3.52	2.72