Long-term trends in reef fish populations in Bonaire Marine Park

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Abstract

Management of reef fish populations requires insight in their resilience to anthropogenic stressors. Studies on temporal variations in reef fish populations and their abundance responses to environmental changes are crucial to the development of ecosystem-based management.

Nineteen years of voluntary fish survey data of reef fish at the west coast of Bonaire Marine Park (Caribbean) were analysed to investigate the effect of environmental changes on local reef fish populations. Various anthropogenic stressors that influence the coral reefs of Bonaire were studied in recent years. This study studies to what extent these stressors and protective management measures can be related to the observed population trends. In addition, reef fish population responses to specific events were analysed. In general fluctuations in sighting frequencies were species-specific and difficult to interpret.

Although some noise in the data couldn't be filtered out they show an overall negative trend in sighting frequencies in the 155 studied species.. A comparison of the average frequencies between the first five years of this study with the last five years resulted in an over 10% decrease in 64 of the species, while 30 species increased over 10%.

Three large parrotfish species decreased by approximately 50% over time and there were indications of a slight negative trend in mid-sized parrotfish as well. In fishery targets, the most intensive fished group, large to mid-sized groupers, decreased strongly. After the abundance of these groupers decreased to near zero, two species belonging to other fish families started to show signs of sequential overfishing.

It is unclear if larval import will compensate for the loss in reproductive capacity of the species in decline. Recent literature on recruitment distances suggest that the level of larval import is low on isolated islands like Bonaire, resulting in dependence of self recruitement.

Another event with strong effect on population dynamics are the mass mortality events in moray eels. Especially in two *Enchelycore* species these resulted in sigmoid like trends. The 2008 and 2022 mass mortality events were first noted at the onset of a period of sea water warming, paralleling various reef fish species in the Red Sea. This gives further support to the hypothesis that the current increase in warming events will lead to more frequent mass mortalities.

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Content

1 Introduction

Management of coral reef fish populations and reef fisheries requires a fundamental insight in their resilience and recruitment. As a result many reef fish studies focus their attention on spatial and temporal variations in populations (e.g. Mellin et al., 2010) and the need for connection between marine protected areas (Beltrán et al., 2017; Green et al., 2015). After the start of this millennium it became clear that marine larval dispersion is more limited than thought before (Cowen et al., 2006) and recent studies of genetic variation reef fish led to the conclusion that larval connectivity between reefs should be considered at scales of a few tens of kilometres (Beltrán et al., 2017; Green et al., 2015; Puebla, Bermingham & McMillan, 2012), although there are considerable differences between species (Almany et al., 2017). Self recruitment appears to be common and to occur consistently through time. This implicates that marine reserves either must be able to sustain focal species within their boundaries or lie close to other protected areas (Beltrán et al., 2017; Green et al., 2015; Puebla, Bermingham & McMillan, 2012).

Apart from this recruitment studies, additional research on abundance and rarity patterns of constituent species are required before relationships of temporal variance with reef resilience can be better understood (Mellin et al., 2010). The data are hard to obtain, as many reefs are affected by anthropogenic impact. Lack of funding of long term studies leads to further scarcity of relevant data. This study made use of REEF voluntary reef monitoring data by 'expert' divers in Marine Park in Bonaire (REEF Environmental Education Foundation, 2023). The long time frame and volume of these sighting data is without precedent in reef fish studies.

The island Bonaire lies in the southern Caribbean 90 km north of the Venezuelan coast. Its coral reefs are commonly considered one of the best conserved in the Caribbean (Hawkins et al., 1999; Jackson et al., 2014) and Pattengill-Semmens (2002) concluded that the number of reef fish species present in Bonaire is high for the Caribbean. However, various studies of Bonaire describe threats caused by eutrophication (De Bakker et al., 2017), sedimentation as a result of land runoff (Van der Geest, Meesters & Mücher, 2020), hurricanes and coral bleaching events (Eckrich et al., 2021; Scheffers and Scheffers, 2006; Steneck et al., 2019) and scuba dive stress on the corals (Hawkins et al., 1999). The common impact of these stressors on the reef communities are relatively well monitored (e.g. Bak, Nieuwland & Meesters, 2005; De Bakker et al., 2017; De Bakker, 2019; Sommer et al., 2011; Steneck et al., 2019), revealing a steady decline of coral cover and an increase in algal turfs. Fish populations are not unaffected by human influences as well. Spearfishing led to the early disappearance of the largest grouper species (Roberts, 2007) and although fishery pressure is considered light to moderate (Boenish and Richie, 2017; De Graaf et al., 2016 ; Hawkins and Roberts, 2004), several authors expressed their concern on the fishing pressure on carnivorous fish (De Graaf et al., 2016; Steneck and Wilson, 2017).

As the effects of various anthropogenic stressors are interrelated it is impossible to ascribe population fluctuations to one specific. Therefore, this study focusses on the effect of stress induced loss of coral cover and on reef fishery as well as on the reaction of the populations to natural or anthropogenic events.

2 Materials & Methods

2.1 Selection criteria and data evaluation

This study is based on REEF volunteer data obtained by the roving diver method as described in Pattengill-Semmens (2002). REEF (Reef Environmental Education Foundation) aims to protect biodiversity and ocean life by actively engaging and inspiring the public through citizen science, education, and partnerships with the scientific community. The data source used is free to use and accessible at https://www.reef.org/database-reports. The volunteer fish survey program carried is out by 'novice' and 'expert' surveyors. Expert REEF surveyors have to pass a fish-identification exam based on at least 90% recognition of at least 200 regional species and experience in 35 surveys. In this study only expert data were used. This study uses data from expert REEF surveyors on readily identifiable species. This is the same selection criterium that the Smithsonian Tropical Research Institute uses for inclusion in their regional biodiversity database (Chollett and Robertson, 2020).

REEF surveys on Bonaire started in 1995, but before 2000 many expert REEF sighting frequencies showed an unaccounted rise in a short period. As the influence of observation experience cannot be excluded, only data after 2000 were used in the trend analyses. Data from 2020-2022 were excluded as during the pandemic in 2020 and 2021 43% and 38% of the surveys were done in one location (Bari Reef) whereas in the years before the maximum was 17%. Especially in 2020 this also lead to a low number of surveys in the areas North, South and Klein Bonaire. The numbers of surveys per year ranged from 262 (2000) to 1357 (2007) with and average of 641 (Figure 1). This study is based on the assumption that the number of surveys largely compensate for observation variation in time and space. Definite conclusions will be avoided after small changes, even when are statistically relevant.

From 2000 to 2019, the annual number of Expert level surveys varied from 271 to 1353 (average 653). This study merely used the sighting frequency data: the percentage of sites at which a species was observed. For species where the sighting frequencies were near 100%, also the log10 based 'density scores' (Pattengill-Semmens, 2002) were analysed.
To avoid excessive influence of coincidence, species with sighting frequencies that reached less than 10% in any of the observation years were excluded. This resulted in data processing and graphical representation of 155 species (Supplementary file). The text of this study primary focusses on large bodied species.

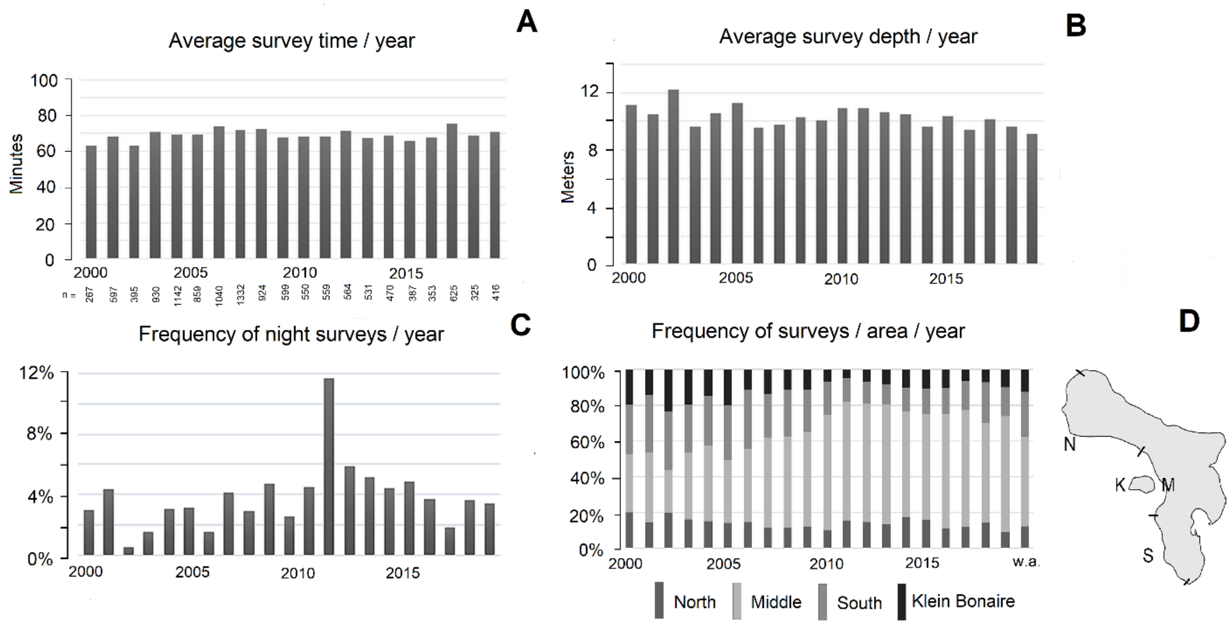

Figure 1. REEF surveys on the west coast of Bonaire over the period 2000-2019.

A. Average divetime **B**. Average maximum depth. **C**. Frequency of night surveys. **D**. Percentage of surveys in four subareas on the west coast of Bonaire. N – North: dive sites 0-20; M – Middle (Kralendijk area): dive sites 21-40; S – South dive sites 41-60, K – Klein Bonaire dives sites A-Z. Dive-site numbers according to the Bonaire Dive Map (Infobonaire, 2023). W.a. = represents the weight of each area in the yearly weighted averages (see text).

Metadata of the survey dives where not available per survey or per individual observer. Figure 1 shows available metadata on a yearly basis. The average dive time, maximum dive depth and percentage of night dives showed relative small variations per year (Figure 1 A, B, D). Unfortunately these variations could not be filtered out with the dataset to my disposal, which leads to noise in the data. The strongest variation occur in the percentage of night dives (surveys between 18:00 and 6:00). In most years the percentage of these night dives was below 5%. The highest yearly percentage was 11.8% in 2012, deviations in this year should be neglected.

Variances in subareas of West Bonaire that were surveyed through the years were compensated. REEF surveys are made at dive sites preferred by the volunteers. Changes in preferences may influence the time series. A division of the west coast of Bonaire in four sub-areas (North, Middle, South and Klein Bonaire) showed the Middle becoming more popular over the years (Figure 1 D). Where frequencies or densities for the total west coast were calculated, weighted averages were used according the formula (1*N+4*M+2*S+1*K)/8. (w.a. in Figure 1). The weighted averages have two advantages over means, biases caused by varying subarea attention over the years are compensated, and data from less surveyed areas weight less in the results. Sub-areas were chosen on basis of the vicinity of an urban area (M), and well developed reefs with less sandy patches (N and K) .

As a reference assessment data were used from the 2019 from the baseline survey by Naturalis Biodiversity Center, Leiden and ANEMOON Foundation (Bennema and Van Moorsel, 2022). In order to compare with REEF data, only observations made in daytime on the west coast of Bonaire were used, resulting in 30 observations on 29 sites. These data contain background information on depth distribution of local fish species between 0-10m and 10-30m. A pairwise t-test for means showed a strong positive association between the 2019 sighting frequencies of this baseline survey and the REEF data for the 155 analysed species (Difference between means=0; Pearson value =0.89).

Concluding remark: The noise in the data calls for prudence in its usage. There are no indications that their level is so strong or unidirectional that it provokes the clear long-term trends presented in this paper. Availability of such long-term data is so unique that it is considered to be a valuable source for park management.

2.2 Data analysis

De trendlines in the REEF data plots were calculated in a generalized adaptive model (Wood, 2017). Grey areas in the resulting 'gam plots' represent 95% confidence intervals. The statistical software R 3.6.2 (R Core Team, 2023) as used with the packages ggplot2, cowplot and mgcv with a geom_smooth confidence interval of 0.95. Note this method resulted in plots with different ordinates.

The fact that the 95% confidence limits in the gam plots in most cases lay close to the calculated lines, certainly on a 0-100% scale. (Supplementary file) inspires confidence in the sighting data.

3 Results

Literature shows that at the start of the studied period reef fish and corals in Bonaire were already affected by human impacts. Roberts (2007) describes how the largest grouper disappeared and sharks had become rare. Yet voluntary REEF research data showed that reef fish species richness around 2000 was high for the Caribbean (Pattengill-Semmens, 2002). Concern on the level of herbivory led to a ban on parrotfish fishery in 2010. A ban on shark fishery was implemented in 2015.

Although some noise in the data couldn't be filtered it shows an overall negative trend in sighting frequencies in the 155 studied species.. A comparison of the average frequencies between the first five years of this study with the last five years resulted in an over 10% decrease in 64 of the species, while 30 species increased over 10%. Trends in 155 individual species can be found in the Supplementary file.

In the results we will discuss reef fish families that play an important role in the park's ecosystem, that are known to be targeted by fishery, and that are known to have taken part in notable 'events' in the studied period. At the end it will be discussed whether trends in the populations could be ascribed to changes in coral cover in Bonaire National Park.

3.1 Parrotfish Scaridae

Parrotfish are considered to play a key role in coral reefs for their ability to reduce algal grow. Concern on the level of herbivory led to a ban on parrotfish (Scaridae) fishery in 2010. Yet, Steneck et al. (2019) concluded that the density declined after 2010.

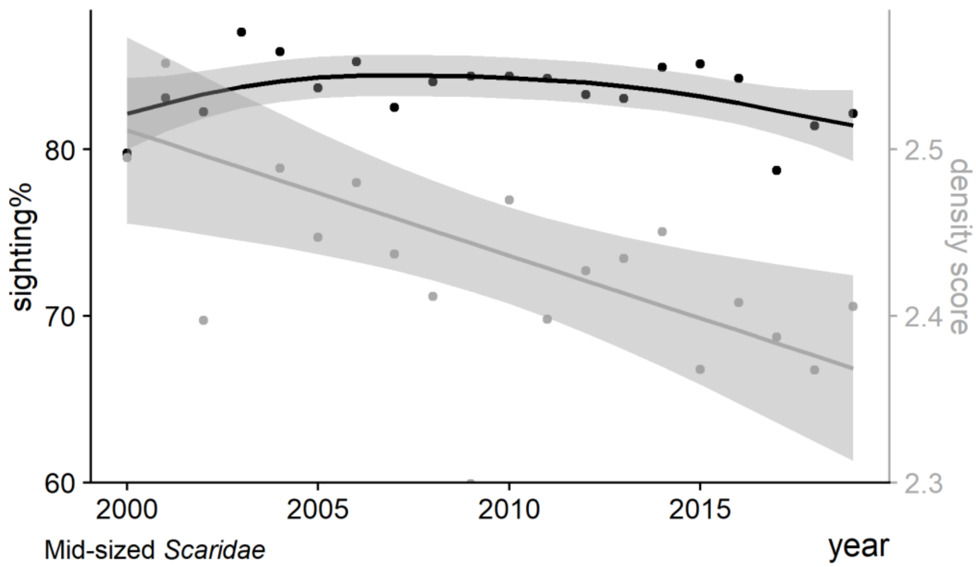

Figure 2. Mean of sighting frequencies and density scores of seven mid-sized *Scarus* and *Sparisoma* species A density score of two represent few (2 to 10) and of three many (11-100) individuals observed per survey. Data from the west coast of Bonaire. Individual species in the Supplementary file.

The REEF data show a negative trend in sighting frequencies of seven mid-sized parrotfish species (Figure 2) after 2010, but this trend is not statistically significant (Kendall's Rank correlation, p=0.2595) . However, as four species were so abundant that their frequencies were mostly 100%, their trends could be masked in the sighting frequency data. To mitigate this risk, REEF's density scores (Figure 2 and Methods) were also taken into account. This score indicates that the average densities of this seven species decreased (Kendall's Rank correlation, p= 0.00184) over the whole period. Also the abundance, defined in Pattengil-Semmens (2002) as sighting frequency x density, declined (Kendall's Rank correlation, p= 0.04677). As the decrease in density is small, it is at most considered as an indication of decrease (see Methods).
The rise in parrotfish densities in 2017, observed by De Bakker (2019) and Steneck et al. (2019) is not confirmed by the REEF data (Figure 2)

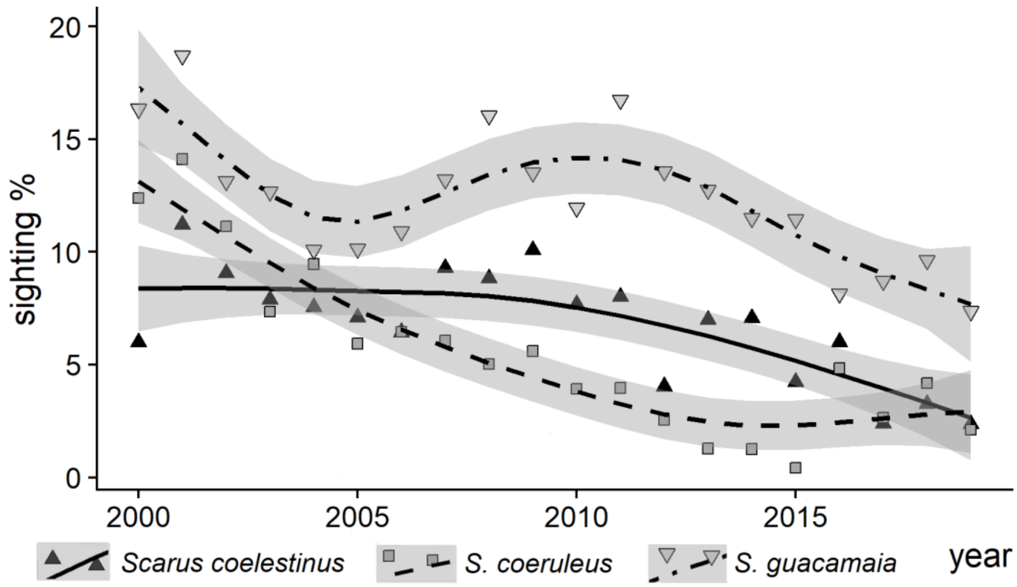

Figure 3. Large Scaridae REEF sighting frequencies on the west coast of Bonaire.

The three largest Caribbean parrotfish species showed a decline over the two decades (Figure 3). Probably their population densities were already relatively low in 2000. Their densities in a no fishing-area in the Venezuelan Los Roques Archipelago, rated in 400 x 15m transects, are +- 10/1000m^2 for *Scarus coelestinus*, *S. guacamaia* and +- 5/1000m2 for *S. coeruleus* (*Debrot et al., 2007*). Assuming that a roving diver covers at least 500m^2 (at least a 50m stretch with a view of 10m breath in case of these conspicuous species) it is expected that such a diver would observe these species on most of the dives.

The influence of the ban on parrotfish fishery in Bonaire on these results is unclear. The ban was implemented in 2010 to secure herbivory on the reefs (Steneck, Mumby & Arnold, 2007), but parrotfish were not commonly targeted by fishermen in Bonaire (Hoetjes et al., 2002; Nenadovic., 2007) and the ban was not was not 100% effective (De Graaf et al., 2016).

3.2 Fishery targets

Reef fish in Bonaire are landed by both the shore-based and boat-based fisheries. In addition to grunts, larger carnivores from are the main fishery targets on the reefs (De Graaf et al., 2016). Considering targeted fish families as a whole, the REEF data show rather stable trends in three families and a considerable decline in groupers (Figure 4).

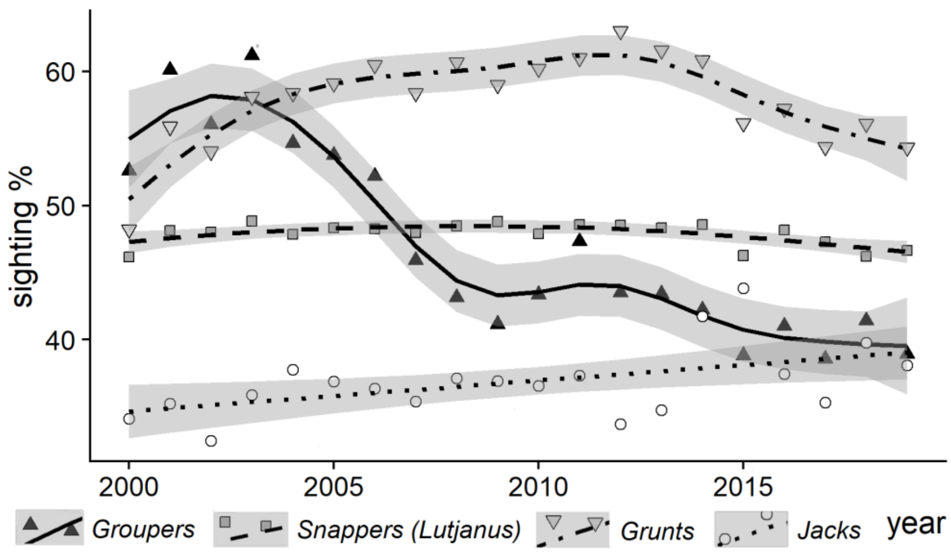

Figure 4. Mean REEF sightings of fishery target species at the west coast of Bonaire.

3.2.1 Groupers large Serranidae

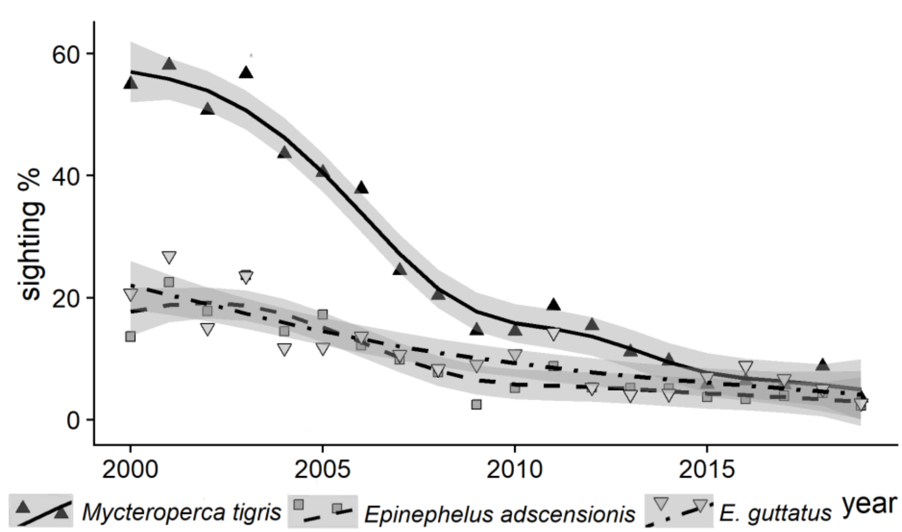

Figure 5. REEF sightings of the most frequent mid-sized groupers in 2000, Tiger grouper *Mycteroperca tigris,* Rock Hind *Epinephelus adscensionis and* Red Hind *E. guttatus* on the west coast of Bonaire.

Groupers larger then one meter (maximum length in Fishbase) are rare in Bonaire. *Epinephelus* species larger then 1 meter were rare, or had already disappeared in the 1990's (Pattengill-Semmens, 2002). The only large to mid-sized groupers that where still frequent in 2000 where the Tiger grouper *Mycteroperca tigris,* Rock Hind *Epinephelus adscensionis and* Red Hind *E. guttatus*. Since then their densities decreased dramatically (Figure 5). Frequencies of the less frequent mid-sized grouper species diminished as well (Supplementary file).

Frequencies of the small groupers (graysby *Cephalopholis cruentata* and coney *C. fulva* varied over time. Those of the former species showed an increase while those of latter declined in the last years (Figure 6).

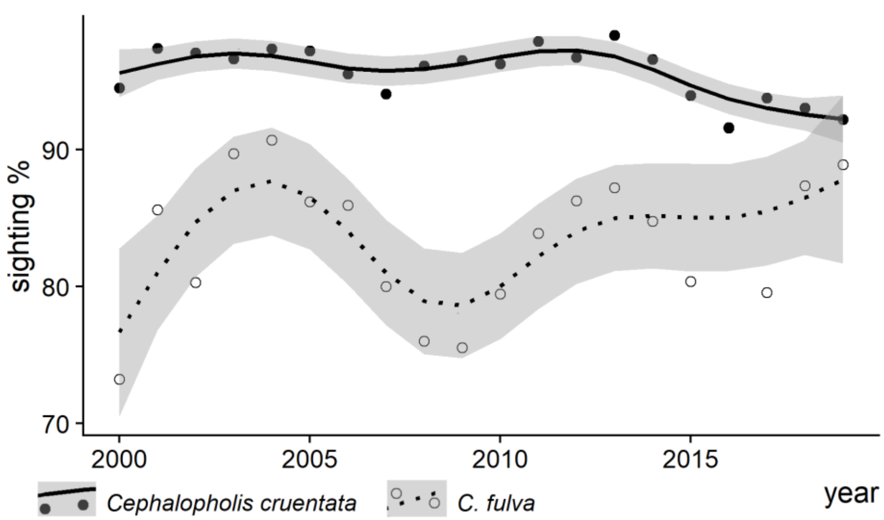

Figure 6. *Cephalopholis* (small groupers) REEF sighting frequencies of two small grouper species on the west coast of Bonaire.

3.2.2 Yellowtail sapper Ocyurus chrysurus and boga Haemulon vittatum

Apart from groupers some other fishery target species showed an decline in recent years. This trend was most apparent in two popular fishing targets, the yellowtail snapper *Ocyurus chrysurus* (Figure 7a) and the boga *Haemulon vittatum*, which declined by 80% (Figure 7b).

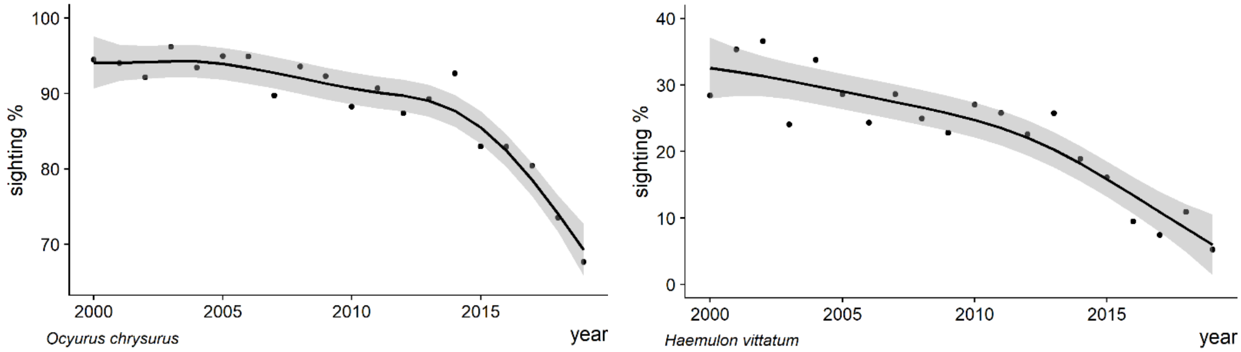

Figure 7. REEF sighting frequencies of (a) yellowtail snapper *Ocyurus chrysurus* and (b) boga *Haemulon vittatum* on the west coast of Bonaire.

3.3 Moray eels Muraenidae mass mortality events

From July to November 2008 divers reported a large number of dead moray eels at the west side of the Bonaire coast. Kozak (2008) suggested this was not the first time eel-die-offs occurred in Bonaire. Kozak summarised the mortality data and concluded that the mass die-off was possibly caused by the bacterium *Vibrio vulnificus*. The majority of moray eel species reported dead were the Spotted moray, *Gymnothorax moringa*, with a total of 57 mortalities, followed by the Green moray *G. funebris* (9) and the Viper moray *Enchelycore nigricans* (5) (Kozak, 2008). In September 2022 Bonaire park management reported a next mortality event in moray eels (Stinapa, 2022).

REEF moray eel sightings, especially of the two *Enchelycore* species, show remarkable fluctuations over time with a dip around 2010 (Figure 8). The trends in both *Enchelycore* species are almost identical, with a sharp decrease after 2009, the decline in *Gymnothorax* species was a year earlier.

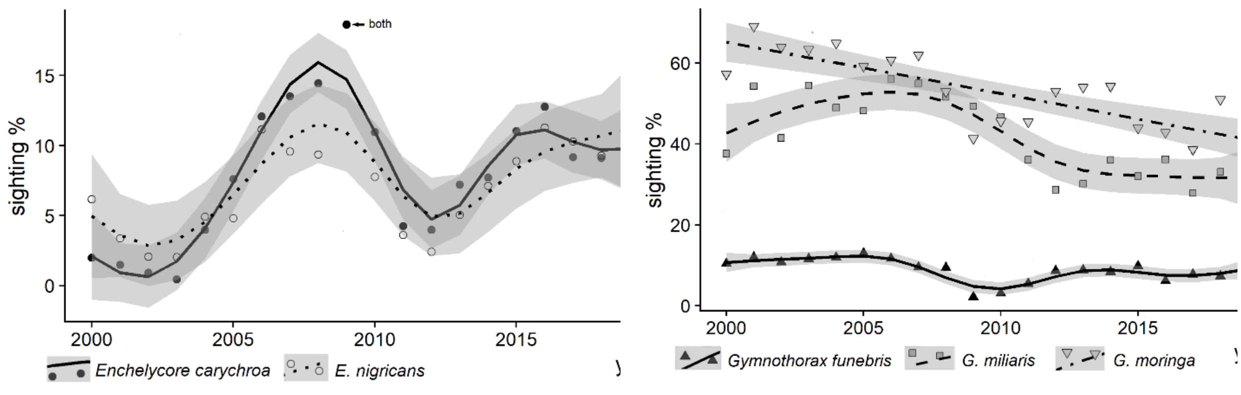

Figure 8. Muraenidae REEF sighting frequencies of two moray species on the west coast of Bonaire.

Remarkably the sightings of both *Enchelycore* species in 2009 were the highest of the whole studied period. A possible explanation could be the increased conspicuousness of the infected morays. Divers reported of morays, which are normally cryptic during daylight hours, being out in open areas and that they 'were attacking their own abdomen' (Kozak, 2008).

3.4 Invasion of the scorpionfish *Pterois* sp.

The invasive scorpionfishes *Pterois volitans and P. miles* rapidly spread over the Caribbean after 2000. Many authors assume a negative effect on local fish population (e.g. De León et al., 2013). However, after four years of study Hackerott et al. (2017) concluded that Invasive lionfish had no measurable effect on prey fish community structure across the Belizean Barrier Reef.

The invasive lionfish was first sighted in Bonaire in 2009 (De León et al., 2013). After it's initial success numbers dropped after 2014 (Figure 9). The hunting permission policy on this species appears successful to keep the numbers down. The steady decline of sightings of the congeneric spotted scorpionfish *Scorpaena plumieri* started well before 2009 (Figure 9), so there seems to be no relation. Looking for influences on Caribbean species favored by Lionfish (*Valdez-Moreno et al., 2012*) in the analysed REEF data (Supplementary file), there is an apparent decrease from 2009 to 2011 only in the belted cardinalfish *Apogon townsendi,* the clown wrasse *Halichoures maculipina* and the pallid goby *Coryphopterus eidolon* but not in many of their congeners, giving the impression of a moderate effect.

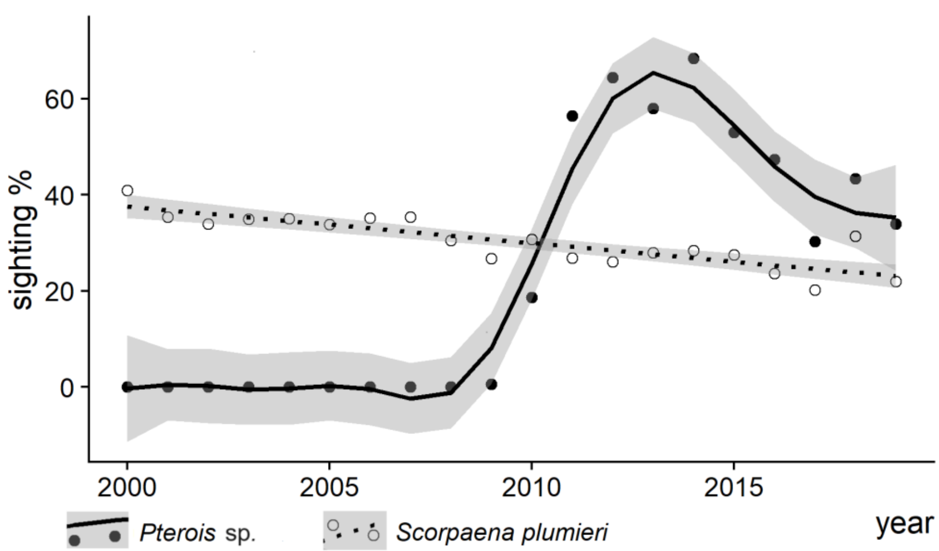

Figure 9. Scorpionidae REEF sighting frequencies of two Scorpionidae species on the west coast of Bonaire.

3.5 Mass recruitment of balloon fish *Diodon holocanthus*

In 1994 local divers with mor than 30 years experience noted a rare mass recruitment event of the balloon fish *Diodon holocanthus* (Debrot and Nagelkerken 1977). Visual censuses of juvenile balloon fish in 1994 and 1995 showed elevated juvenile balloon fish densities on the islands Curaçao, Aruba and Bonaire.

REEF sightings of balloon fish dropped from around 40% in 2000 to less then 10% in 2010, while those of the congeneric porcupinefish *D. hystrix* increased from 40% to 60%. (Figure 10). Tentatively the increase in the porcupinefish could be assigned to the declining competitive interaction, but continuation of this positive trend after 2010 discontinue this negative relation.

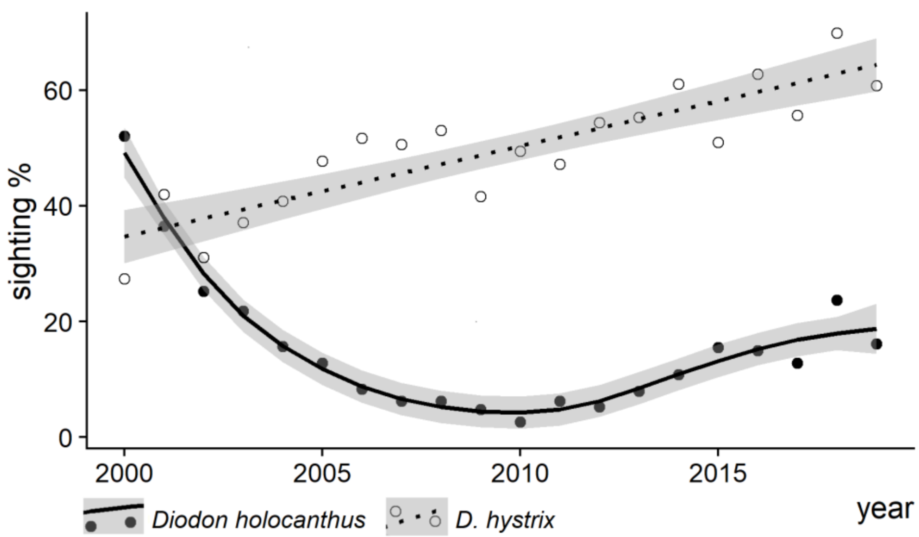

Figure 10. Diodontidae. REEF sighting frequencies of two porcupine fish species on the west coast of Bonaire.

3.6 Establishment of a Fish protected area in 2008

In 2018 the management of the National Marine Park Bonaire (Stinapa, 2018) concluded that several recent studies are showing a small increase in the density and biomass of small carnivorous fish in the fish protected areas. The same message noted that the protection is not fully effective, illegal poaching is still occurring in these areas.

Concern about overfishing (De Meijer and MacRae, 2006) led to two fishery protected areas (FPA's) of approximately 1km^2 and 0.2km^2 in Bonaire which were implemented in 2008. The two areas lie adjacent to the town Kralendijk. In our division of West Bonaire (see Methods) the FPA's cover about 30% of the urbanized Middle area of west Bonaire. In two areas next to the FPA's both fishing and snorkel fishing is allowed.

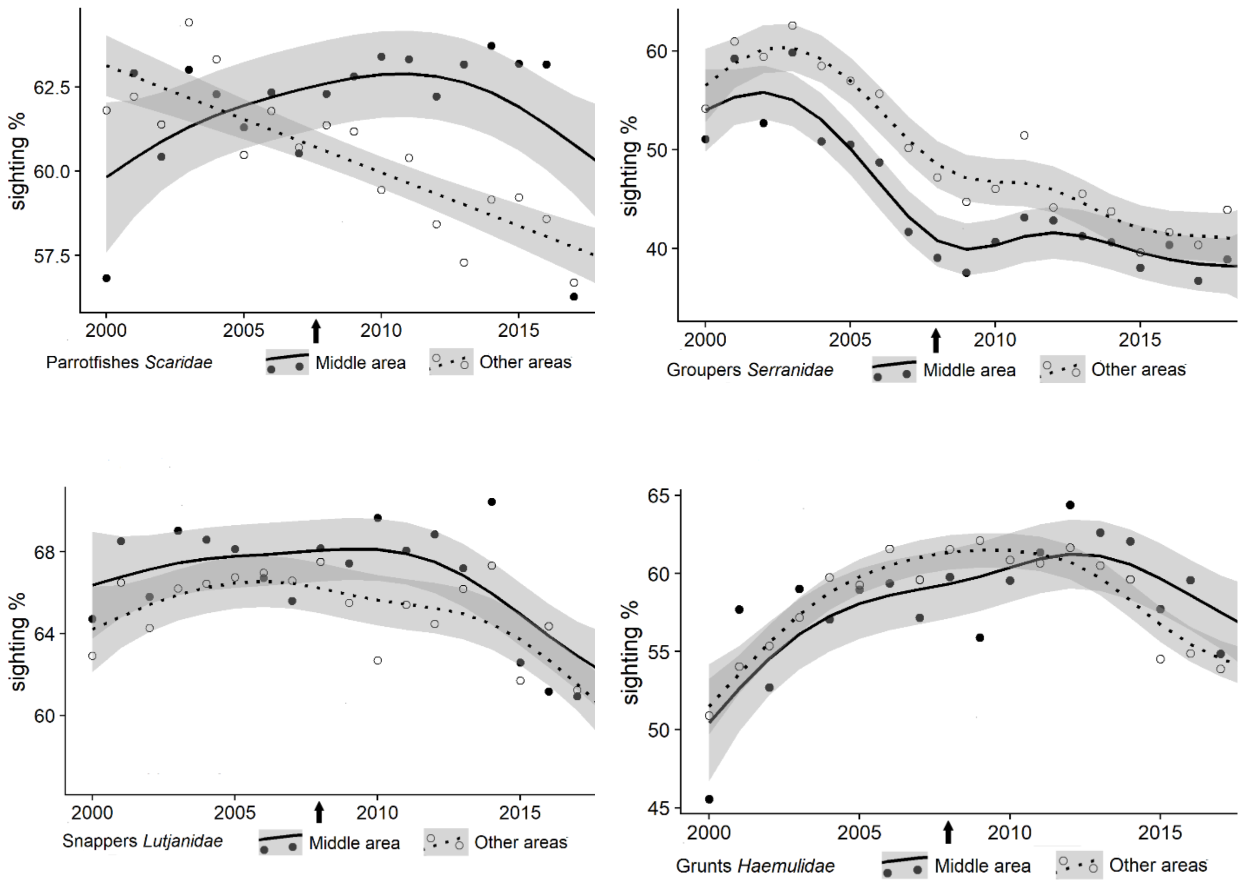

Figure 12. Mean reef sighting frequencies of (a) Scaridae (b) Serranidae (c) Lutjanidae and (d) Haemulidae in the Middle and in other areas (see Methods) of the west coast of Bonaire. The arrow indicates the year of establishment of two fish protected areas inside the middle area.

Inside the urbanized Middle area of Bonaire (see Methods) trends of parrotfish, groupers, snappers and grunts were analysed in- and outside the FPA's. The only positive effect after the implementation of the FPA's was the flattening of the negative trend in groupers inside the FPA's. Eventually the sighting frequencies inside the FPA ended at the same levels as outside (comparable to Figure 12). As De Bakker (2019) reported that several sites in, or directly adjacent to, the no-fishing zone harbour a considerable fish biomass relative to the rest of the reefs, a comparison is made between the Middle area and the three other areas on the west coast (Figure 12). Only in parrotfish, the sighting frequencies became clearly higher in the Middle area after 2008. For groupers the decrease in average sighting frequencies in the Middle area stopped at 40% after 2008 and stabilized at the same level as in the other areas. This could be an indication that the implementation of the FPA's had a positive effect on parrotfish and groupers.

3.7 May observed trends be ascribed to changes in coral cover?

Decrease in coral cover in reefs shallower than 20 m, as a result of bleaching and hurricanes, already started in at least the 1970's (Bak, Nieuwland & Meesters, 2005). In the studied period hurricanes Lenny (1999) and Omar (2008) in combination with several bleaching events led to the devastation of almost all local *Acropora cervicornis* fields (Bries, Debrot & Meyer, 2004; IUCN, 2011; Meesters, Bak & Van Duyl, 2020, Sommer et al., 2011). Disturbances by hurricane Omar and a serious bleaching event in 2010 resulted in a 22% coral decline (Steneck et al., 2019), followed by other events from 2014 to 2017 causing coral an unaccounted degree of mortality (Eckrich et al., 2021). In the period after 2014, De Bakker et al. (2017) observed indications of stabilization. Steneck et al. (2019) reported stabilisation in coral cover after 2011 and a recovery after 2015. In response, Meesters, Bak & Van Duyl (2020) discussed the methodology used by Steneck et al. could lead to false interpretations of coral cover trend data.

Few studies report a direct effect of hurricanes on reef fish populations, the fish are thought to reduce mortality by moving to deeper water during storms (Bacheler, 2019). Emphasis is laid to a prolonged effect as a result of habitat degradation. As hurricanes and bleaching are mutually enforcing in their damage to reefs (Bries, Debrot & Meyer, 2004) their separate effects on fish populations are hard to study. Following Steneck et al. (2019) this study concentrates on the changes after 2008-2010, a period wherein hurricane Omar in 2008 and the severe bleaching event in 2010 took place.

Twenty three of the 155 analysed species, among which 19 were bottom-living, had their lowest number in 2011 or 2012(Supplementary file part B). This result was most apparent in gobies Gobiidae, where almost all 8 non-cleaner species declined in sighting frequencies from 2003-2005 to 2011-2012 after which the sightings of most of them increased again. Yet in the case of these small species coral rubble may have hindered their visibility.

There were no clear general trends in the three facultative corallivorous butterflyfish species Chaetodontidae and the three spongivorous angelfishes Pomacanthidae in this study (Supplementary file). Also in the herbivorous fish species and the four carnivore families there are no specific trends that can be attributed to these 2008 and 2010 events (Figure 2, 3 and the Supplementary file).

3.8 Comparison with Bonaire reef fish trends found in other studies

Fish population trends on Bonaire are studied over many years, not only in long-term studies but also by shorter surveys. This gives the chance to compare present data with notes with notes on reef fish trends in these researches. In many cases the REEF data on abundances do not confirm with notes based on short terms (Table 2). These differences in results resemble the conclusion by Barrett et al. (2007) that one-off studies (in his case on the effectiveness of MPA's) led to other results than long-term studies.

Conclusions on fish population trends	**Research years**	**Based on years of study**	**Confirmed in this study**	**Paper or report**
Parrotfish biomass and population densities decline from 2003 to 2009		14	+	*Steneck et al.* (*2019*)
Parrotfish decline between 2003 and 2011	Various sources in literature	18	+	*De Graaf et al.* (*2016*)
The larger Parrotfish species (Rainbow, Blue and Midnight Parrotfish), were less abundant compared to 2014.	2014-2017	3	+	*De Bakker* (*2019*) p. 131
in 2017 parrotfish densities increased sharply'		14 (based on 2017 surveys)	-	*Steneck et al.* (*2019*)
More Parrotfish were seen in 2017, their mean biomass did not increase significantly.	2014-2017	3	-	*De Bakker* (*2019*) p. 131
Parrotfish and surgeonfish were less common in the "No Fishing" zone	2014	1	-	*De Graaf et al.* (*2016*)
Surgeonfish increased in abundance and biomass	2014-2017	3	-	*De Bakker* (*2019*) p.131
Little change in snappers in Bonaire since 2003	2003-2007	4	+	*Alvarado in Steneck et al.* (*2007*)
Increase of both Stegastes species between 2003 and 2007	2003-2007	4	-	*Steneck, Mumby & Arnold* (*2007*)
Bonaire's average carnivorous fish density showed no change from 2015 to 2017, there was a notable increase in biomass	2015-2017	2	- (decrease in density)	*Boenish* (*2017*).
The FPA sites showed no statistically significant difference in density from the control sites and did not differ significantly from the corresponding 2015 numbers	2015-2017	14 (after 2 years FPA's)	+ / - (- for parrotfish)	*Boenish* (*2017*).
The designation of no-fishing zones does appear to lead to slightly higher abundance and biomass of fish in general, including herbivorous fish.	2014-2017	2	+/ - (+ for parrotfish)	*De Bakker* (*2019*) p.131
Compared to 2014 there appears to be a slight increase in total fish abundance and biomass	2014-2017	2	-	*De Bakker* (*2019*) p.131
An increase in the abundance of commercial fish (groupers and snappers) was observed	2014-2017	2	-	*De Bakker* (*2019*) p.131

4 Discussion

Disturbances in coral reef caused by climate change and other anthropogenetic influences lead to a worldwide decline of coral reef fish diversity. This effect is less pronounced in the Caribbean than in high diversity areas like the Indo-Australia region (Pratchett et al., 2011). In Bonaire coral cover declined on both shallow as on deeper (>20m) reefs over the last decades and continued in the period of this study with a possible stabilization or recovery after 2014 (De Bakker et al., 2017; Steneck et al., 2019; Sommers et al., 2010). Sighting frequencies of reef fish in this period showed differing trends, confirming the suggestion by Barrett et al. (2007) that reef fish responses to changes are species-specific, slow and complex. Overall, decreases prevailed over increases. Negative trends were strong in large bodied species, sighting frequencies of three large parrotfish species and several mid-sized groupers reached low levels, but it has to be taken in account that abundance of groupers is higher at the exposed east coast of the island (De Graaf et al., 2016). It is unclear if larval import will compensate for the loss in reproductive capacity. Prevailing wind and currents in the area are westwards, indicating that he closest source of larval import is the remote Las Aves archipelago at 60 km and the larger, protected, Los Roques archipelago at 150km. Fish densities in both archipelagos are relatively high for the Caribbean (Debrot, et al., 2007; Debrot, Yranzo & Arocha, 2019). However, the distance of these areas from Bonaire suggests a weak larval connection (see introduction). Also the small size of the Los Aves archipelago (3.35 km^2) will lower the level of larval import. This implicates a high level of self recruitment of reef fish in Bonaire, increasing the chance of local extinction.

A clear exception is the mass recruitment of balloonfish *D. holocanthus* in 1994 (Debrot and Nagelkerken, 1997) of which the authors indicated that the recruitment event had spanned a linear distance of at least 200 km and possibly was a Caribbean-wide phenomenon (Debrot and Nagelkerken, 1997). The authors suggest that the species primarily recruits in mass events, a recruitment strategy not uncommon in Tetraodontiformes (Piedra-Castro and Araya-Vargas, *2018*). Support for this suggested family trait can be found in the sharp extreme high densities of juvenile sharpnose puffer *Canthigaster rostrata* in Bonaire in 2023, which reached to 'hundreds per dive' (Godfried van Moorsel, 2023, pers. comm.). The lifespan of *D. holocanthus* in the wild is unknown but aquarium owners inform on internet that they can live at least 10 to 15 years in captivity (Shay, 2022). The convex downward curve till 2010 matches what would be expected after the mass recruitment event of 1994. The observed decline from 2000 to 2010 till nearly zero can be explained as the aftermath of the mass recruitment in 1994 and suggests dependence of the balloon fish population on mass recruitments.

Another factor seldom discussed in literature is the effect of mass mortality on reef fish populations. The 2008 event led to strong fluctuations in the sighting frequencies of several moray eel species. Kozak (2008) suggested that this as not he first time in Bonaire. This, and a next mass mortality event in moray eels in 2022 (Stinapa, 2022), suggests that these events are repetitive. Following this line of reasoning the ‘2003 dip’ in the *Enchelycore* species could be caused by an earlier outbreak. Mass mortality in fish caused by pathogens has repeatedly been ascribed to seawater warming events, possibly as a result of a suppressed immune response to pathogens (Genin et al., 2020). The authors found that, instead of the maximum temperature and duration of the warming event, the rate of warming at the onset was the likely trigger of mass mortality of coral reef fishes in the Red Sea. This was also the case in the 2008 and 2022 moray eel mortality events, which started at the onset of a NOAA coral reef warning period for Aruba, Curaçao and Bonaire (NOAA, 2023). Increase in warming events carries the risk of more frequent mass mortalities.

It is concluded that volunteer sighting data, when used with caution, prove to be a valuable source for long-term studies of reef fish populations. In this case the data show that the many threats to the reefs on Bonaire had a moderate impact on many fish species, with the exception of large bodied species. The fishery ban on parrotfish works well for mid-sized species, but population sizes of the three larger species is reason to concern. The only plausible explanation for the decimation of the mid-sized groupers is the high fishing pressure on this group. De Graaf et al calculated that yearly c.a. 13t of reef fish where harvested from the west coast of Bonaire. The yield (2.1 t/km2/year) was modest, ca. 5% of the standing stock, but differed significantly between fish families. In grouper species combined this percentage was 18%, indicating a high fishing pressure. There is an increased risk that the mid-sized groupers will suffer the same fate as the larger groupers of (*Roberts, 2007*) and there already signs of sequential overfishing in other fish families. This mechanism probably explains the strong recent decline of the yellowtail snapper *O. chrysurus* and the boga *H. vittatum.* Effective protection of reef fish in Bonaire would not only be beneficial to the biodiversity of the reefs and the attractiveness to dive tourists, but eventually also to artisanal fishery in Bonaire.

5 Conclusions

Abundance responses of reef fish populations to environmental changes on the relatively reproductive isolated west coast of Bonaire were studied using volunteer sighting observation data. The reaction of populations to changes in coral cover were specific and complex. Temporal variations in abundances at family level could not be ascribed to their trophic preferences, in many cases temporal trends differed strongly within families. Exceptions to this lack of conformity at higher taxonomic levels were the decrease in bottom-living gobies in a period of extreme coral bleaching and hurricane events, and the strong variations in population size of moray eels as a result of repetitive infections by pathogens.

Evaluation of long-term changes shows that large bodied species in groupers and parrotfish declined in the studied period. In case of groupers the decrease could only be ascribed to the high fishing pressure described by other authors. In addition there are indications that their depletion leads to successive overfishing in species of other families.

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Supplementary material

Supplementary material is provided in Reef_fish-Bonaire_2000-2019_Supplement.pdf.

References

Almany, G.R., Planes, S., Thorrold, S.R., Berumen, M.L., Bode, M., Saenz-Agudelo, P., Bonin, M.C., Frisch A.J., Harrison H.B., Messmer V., Nanninga G.B., Priest M.A., Srinivasan M., Sinclair-Taylor T., Williamson, D.H., Jones, G.P., 2017. Larval fish dispersal in a coral-reef seascape. *Nature Ecology & Evolution* 1(6):0148. DOI 10.1038/s41559-017-0148

Alvarado, N.A., Mumby, P., Steneck, R., 2017. Trends in distribution and abundance of carnivorous and herbivorous reef fish populations on Bonaire. I*n*: Steneck, RS, Wilson, M,(Eds.):Status and Trends of Bonaire's Reefs in 2017: Clear signs of resilience:14-22. https://www.dcbd.nl/sites/default/files/documents/Steneck_Bonaire-Report_2007.pdf (Accessed: 8-11-2023)

Bacheler, N.M., Shertzer, K.W., Cheshire, R., MacMahan J.H., 2019. Tropical storms influence the movement behavior of a demersal oceanic fish species. *Scientific Reports* 9:1481. DOI 10.1038/s41598-018-37527-1

Bak, R.P.M., Nieuwland G., Meesters E.H., 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs* 24: 475–479. DOI 10.1007/s00338-005-0009-1

Barrett, N.S., Edgar, G.J., Buxton, C., Haddon, M., 2007. Changes in Fish Assemblages Following 10 Years of Protection in Tasmanian Marine Protected Areas. *Journal of Experimental Marine Biology and Ecology* 345(2):141-157. DOI 10.1016/j.jembe.2007.02.007

Beltrán, D.M., Schizas N.V., Appeldoorn R.S., Prada C., 2017. Effective dispersal of Caribbean reef fish is smaller than current spacing among marine protected areas. *Scientific Reports* 7: 4689. DOI 10.1038/s41598-017-04849-5

Bennema, F.P., Van Moorsel, G.W.N.M., 2022. Reef fishes: 68-75. In: Hoeksema B.W.(ed) 2022. Marine biodiversity of Bonaire: a baseline survey (2nd edition). Naturalis Biodiversity Center, Leiden, and ANEMOON Foundation, Bennebroek. 78 pp. https://research.rug.nl/files/239819953/90526600_8048951_MARINE_BIODIVERSITY_OF_BONAIRE_1_6.pdf (Accessed: 8-11-2023)

Boenish R., Richie M., 2017. Patterns of predatory fish biomass and density within and around Fish Protection Areas of the Bonaire Marine. *In*: Steneck, RS, Wilson, M,(Eds.):Status and Trends of Bonaire's Reefs in 2017: Clear signs of resilience:52-63. https://www.dcbd.nl/sites/default/files/documents/Steneck_Bonaire-Report_2007.pdf (Accessed: 8-11-2023)

Bries, J.M., Debrot A.O., Meyer, D.L., 2004. Damage to the leeward reefs of Curacao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. *Coral Reefs* 23:297–307. DOI 10.1007/s00338-004-0379-9

Chollett I., Robertson D.R., 2020. Comparing biodiversity databases: Greater Caribbean reef fishes as a case study. *Fish and Fisheries* 21(6):1195-1212. DOI 10.1111/faf.12497

Cowen, R.K., Pari, C.B., Srinivasan, A., 2006. Scaling of Connectivity in Marine Populations. *Science* 311:522-527. DOI 10.1126/science.1122039

De Bakker, D.M., Meesters, E.H., Bak, R.P.M., Nieuwland, G., Van Duyl, F.C., 2017. Long-term Shifts in Coral Communities On Shallow to Deep Reef Slopes of Curaçao and Bonaire: Are There Any Winners? *Frontiers in Marine Science* 3: 247. DOI 10.3389/fmars.2016.00247

De Bakker, D.M., 2019. 40 years of change on the coral reefs of Curaçao and Bonaire. PhD Thesis. Wageningen University. Wageningen, Netherlands. 191pp. DOI 10.18174/468014

Debrot A.O., Nagelkerken I., 1997. A rare mass recruitment of the balloonfish(*Diodon holocanthus* L.) in the Leeward Dutch Antilles, 1994. *Caribbean Journal of Science* 33(3-4):284-286.

Debrot, A.O., Yranzo, A., Arocha, D., 2019. Los Roques and las Aves Archipelagos, Venezuela : A marine ecological and conservation reconnaissance of two little-known Southeastern Caribbean oceanic Archipelagos. *Atoll Research Bulletin* 622. Smithsonian Institution Scholarly Press. 27pp. https://edepot.wur.nl/477600

Debrot, D., Choat J.H., Posada J.M., and Robertson D.R., 2007. High Densities of the Large Bodied Parrotfishes(Scaridae) at Two Venezuelan Offshore Reefs: Comparison Among Four Localities in the Caribbean. Proceedings of the 60th Gulf and Caribbean Fisheries Institute November 5 - 9, 2007 Punta Cana, Dominican Republic: 335-338. https://www.semanticscholar.org/paper/High-densities-of-the-large-bodied-parrotfishes-at-Debrot/2e5c695ce15aa694df87e814de296e8650ebb693 (Accessed: 30-3-2023)

De Graaf M., Houtepen E., Tichelaar E., Miller D.C.M., Brunel T., Nagelkerke L.A.J., 2016. Status and trends reef fish and coastal fisheries Bonaire(Caribbean Netherlands):report card 2014–2015. Wageningen: Wageningen Marine Research report C087/16. 70 pp. https://edepot.wur.nl/424549

De León, R., Vane, K., Bertuol, P., Chamberland, V.C., Simal, F., Imms, E., Vermeij, M.J.A., 2013. Effectiveness of lionfish removal efforts in the southern Caribbean. *Endangered Species Research* 22(2):175-182. DOI 10.3354/esr00542

De Meijer, K., MacRae, D, 2006. Bonaire National Marine Park management plan 2006. Stinapa. 107pp. https://www.dcbd.nl/sites/default/files/documents/Stinapa%282006%29_BonaireNationalMarinePark2006ManagementPlan.pdf (Accessed: 8-11-2023)

Eckrich, C., Francisca, R.L.,Rempel, H.S, Ren, E., 2021. Coral Bleaching in the Bonaire National Marine Park 2016-2020. Stinapa Natural Parks Foundation. Bonaire. 14pp. https://www.dcbd.nl/sites/default/files/documents/EckrichEtAl%282021%29_coralBleaching2016to2020_v2.pdf (Accessed: 8-11-2023)

Fishbase. https://www.fishbase.se (Accessed: 8-11-2023)

Genin, A., Levy, L., Sharon, G., Raitsos, D. E., Diamant, A., 2020. Rapid onsets of warming events trigger mass mortality of coral reef fish. *Proceedings of the National Academy of Sciences of the United States of America* 117(41):25378-25385. DOI 10.1073/pnas.2009748117

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews of the Cambridge Philosophical Society* 90(4):1215-1247. DOI 10.1111/brv.12155

Hackerott, S., Valdivia, A., Cox C.E., Silbiger, N.J., Bruno, J.F., 2017. Invasive lionfish had no measurable effect on prey fish community structure across the Belizean Barrier Reef. *PeerJ* 5:e3270. DOI 10.7717/peerj.3270

Hawkins, J.P., Roberts, C.M., Van't Hof, T., De Meyer, K., Tratalos, J., Aldam, C., 1999. Effects of Recreational Scuba Diving on Caribbean Coral and Fish Communities. *Conservation Biology* 13(4):888-897. DOI 10.1046/j.1523–1739.1999.97447.x

Hawkins, J.P., Roberts C.M.. 2004. Effects of Artisanal Fishing on Caribbean Coral Reefs. *Conservation Biology* 18(1):215-226. DOI 10.1111/j.1523–1739.2004.00328.x

Hoetjes, P., Kong, A.M., Juman, R., Miller, A., Miller, M., De Meyer, K., Smith,A., 2002. Status of coral reefs in the Eastern Caribbean: the OECS, Trinidad and Tobago, Barbados, and the Netherlands Antilles. In Status of coral reefs of the world: 2002. Wilkinson(ed.):325-342. https://www.icriforum.org/wp-content/uploads/2019/12/GCRMN_2002.pdf (Accessed: 8-11-2023)

Hughes T.P., 1994. Catastrophes, phase shifts, and large–scale degradation of a Caribbean coral reef. *Science* 265(5178):1547-1551. DOI 10.1126/science.265.5178.1547

Infobonaire, 2023. https://infobonaire.com/scuba-diving/dive-site-map/ (Accessed: 8-11-2023)

IUCN, 2011. Coral Reef Resilience Assessment of the Bonaire National Marine Park, Netherlands Antilles. Gland, Switzerland: IUCN. 51pp. https://www.dcbd.nl/sites/default/files/documents/IUCN%25202011%2520Bonaire_coral_reef_resilience_report.pdf(Accessed: 8-11-2023)

Jackson J., Donovan M., Cramer K., Lam V., 2014. Status and trends of Caribbean coral reefs: 1970–2012. Washington: Global Coral Reef Monitoring Network. 304 pp. https://portals.iucn.org/library/efiles/documents/2014-019.pdf (Accessed: 8-11-2023)

Kozak, K., 2008. Physis: Journal of Marine Science IV 19: 7-12 from CIEE Bonaire. https://www.dcbd.nl/sites/default/files/documents/Physis%20Vol%204.pdf (Accessed: 8-11-2023)

Meesters, E.H., Bak, R.P.M., Van Duyl, F.C., 2020. Commentary: Managing Recovery Resilience in Coral Reefs Against Climate-Induced Bleaching and Hurricanes: A 15 Year Case Study From Bonaire, Dutch Caribbean Frontiers in Marine Science 7:346. DOI 10.3389/fmars.2020.00346

Mellin, C., Huchery, C., Caley, M.J., Meekan, M.G., Bradshaw, C.J.A., 2010. Reef size and isolation determine the temporal stability of coral reef fish populations. *Ecology* 91(11):3138–3145. DOI 10.1890/10-0267.1

Nenadovic, M., 2007. The impact of traditional fishing practices on the abundance of major herbivorous fish species in Bonaire, Netherlands Antilles. In: Steneck, R, Mumby, P and Arnold, S(Eds.):A report on the status of the coral reefs of Bonaire in 2007 with results from monitoring 2003-2007:71-80. University of Maine.

NOAA, 2023. 5 km Regional Virtual Stations Latest Stress Level, Data, and Graphs. https://coralreefwatch.noaa.gov/product/vs/data.php (Accessed: 8-11-2023) .

Pattengill–Semmens, C.V., 2002. The reef fish assemblage of Bonaire Marine Park: an analysis of REEF fish survey data. Proceedings 53rd Gulf and Caribbean Fish Institute 53:606–622.

Piedra-Castro, L., Araya-Vargas, A., 2018. Mass mortality of *Canthigaster rostrata*(Tetraodontiformes: Tetraodontidae) on the southern Costa Rican Caribbean coast. *Journal of Marine and Coastal Science* 10(1):31-37. DOI 10.15359/revmar.10-1.2

Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V., Graham, N.A.J, 2011. Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity* 3:424-452. DOI 10.3390/d3030424

Puebla, O., Bermingham, E., McMillan, W.O, 2012. On the spatial scale of dispersal in coral reef fishes. *Molecular Ecology* 21(23):5675-5688. DOI 10.1111/j.1365-294X.2012.05734.x

R Core Team (2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (Accessed: 8-11-2023)

REEF Environmental Education Foundation, 2023. Reef Environmental Education Foundation Volunteer Fish Survey Project Database. World Wide Web electronic publication. www.REEF.org (Accessed 31-3-2023).

Roberts C.M., 2007. The unnatural history of the sea. Washington. Covelo, Island Press, London.

Scheffers, A., Scheffers S., 2006. Documentation of the Impact of Hurricane Ivan on the Coastline of Bonaire(Netherlands Antilles). *Journal of Coastal Research* 226:1437-1450 DOI 10.2112/05-0535.1

Shay, K., 2022. What You Should Know Before Getting a Porcupine Puffer. https://pethelpful.com/fish-aquariums/porcupine_puffer_basics (Accessed: 8-11-2023) .

Sommer, B., Harrison, P.L., Brooks, L.,Scheffers, S.R., 2011. Coral community decline at Bonaire, Southern Caribbean. *Bulletin of Marine Science* 87(3):541-565. DOI 10.5343/bms.2010.1046

Steneck, R., Mumby, P., Arnold, S, 2007. A report on the status of the coral reefs of Bonaire in 2007 with results from monitoring 2003-2007. University of Maine. 94pp. https://www.dcbd.nl/sites/default/files/documents/Steneck_Bonaire-Report_2007.pdf (Accessed: 8-11-2023)

Steneck, R.S., Wilson, M., 2017. Status and Trends of Bonaire's Reefs in 2017: Clear signs of resilience. University of Main. 118pp. https://www.dcbd.nl/sites/default/files/documents/2017_-Steneck-Wilson_Status-and-Trends-of-Bonaire%E2%80%99s-Reefs-in-2017-.pdf (Accessed: 8-11-2023)

Steneck, R.S., Arnold, S.N., Boenish, R., De León, R., Mumby, P.J., Rasher, D.B., Wilson, M.W.., 2019. Managing recovery resilience in coral reefs against climate induced bleaching and Hurricanes: a 15 year case study from Bonaire, Dutch Caribbean. *Frontiers in Marine Science* 6:265. DOI 10.3389/fmars.2019.00265

Stinapa, 2018. No Fishing zones.(Facebook).

https://www.facebook.com/Bonaire.STINAPA/posts/no-fishing-zonesbonaire-has-two-no-fishing-areas-that-were-established-in-2008-o/2129032907113934/ (Accessed: 8-11-2023)

Stinapa, 2022. Bonaire National Park Sightings. Facebook. https://www.facebook.com/Bonaire.STINAPA/posts/pfbid02Z3bpV1WBfdXuRL6Ju5mt4EEhzdh2o53AmDy2VvubMftrMTE4x8tyWYyXaWcJj6kul (Accessed: 8-11-2023)

Valdez-Moreno, M., Quintal-Lizama, C., Gómez-Lozano, R., García-Rivas M.d.C., 2012. Monitoring an Alien Invasion: DNA Barcoding and the Identification of Lionfish and Their Prey on Coral Reefs of the Mexican Caribbean. *PLoS ONE* 7(6):e36636. DOI 10.1371/journal.pone.0036636

Van der Geest, M., Meesters, E., Mücher, S., 2020. Impact of terrestrial erosion on coral reef health at Bonaire: a plea for nature-inclusive “watershed-to-reef” based coastal management. Wageningen University & Research report C055/20. 32pp. https://edepot.wur.nl/524688

Wood, S.N., 2017. Generalized Additive Models. An Introduction with R, Second Edition. New York: Chapman and Hall/CRC. DOI 10.1201/9781315370279