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INVASION NOTE

# The levelling-off and recent rapid decline in population density of the highly prolific invasive lionfish on the Saba Bank, Eastern Caribbean

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**Abstract** Since its introduction in the Western Atlantic more than 30 years ago, the lionfish (*Pterois volitans/miles* complex) has spread throughout the Gulf of Mexico, the Caribbean and the Western Tropical Atlantic, with massive and unprecedented ecological impacts. This invasion is among the most studied marine fish invasions but very little is still really known about the population dynamics of the species and the factors ultimately governing its abundance. The species was first documented on the Saba Bank in 2010 and rapidly increased in abundance till the end of 2014. In this note we document its rise and subsequent decline in density and thereby describe the species' third apparent local population boom-bust event for the Greater Caribbean. We also document gradual increases in the mean size of lionfish of the Eastern Caribbean Saba Bank that coincided with the increase and subsequent decline in abundance. Contrary to the previously documented epizootic disease outbreak associated with the population crash observed in the Gulf of Mexico we were unable to find any signs of the occurrence of epizootic disease. We suggest that the population decline on the Saba Bank might have been due to non-local causes. Boom-bust dynamics are often witnessed in biological invasions and have critical implications for both understanding and managing invasive species. While the underlying cause for the boom-bust event we document remains unknown, our work suggests that in the region, ecological feedback mechanisms are gradually developing that can help level-off deleterious population excesses of this invasive species.

**Keywords** Marine fish invasion · Boom-bust

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## Introduction

Non-native invasive species are a major threat to marine biodiversity worldwide, including that of the marine protected areas of the Dutch Caribbean where 27 exotic and cryptogenic marine species have been previously recorded for one or more islands of the Dutch Caribbean (Debrot et al. 2011). Two models of invasion kinetics have been proposed (Boudouresque and Verlaque 2012). These are the "natural fluctuation model" whereby an invading species will gradually increase and stabilize at a "plateau" in density and the "boom-bust model", whereby an invading species will increase rapidly after invasion ("boom") to later decline in abundance and density to a much lower ("bust") level. Especially in the boom-bust model, "settling in" after the initial expansion phase may occur with population crashes due to any number of ecosystem feed-backs such as evolutionary limits (Lankau et al. 2009), low genetic diversity of the founding population (Boudouresque and Verlaque 2012), competition (Moore et al. 2012), habitat limitations (Larson et al. 2019), or pathogens (LeBrun et al. 2022).

The Indo-Pacific lionfish (*Pterois volitans/miles* complex) is a highly prolific and invasive species that has become well-established in the Greater Caribbean marine environment. It has been documented to prey on large numbers of juvenile native Caribbean fishes and crustaceans and is expected to have serious detrimental effects on native coral reef fish populations, even affecting or endangering endemic undescribed fish faunas (Tornabene and Baldwin 2017). Since their first release into the wild in Florida likely dating from 1985, the species has spread throughout the Caribbean and is now establishing itself in tropical Brazil (Luiz et al. 2021). The lionfish is capable of rapid population growth after establishment and is one of the most successful and most-studied marine fish invasions documented so far (Côté and Smith 2018). While apparent population "levelling-off" was first witnessed for the lionfish in the Bahamas in 2012 (Benkwitt et al. 2017), population crashes of up to 75% have been observed in the Gulf of Mexico associated with a high rate of incidence of an ulcerative skin lesion (Harris et al. 2020). Similar population crashes have not yet been reported for the rest of the Caribbean. On the Saba Bank in the Eastern Caribbean, lionfish were not reported from commercial snapper and lobster trap catches prior to 2008 (Toller and Lundvall 2008, Toller et al. 2010; Williams et al. 2010), but in or just before 2010, when the species was first were first reported as bycatch in the fisheries (Debrot et al. 2011). In this paper we report the rapid rise and subsequent population decline of lionfish for the Saba Bank as documented on the basis of lionfish Catch per Unit of Effort (CPUE) in the bank's commercial trap fisheries and present limited data on size-frequency developments and skin lesion infection rates. In doing so we present some rare new evidence of the species showing signs of ecological "settling-in" in the Caribbean Sea, after three decades of purely expanding populations.

## Methods and materials

### The Saba Bank

In this study we assessed lionfish on the Saba Bank, a large 2200 km$^2$ submarine plateau southwest of the island of Saba. It is located 3–5 km southwest of Saba and 25 km west of St. Eustatius in the Dutch Caribbean (Fig. 1). Water depth varies between 20 and 50 m for most of the bank, except for an area of about 230 km$^2$ along its eastern margin, which lies at depths of 10–20 m (Toller et al. 2010). The surrounding sea floor goes to depths of about 1000 m. Most coral development is found in a narrow band of 55 km along the eastern and south-eastern edges of the bank. The bank lies fully within the Dutch Kingdom's Caribbean Exclusive Economic Zone waters. In recent years, it has gained international recognition as an area of exceptional biodiversity value and been accorded increasingly higher and more extensive conservation status. For instance, in 2012 it was accorded "Particularly Sensitive Sea Area" status by the International Maritime Organization which forbids tanker traffic, while in 2015 it became part of the "Yarari Marine Mammal and Shark Sanctuary", emphasizing its value to both endangered cetaceans and sharks (Debrot et al. 2017).

### Saba Bank fisheries

In recent years the fleet size of Saba involved in fishing on the bank has generally fluctuated between eight and ten Maine lobster boats, of 9–12 m length, operating all year round. Basic data on catch, effort, species composition and length frequency of the fishery were collected weekly by Saba Bank Management Unit as described by de Graaf et al. (2017) and Brunel et al. (2021). The West-Indian spiny lobster, *Panulirus argus*, is the most important targeted species and is fished with lobster traps (West-Indian arrowhead traps) up to depths of 45 m. This fishery began during the 1980s with the advent of mass-tourism on St. Maarten. The second-most important

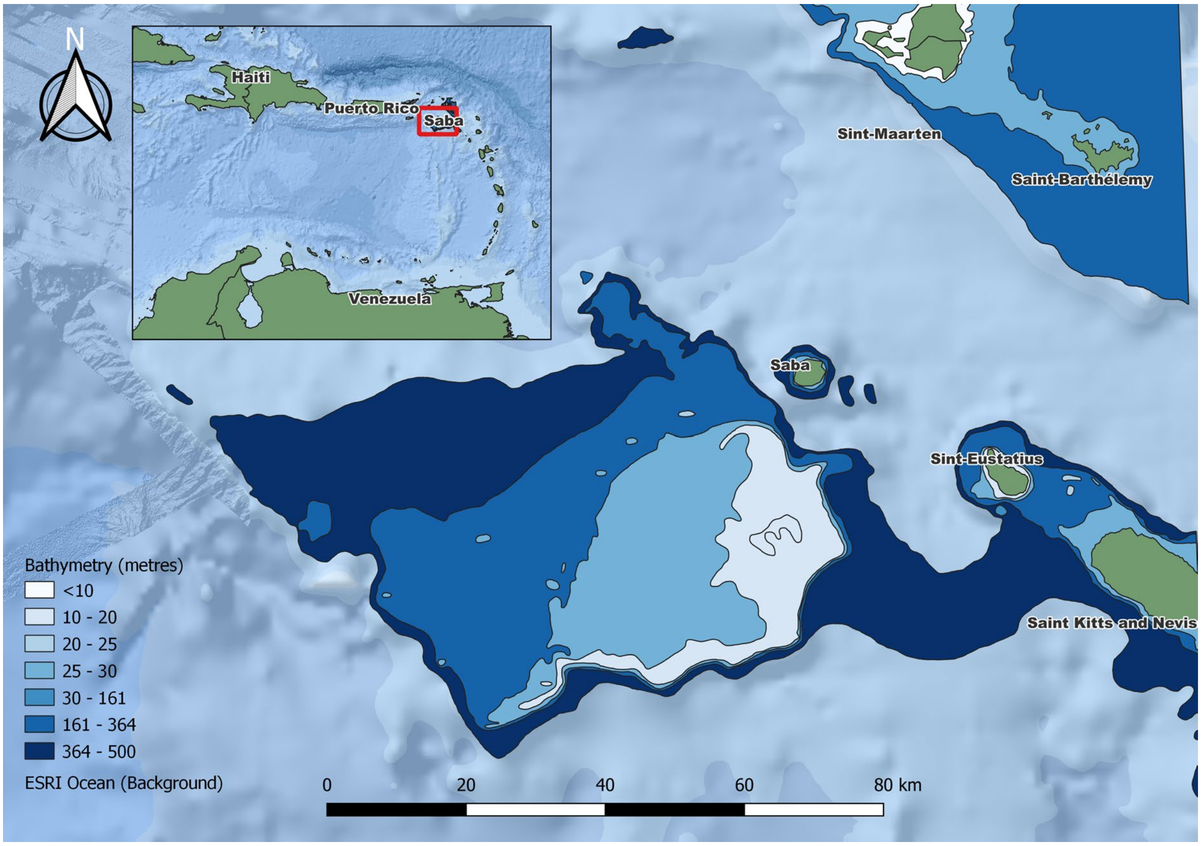


**Fig. 1** Map of the Western Tropical Atlantic showing the location of the Saba Bank in the Eastern Caribbean

fishery is the "redfish" (snapper) fishery which is also largely conducted using the same traps but at deeper depths (de Graaf et al. 2017). These are typically deployed at depths of 50–250 m and catch mainly silk snapper, *Lutjanus vivanus*, followed by blackfin snapper, *Lutjanus buccanella,* and vermillion snapper, *Rhomboplites aurorubens* (Brunel et al. 2021). These are the only two fisheries taking lionfish on the bank as a limited part of the bycatch. The traps are made of coated wire mesh, with mesh sizes of $1\times2$ to $2\times2$ inch (2.5–5 cm). Fish and lobster traps differ in funnel size, with the funnel of fish traps being narrower and longer. Salted cow hides ($20\times20$ cm), are used as bait and are attached inside the traps with plastic-coated wires (Toller and Lundvall 2008).

## Fisheries data

Since 2012, the fisheries on Saba Bank are monitored through a survey-based monitoring program conducted from the sole fishing port of Saba Island (see Brunel et al 2021 for a full description). Part of this program consists of conducting interviews with the fishers when they return from a fishing trip. The "logbooks" that are filled, contain information about the fishing operations (type and number of gear, location, duration) and catches per trips for a number of species, including lionfish. Biological sampling is also conducted, both on the landings (at the harbour) and on the catches (onboard) to establish catch species composition and length composition, including the lionfish when present.

The logbook surveys and biological sampling are conducted according to an opportunistic strategy—rather than a pre-established sampling schedule—and they are greatly dependent on the fishers availability and willingness to collaborate. As a result, the coverage of both sampling activities can vary greatly between boats and months (on average, a total of 60 trips per year are covered by the biological sampling activity, and logbooks cover 410 trips per year). Since 2015, lionfish have had commercial value in Saba and, notwithstanding their small contribution to the bycatch of the lobster and snapper fisheries, they are landed and sold locally for consumption as an environmental specialty. Before 2015, nearly all lionfish caught in any type of trap were only killed and discarded.

### Abundance trends

The annual mean of the catches of lionfish per fishing trip was calculated from the logbooks data for the two main gears (lobster traps and redfish traps) to investigate the existence of temporal changes in lionfish abundance. A non-parametric Mann–Kendall test was then applied to the annual means to test for the existence of monotonous temporal trends.

### Length-frequency analysis

Length measurement data on lionfish were less numerous than the logbook data, and there were several years for which too few measurements were available to describe the length-frequency distribution of the catches (no lionfish measured between 2013 and 2015, and less than 15 in 2016 and 2020). The analysis of the length-frequency data therefore only included the years with higher numbers of lionfish measured (between 29 and 71 fish measured annually for the years 2012, 2017, 2018, 2019 and 2021). Lionfish length was modelled as function of the year, used as categorical variable and using a GLM with a Gamma error distribution. A Turkey's "Honest Significant Difference" test was then applied to conduct pairwise comparisons of the differences in lionfish length between pairs of years.

### Fisheries-independent depth trends in population density and size-frequency distribution

Population size-frequency and density comparisons for different depths using fisheries-dependent catch data is complicated for the Saba Bank based on the fact that lobster traps and snapper traps differ greatly in shape and selectivity and are deployed at greatly different depths, with little overlap. Therefore, in addition to the data obtained from port sampling of lionfish landings we studied population density and size-distribution in relation to depth on the bank based on directed fisheries-independent experimental lionfish trapping, conducted between June and November 2018. Trapping was done using traditional arrowhead fish traps and modified arrowhead traps with "escape" funnels (in an attempt to reduce by catch of other fish species), here termed "modified arrowhead traps" (Supplement 1). Both traps used had a grid size of 2.5 × 2.5 cm. A total of 183 trap lifts were done from depths varying between 19 and 142 m, using a soaking time of 7 days. There were no significant differences in catch rate or size-structure between the arrowhead and modified arrowhead trap types, and therefore the data from both types of traps was pooled for analysis.

### Skin ulcer incidence

Up to 2020, no notice was made of any skin lesions on any of the (217) Saba Bank lionfish measured but in 2021, a focussed examination was conducted. This yielded a sample of 47 fish. We compared the incidence of skin disease of our sample to the values established for the Gulf of Mexico using a standard test for the difference between two proportions for large sample sizes from binomial populations whereby a normal distribution can be assumed (Walpole and Meyers 1978). As the sample sizes for comparison with our limited data were very large, we tested for the difference in proportions assuming a tenfold smaller reference sample size than Harris et al. (2020) had actually obtained (August 2017, n = 988; December 2017, n = 1228).

## Results

### Lionfish population trends

For the period covered by the logbook data, the annual mean catch of lionfish per trip showed a short increasing phase follow by a decrease for both gears (Fig. 2). Mean catch per trip increased from 2012 to 2014 in the deep-water redfish traps and to 2015 in the shallow-water lobster traps (although the trend was not significant, Man–Kendal test, $p = 0.30$ for 2012–2014 and $p = 0.09$ for 2012–2015 for redfish and lobster traps respectively). After this increase, the mean annual catch

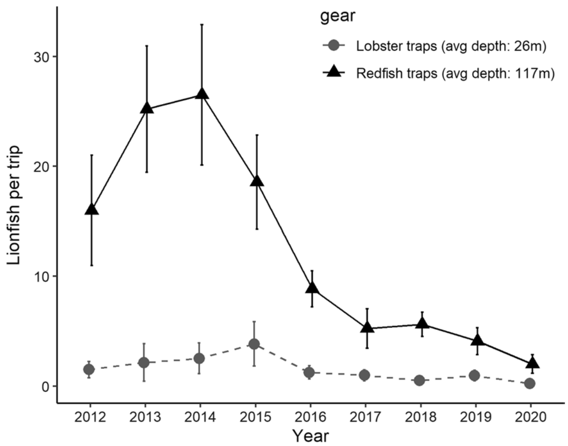


**Fig. 2** Trends in the abundance (annual mean catch per trip) of lionfish in the deep-water redfish traps and shallow-water lobster traps on the Saba Bank. Error bars indicate 95%

per trip declined abruptly (Man–Kendal test, $p < 0.001$ and $p = 0.02$) to reach low levels in the most recent years, especially in the deep-water redfish traps. Catches of lionfish per trip in the redfish traps were 8.4 time higher (average of the annual ratios in mean catches per trip) than in the lobster traps.

## Lionfish length structure and depth distribution

The Gamma GLM indicated that there were significant differences in lionfish length between the years ($p < 0.001$) and the Turkey's HSD test done on the model coefficients showed that the year 2012 (27.4 cm on average) was different from the subsequent years (annual mean between 31.3 and 33.5 cm for the years 2017, 2018, 2019 and 2021, Fig. 3). This indicates that at the beginning of the invasion lionfish were smaller than at present, and after the significant population decline which started in 2014.

Fishing experiments done in 2018 with the arrowhead traps along the whole depth range in which the fisheries operate showed that the length of the lionfish caught was independent from the depth at which the traps were set (Fig. 4). Lionfish density, however, was found to vary with depth, as indicated by the proportion of trap catches containing one or more lionfish (Fig. 5). Lionfish were significantly more likely to be caught in traps set at intermediate depths between 50

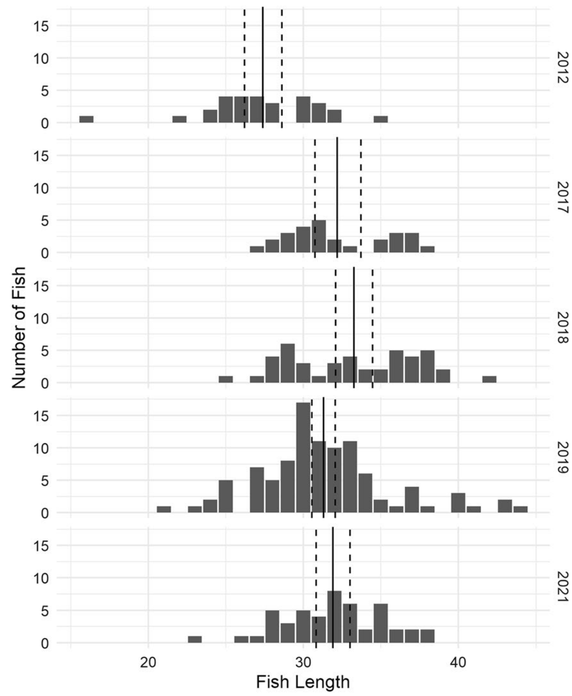


**Fig. 3** Lionfish size-frequency structures for fish caught in the trap fisheries on the Saba Bank for the year 2012, 2017, 2018, 2019 and 2021. Vertical bars indicate the annual mean length (and 95% confidence intervals)

and 100 m than at either deeper or shallower depths ($X^2 = 18.54$, $df = 3$, $p < 0.001$), indicative of higher lionfish population densities at those intermediate depths.

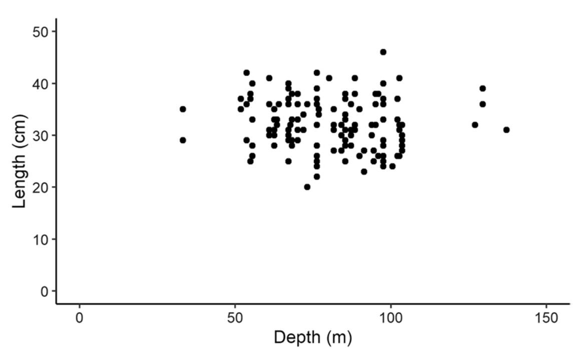


**Fig. 4** Lionfish size (total length in cm) versus depth (m) as caught in fisheries-independent trap sampling on the Saba Bank in 2018

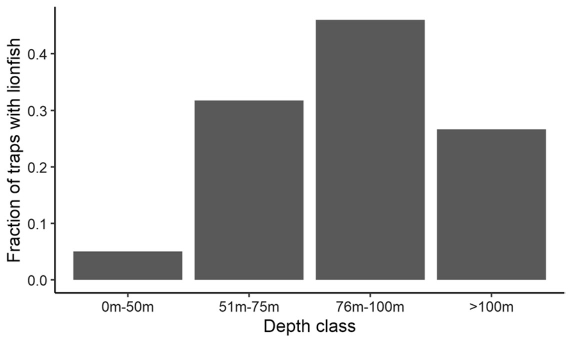


**Fig. 5** Proportion of traps catching one or more lionfish for four different depth intervals using either traditional arrowhead traps or (slightly) modified arrowhead traps

Skin ulcer incidence 2021

The disease prevalence we recorded in 2012 amounted to 0%. Even based on our modest sample size of 47 fishes for the Saba Bank and applying parsimonious assumptions as previously explained, we can conclude that in 2021 the incidence of disease on the Saba Bank was significantly less than the incidence recorded for the Gulf of Mexico in August 2017 (40%) ($z=5.07$, critical region$_{\alpha = 0.001}$: $z>3.10$), The incidence on the Saba Bank in 2021 was also significantly less than the much lower incidence recorded for the Gulf of Mexico in December 2017 (14%) ($z=2.69$, critical region$_{\alpha = 0.01}$: $z>2.33$), applying the same parsimonious assumptions.

## Discussion

Notwithstanding the many studies that are available on the Western-Atlantic lionfish invasion, little still is known about the dynamics of the lionfish and the factors governing its populations in the Caribbean (Benkwitt 2013; McCard et al. 2021). In the meantime the species appears to have reached the final stage of its invasion process, in which it has become firmly established and numerous in a wide variety of habitats and able to reproduce and disperse across a wide geographic range (Harris et al. 2018).

In this study we document a large and rapid population drop for the lionfish following its initial increase in abundance on the Saba Bank in the Eastern Caribbean, after first arriving in 2009 or 2010. Our data, indicate also a gradual increase in mean size of lionfish caught, since they were first recorded on the bank in 2010 and up through 2021. As the data further come from two fisheries operating at different depth ranges but which show no inversely complementary density patterns through time (i.e., a decrease in the shallow depth range in combination with an increase at greater depths), it all but precludes that the population declines observed could be explained by any large scale or ontogenetic vertical migration of the fish. In corroboration of this, our fisheries-independent 2018 studies into lionfish trapping efficiency at different depths on the bank, indicated no evidence of size-dependent depth distribution as is commonly observed in many other reef fish species.

Population size-frequency and density comparisons for different depths using fisheries-dependent catch data is complicated for the Saba Bank based on the fact that lobster traps and snapper traps differ greatly and are deployed at greatly different depths, with little overlap. Hence, the large difference in lionfish catch rates documented between the two fisheries may reflect a depth-related habitat preference for the lionfish, but may also simply reflect a difference in catchability between the two types of traps used. This is because, unlike redfish traps which are designed to target fish, lobster traps have a wider mesh size and a broader funnel. To address this complexity we conducted sampling using the typical arrowhead fish traps and slightly modified arrowhead traps across all depths. The results showed that lionfish population densities were relatively low at the comparatively shallow depths of deployment of the lobster traps and had higher population densities between 50 and 100 m of depth on the Saba Bank. Hence, this density difference certainly contributes to the much lower lionfish catch rates of lobster versus snapper traps. Most traps in the redfish fishery are set in the 50–100 m depth range and can partially explain why the redfish trap fishery had much higher catch rates than the lobster trap fishery.

Several other researchers have examined how lionfish density and population size-structure might differ with depth. Some results indicate lionfish densities are often highest at mesophotic (30–150 m) depths (Andradi-Brown et al. 2017), as do our findings. Like Nuttall et al. (2014), we ascribe the observed density differences with depth especially due to differences in habitat availability. On the Saba Bank, three-dimensional reef structure and hence shelter is limited in the shallower central parts of the bank and most reef cover which lionfish appear to depend on and actively seek, occurs along the outer slopes of the bank (Mckenna and Etnoyer 2010).

As regards potential depth-related size-frequency differences, some studies suggest that lionfish preferentially recruit to shallow areas and then migrate down to deeper reefs (Claydon et al. 2012). However, the studies examining fish in the (larger) size range susceptible to being caught by fish traps conclude that lionfish size structure is not really affected by depth unless shallow-biased culling by divers takes place (Andradi-Brown et al. 2017). Notwithstanding our considerable dataset, in corroboration of the studies cited above, no trend in mean lionfish size with depth could be demonstrated for the Saba Bank where also no culling takes place.

Benkwitt et al. (2017) were the first to suggest that the lionfish invasion might be waning. More recently, Harris et al. (2020) found evidence to suggest that an infectious, undescribed pathogen that causes skin ulceration in lionfish may have caused or at least contributed to a population crash and recruitment failure for this species in the Gulf of Mexico. On the Saba Bank, and based on the data we have, the population crash we document has likely not been accompanied by a similar incidence of the new ulcerative skin disease. Neither past observations during fisheries monitoring up through 2020, nor our directed sampling in 2021, uncovered any instances of skin disease. Hence there is no evidence that disease could play a similar local role on the Saba Bank as has been suggested for the Gulf of Mexico. However, if the skin disease can cause population crashes and reduced reproductive output elsewhere this might result in sharply lower larval densities and transport and ultimately reduce recruitment in other areas. While the cause for the lionfish population decline of the Saba Bank remains unknown, our data indicate in any case that a local outburst of necrotic skin disease is likely not the cause. The fisheries take of lionfish as a minor component of the bycatch from about ten vessels fishing on a 2000 $km^2$ bank is unlikely to have been a meaningful contributor to the population decline documented. Boom-bust dynamics are often witnessed in biological invasions and have critical implications for both understanding and managing invasive species (Strayer et al. 2017). While the underlying cause for the boom-bust event we document remains unknown, it suggests that the Caribbean coral reef ecosystem is starting to develop feedback mechanisms that can level-off deleterious population excesses of this invasive species. Further research is needed to see to what extent other areas in the Western Atlantic have also undergone population changes and what the underlying causes might have been.

Hence, the exact causes for apparent levelling-off of lionfish populations as also seen in different parts of the region remain unknown. Evidence for control by means of predators (e.g. Bejarano et al. 2015) or parasites (e.g. Tuttle et al. 2017) seems weak or largely lacking. For the population levelling seen in the Bahamas, evidence suggest that intraspecific density dependent effects such as local competition for food, cannibalism and/or low genetic diversity may all play a role (Burford Reiskind et al. 2019). The population decline we documented here for the Saba Bank suggests that the need for control efforts will gradually decline as lionfish populations might eventually level-off to a new (and lower) equilibrium density thanks to ecological control mechanisms which are yet poorly understood.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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