Rapid declines in lionfish catches in the Saba Bank lobster and snapper trap fisheries, Dutch Caribbean

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Research Article

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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 and the Caribbean having 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. We here document a large population crash for the lionfish following its rapid increase in abundance on the Saba Bank following its appearance in 2010. In doing so we document the third case of apparent local population boom-bust event for the Greater Caribbean, and the first for the Eastern Caribbean. We also document gradual increases in the mean size of lionfish of the Saba Bank that coincided with the increase and subsequent decline in lionfish 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 crash on the Saba Bank might have been due to non-local causes, such as reduced reproductive output in distant larval source populations. 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 helps improve our understanding of this most serious biological invasion.

Introduction

Non-native species are a major threat to marine protected areas worldwide (Iacarella et al. 2019). This is also the case for the marine protected areas of the Dutch Caribbean where 27 exotic and cryptogenic marine species that have been previously recorded for one or more islands of the Dutch Caribbean (Debrot et al. 2011). The Indo-Pacific lionfish (*Pterois volitans/ miles* complex) is one of those. 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 species 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). A number of ecological characteristics are believed to contribute to this success in establishing itself in the western tropical Atlantic, among which effective predator defence, highly efficient predation and feeding, coupled with a high growth rate and fecundity (Côté and Smith 2018). The only habitats which seems to have a strongly reduced presence of lionfish are non-estuarine shallow tropical lagoons presenting combined hypoxic and osmotic stress and turbid estuarine habitats, both likely due to one or more documented physiological tolerance limits (Trehern et al. 2020).

The species might have spread so rapidly and successfully because it was able to occupy the empty niche that was formerly filled by native piscivores (e.g. groupers) that had already been greatly impacted by man (Curtis et al. 2017). However, Valdivia et al. (2014) present evidence suggesting that native reef predators are not able to control lionfish and that their absence cannot be the reason for the success of the lionfish. It has also been suggested that in time native predators will develop resistance to the lionfish venom which will eventually result in higher predation rates on this species (Muñoz 2017). Indeed, usually invasive species will “settle in” after the initial expansion phase. Such “settling in” may occur with population crashes due to any number of causes. While such 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 lesions (Harris et al. 2020). Similar population crashes have not yet been reported for the rest of the Caribbean. In this paper we report the rapid rise and subsequent population crash of lionfish for the Eastern Caribbean Saba Bank as documented on the basis of lionfish Catch per Unit of Effort (CPUE) in the Bank’s lobster and snapper trap fisheries and present limited data on size-frequency developments and skin lesion infection rates. In doing so we present the first evidence of the species showing signs of ecological “settling-in” in the Caribbean Sea, after three decades of purely expanding populations in the Caribbean.

Methods And Materials

The Saba Bank

In this study we assessed lionfish on the Saba Bank, a large 2,200 km^2 submarine plateau west of the island of Saba. The bank is a flat offshore bank, located 3–5 km southwest of Saba and 25 km west of St. Eustatius in the Dutch Caribbean (Fig. 1). For the most part, depths are 20–50 m, in the eastern section about 230 km^2 lies between 10 and 20 m depth (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 platform. The bank lies fully within the Dutch Kingdom’s Caribbean Exclusive Economic Zone (EEZ) 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 (PSSA)” status by the International Maritime Organization (IMO) 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. Basic data on catch, effort, species composition and length frequency of the fishery were collected weekly by Saba Bank Management Unit (SMBU) 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 (modified Caribbean 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 fishery is the “redfish” (snapper) fishery which is also largely conducted using traps. 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). The traps are made of coated wire mesh, with mesh sizes of 1x2 to 2x2 inch (2..5–5 cm). Fish and lobster traps differ in funnel size, with the funnel of fish traps being narrower. Salted cow hides (20 x 20 cm), are used as bait and are attached to the traps with plastic-coated wires (Toller & Lundvall, 2008).

Fisheries data

Following piloting trials in 2010, a sample-based fishery survey was implemented in September 2011 at the sole fishing port of Saba Island from whence the Saba Bank fisheries take place. Within this program, fishers fill in logbooks at the end of fishing trips, in which they report information about the fishing operations (type and number of gear, location, duration) and catches per trips for a number of species, amongst which the lionfish. Sampling was also conducted for a number of trips per week, both on the landings (at the harbour) and one the catches (onboard) to establish catch species composition and length composition, including the lionfish when present. The number of trips sampled for landings length-composition averaged 60 per year. Since 2015, lionfish have had commercial value in Saba and are landed and sold locally for consumption. Before 2015, nearly all lionfish caught in any type of trap were killed and discarded.

Abundance trends

The number of lionfish caught per fishing trip reported in the logbooks were analysed to investigate the existence of temporal changes in the lionfish abundance. A GLM with a negative binomial distribution was fitted to estimate year and gear type effect, and their interaction. The number of trap lifted during each trip was not included in the model because it was strongly co-linear with the type of gear (more traps are lifted in a trip for the lobster fishery than for the redfish fishery) and GLMs fitted separately on the data for each fishery did not show a significant effect of the number of traps. In addition to estimating year and gear effects, the existence of monotonous temporal trends in the catches of lionfish was tested using the non-parametric Mann-Kendall test.

Length-frequency analysis

While ample logbook information was available for each year over the period 2012–2020, there were years with very few lionfish length measurements (none sampled between 2013 and 2015, and less than 10 in 2016, 2017 and 2020). Differences in mean lionfish length between the years was tested by first conducting an ANOVA (to test for overall year effects) followed by a pairwise comparison test using the Tukey's ‘Honest Significant Difference’ method (to test which years individually differ from the others). Only the years with higher numbers of lionfish measured (between 28 and 71 fish measured annually for the years 2012, 2018, 2019 and 2021) were used in this analysis. Logbook data for the piloting port sampling monitoring trials of 2010 and 2011 were excluded.

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 a modified arrowhead trap with "escape" funnels in an attempt to reduce by catch of other fish species, here termed "modified arrowhead traps". Both traps used had a grid size of 2.5 x 2.5 cm. A total of 183 trap lifts were done from depths varying between 19 m 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 10-fold smaller reference sample size than Harris et al. (2020) had actually obtained (August 2017, n = 988; December 2017, n = 1228).

Results

Lionfish population trends

Lionfish were not reported from catches by either Toller and Lundvall (2008), Toller et al. (2010) or Williams et al. 2010), confirming the arrival of lionfish on the Saba Bank after 2008 but before 2010 when we started recording it from the catches sampled in the Fort Bay port of Saba. In fact, the species was first were first reported for Saba and Saba Bank in 2010 (Debrot et al. 2011).

The abundance of lionfish in shallow-water lobster traps appear to have peaked between 2012 and 2015 but to have declined since then. Similarly, in the deep-water redfish traps, lionfish initially increased between 2012 and 2014 and then continuously declined to reach its lowest value in 2020 (Fig. 2). The GLM model indicated that the effect of year, gear and their interaction were all significant. Predicted lionfish catches per year and gear showed a first period of increase from 2012 to 2015 in the redfish traps followed by a decline until 2020 (figure 2). The trends for both period were significant (Man-Kendal test, $p = 0.01$ for 2012-2014 and $p < 0.001$ for 2014-2020). Catches in the lobster traps were 10.7 time lower than in the redfish traps (<0.001). Catches in the lobster traps increased until 2015 and decreased afterwards. The Man-Kendal test indicated that the declining trend after 2015 was significant ($p = 0.82$ for 2012-2015 and $p < 0.001$ for 2015-2020).

Lionfish size structure and depth distribution

The size structure data indicate a rapid increase in average size of trap-caught lionfish between 2012 and 2016, with mean sizes ultimately stabilizing at about 32 cm TL (Fig. 3). Pairwise comparisons of mean length between the years (2012, 2018, 2019 and 2021) indicated significant differences ($p \leq 0.01$) in mean fish size between 2012 and the most recent years (2018, 2019, 2021). This indicates that at the beginning of the invasion animals were smaller than at present, and after the significant population decline which started in 2014. Fisheries-independent deployment of arrowhead traps done in 2018 along the whole depth range in which these fisheries operate (as described above) showed that the size of the lionfish caught was independent of the depth at which the traps were set (Fig. 4). In contrast to the lack of fish size trends with depth (Fig. 4), fish density, as indicated by the proportion of trap catches containing one or more lionfish, did differ significantly with depth (Fig. 5). Lionfish were significantly more likely to be caught in traps set at intermediate depths between 50 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.

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 (McCard et al. 2021). Even such a fundamental process as lionfish larval transport has only most recently been documented (Sponaugle et al. 2019). 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 is able to reproduce and disperse across a wide geographic range (Harris et al. 2018). The lionfish preys 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).

In this study we document a large population crash for the lionfish following its rapid increase in abundance on the Saba Bank in the eastern Caribbean, a few years following its arrival in 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 still show the same pattern of peaking lionfish abundance followed by rapid decline, 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 common 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 catch rate of lobster versus snapper traps. Many trap 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 elsewhere. While the cause for the lionfish population crash of the Saba Bank remains unknown, our data indicate that in any case that a local outburst of necrotic skin disease is likely not the cause. 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, our work helps improve our understanding of this most serious biological invasion. 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.

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 crash we documented here for the Saba Bank suggests that control efforts will altogether be unnecessary as lionfish populations might gradually level off to a new (and lower) equilibrium density thanks to ecological control mechanisms which are yet poorly understood.

Declarations

Acknowledgments

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

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Figures

Figure 1

Map of the Western Tropical Atlantic showing the location of the Saba Bank in the eastern Caribbean.

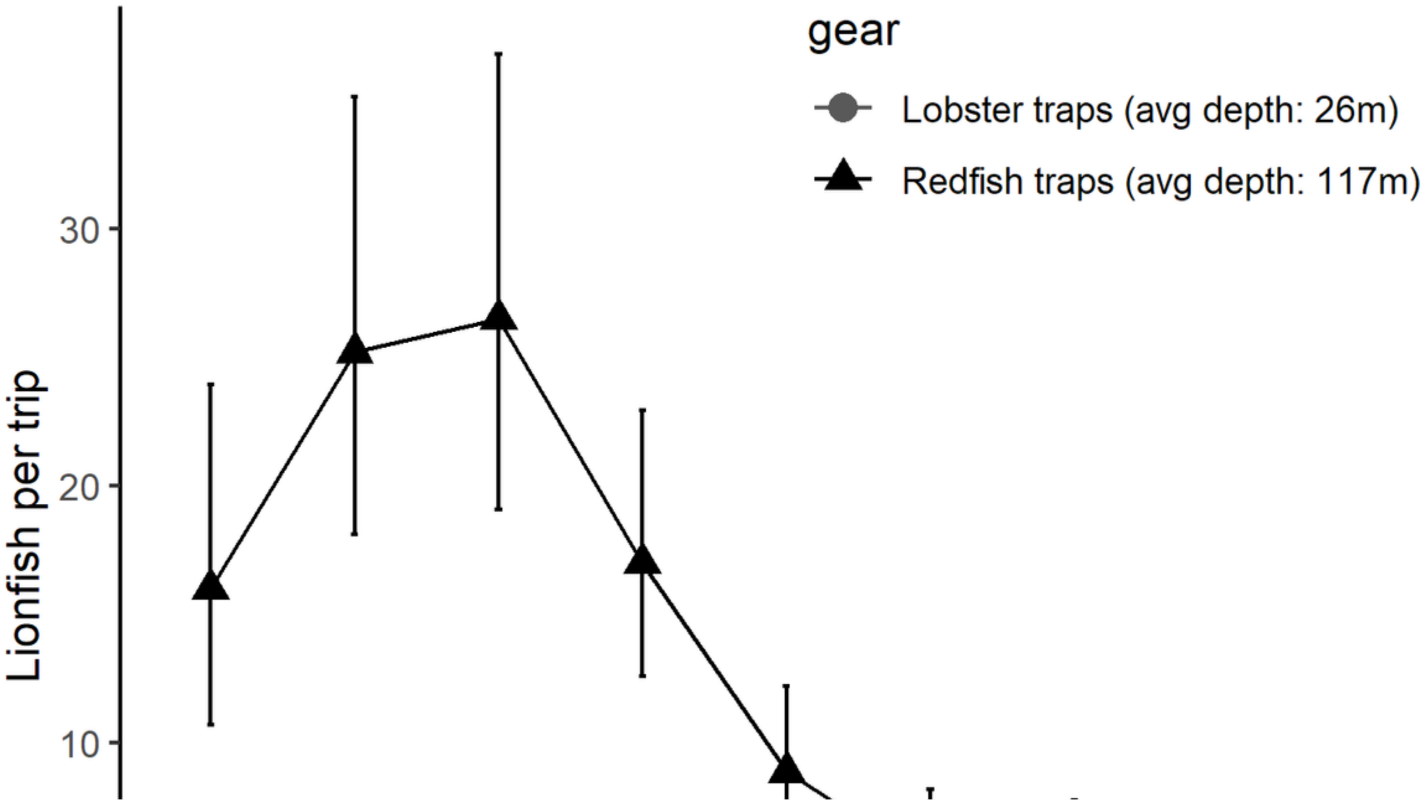

Figure 2

Trends in the abundance (measured as catch per trip and predicted using a GLM model) of lionfish in the deep-water redfish traps and shallow-water lobster traps on the Saba Bank. Error bars indicate 95% CI of the yearly predicted values.

Figure 3

Lionfish size-frequency structures for fish caught in the trap fisheries on the Saba Bank for the year 2012, and from 2016 to 2021. Vertical bars indicate the annual mean length (and 95% confidence intervals).

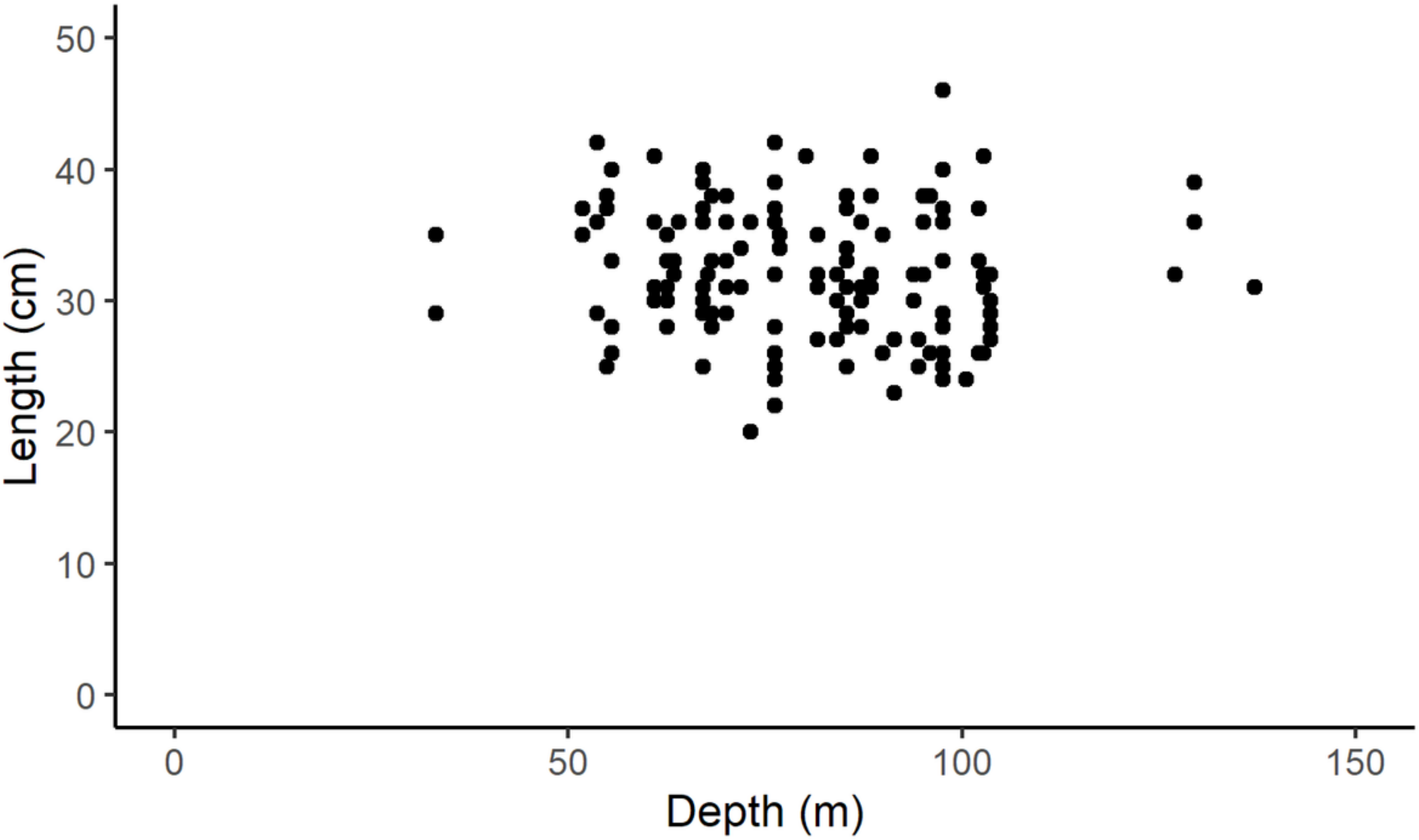

Figure 4

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

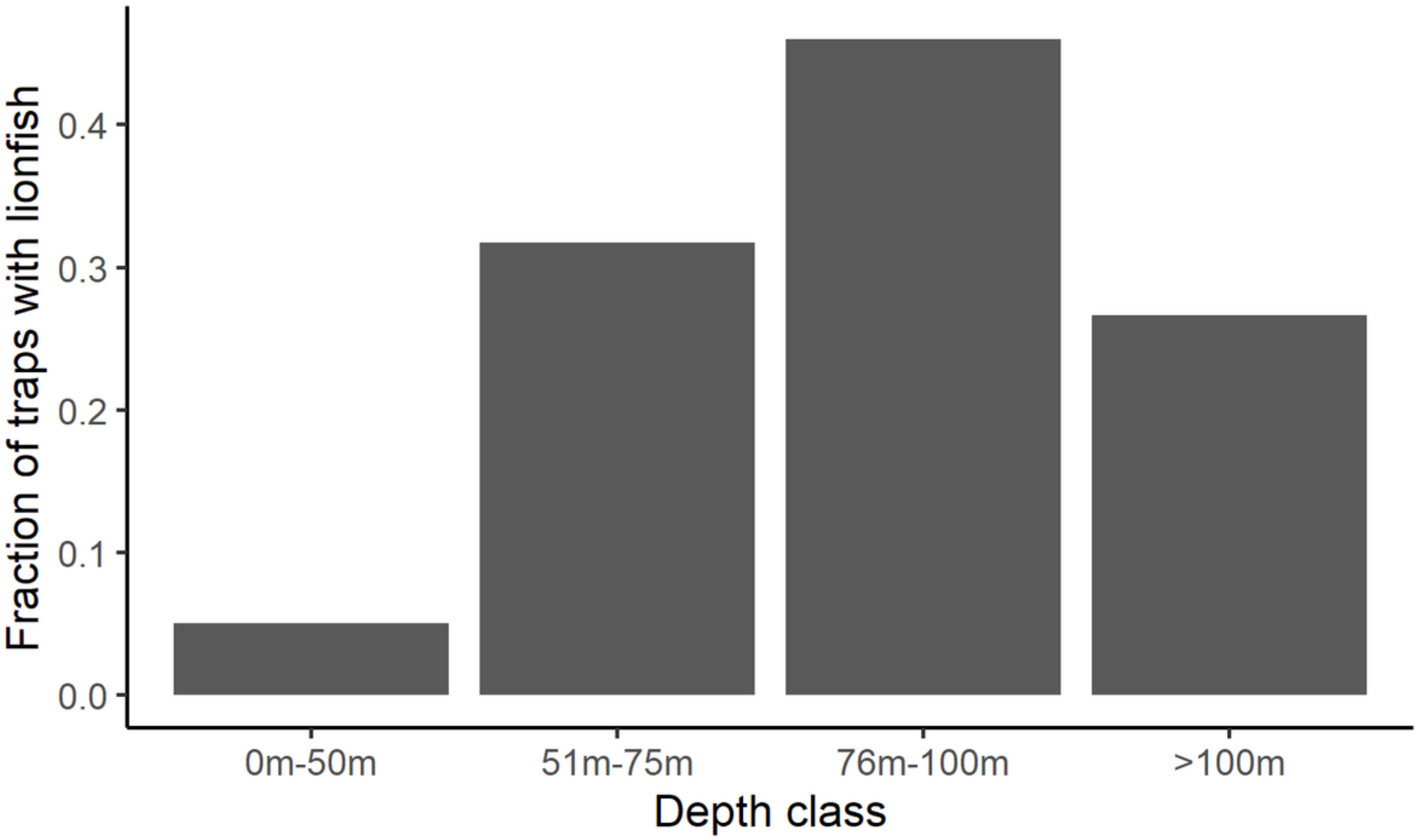

Figure 5

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