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# Managing invasive lionfish in Belize's Marine Protected Areas

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## Abbreviations

BCMR – Bacalar Chico Marine Reserve
CCMR – Caye Caulker Marine Reserve
GUZ – General Use Zone
HCMR – Hol Chan Marine Reserve
IAS – Invasive Alien Species
LFS – Lionfish Focused Search
MPA – Marine Protected Area
NTZ – No Take Zone
PHMR – Port Honduras Marine Reserve
SWCMR – South Water Caye Marine Reserve

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# Executive Summary

***"For marine protected areas to function as conservation areas, it's important that the biology and ecology be conserved to the highest level possible, and that now requires lionfish control."***

***– James Morris (2014) in Nature.***

Across the Caribbean, the invasion of red lionfish (*Pterois volitans*) poses a pervasive threat to marine ecosystems and coastal fishing communities. First recorded in Belize in 2008, lionfish have become well established across the country's entire marine environment. Uncontrolled, invasive lionfish populations disrupt marine food webs, negatively impacting coral reef health and fisheries productivity, thereby undermining the resilience of coral reefs and reef-associated systems to global change. Basic data on lionfish populations are lacking from the majority of Belize's marine reserves, which has made it impossible to develop, implement or evaluate lionfish management targets and action plans. This report presents the most thorough population census to date for invasive lionfish and associated native fish communities in Belize. By adapting an approach by Green (2014) we have been able to develop site specific threshold density estimates of lionfish within five Belizean marine reserves and provide specific recommendations for the adaptive management of lionfish across the Belize Barrier Reef Reserve System (BBRRS).

Invasive lionfish present a real and present threat to the status of coral reefs, with first impacts observed lower down the food web and cascading, longer-term impacts leading to losses in commercial fish and apex predators, if left unmanaged over several years [29]. Devastating impacts on reef fish communities in particular have been observed in the Bahamas, and food web models show long term serious impacts to biomass for many key native fish species [29]. Our vision is to establish effective lionfish control and provide a framework for effective population suppression in prioritised conservation areas across Belize and its invaded range by 2023 - supporting the Aichi Biodiversity Target 9 to identify, control and eradicate invasive alien species and the wider objectives of the National Lionfish Management Strategy (2019-2023).

Since 2009, lionfish control and awareness efforts have been taking place throughout Belize. However, lionfish have spread rapidly and widely across the region due to high fecundity, a generalist diet and lack of predators, and total eradication is no longer considered possible. The first challenge to achieving effective lionfish management is understanding what effective control looks like. In 2014, an important ecological model was published , which provided evidence for optimism: lionfish population suppression below site-specific management targets allows native fish populations to recover[57]. This report shares how we calculated these targets for five marine reserves in Belize, and presents a broad overview of control actions and approaches that have been taken across the wider Caribbean region. Our results show that at the time of survey, lionfish populations were generally low across all five regions. Lionfish were also observed at higher densities and as larger individuals within no-take zones (NTZs), which corresponded with higher prey biomass observed within these zones. In total, 22% of surveyed sites exceeded the predicted threshold density, with 18% of these designated as NTZs. This is an important result and suggests that the majority of reefs that were found to be ineffectively managed for lionfish occur within NTZs. Thus, if lionfish populations are left unchecked, NTZs will cease to function as fish replenishment zones that sustain biodiversity.

By developing specific management targets and thresholds for protected areas, using the best available science and the precautionary principle, MPA managers can prioritise sites, create removal targets and direct removal efforts only towards areas identified as vulnerable to the impacts of lionfish invasion. This is an important benefit for conservation practitioners seeking to allocate resources in a way that sustains sufficient invasive species control over the long term, in priority habitats.

# Introduction

## Lionfish – a background to the invasion

Native to the Indo-Pacific and Red Sea, the distinct appearance of lionfish (in particular species of the genus *Pterois*) has made them prized by aquarists the world over (Fig. 1). *P. volitans* was among the most commonly imported live marine tropical fishes to the USA in 2005 [1]. This international trade, and the subsequent release of imported aquarium fish into the ocean, is considered the most likely route by which two species of lionfish (*P. volitans* and *P. miles*) became established in the Tropical Western Atlantic [2].

**Figure 1: The red lionfish (P. volitans) photographed in Turneffe Atoll, Belize. Photo credit: Gordon Kirkwood**

Lionfish are considered highly invasive; they are ecological generalists, able to thrive in a broad range of habitats and environmental conditions [3–5]. In non-native environments, they have been recorded at densities far higher [6] than those observed in their native range. The success of lionfish is in part due to their life history characteristics: lionfish grow more quickly and become reproductively mature earlier than comparable mesopredators on Atlantic reefs [4]. They also remain reproductively active throughout the year compared to once a year in native counterparts [7], and have few natural predators, likely due to the 18 venomous spines located on their dorsal, ventral and anal fins [7,8].

The first confirmed lionfish sighting in the Tropical Western Atlantic was in Florida, USA in 1985 [9] with subsequent releases believed to have occurred over the following decade [6]. No further reports were made until 2000, when numerous lionfish sightings were reported and confirmed along the Atlantic coast of mainland USA, as well as in Bermuda and The Bahamas [2,10]. Sporadic reports were subsequently made with increasing frequency across the Caribbean and Gulf of Mexico, until a report made in Trinidad and Tobago in 2012 [11] indicated that the entire region had been successfully invaded (Fig. 2).

Genetic analysis confirms that there are two species present in the invaded range: *P. volitans* and *P. miles.* The species are morphologically indistinguishable but genetic analysis suggests that *P. volitans* may be the only species to have become established [12].

Lionfish populations in the Tropical Western Atlantic are associated with a strong founder effect: that is, a low genetic diversity compared to that in the native range of the species [12]. This suggests that the invasive lionfish population can be traced to a relatively small pool of individuals that share a common geographic origin. The first report of an invasive lionfish in Brazil was made in 2014 and the mitochondrial DNA of the captured individual strongly indicates a further range expansion of the Tropical Western Atlantic invasion rather than an independent release [13].

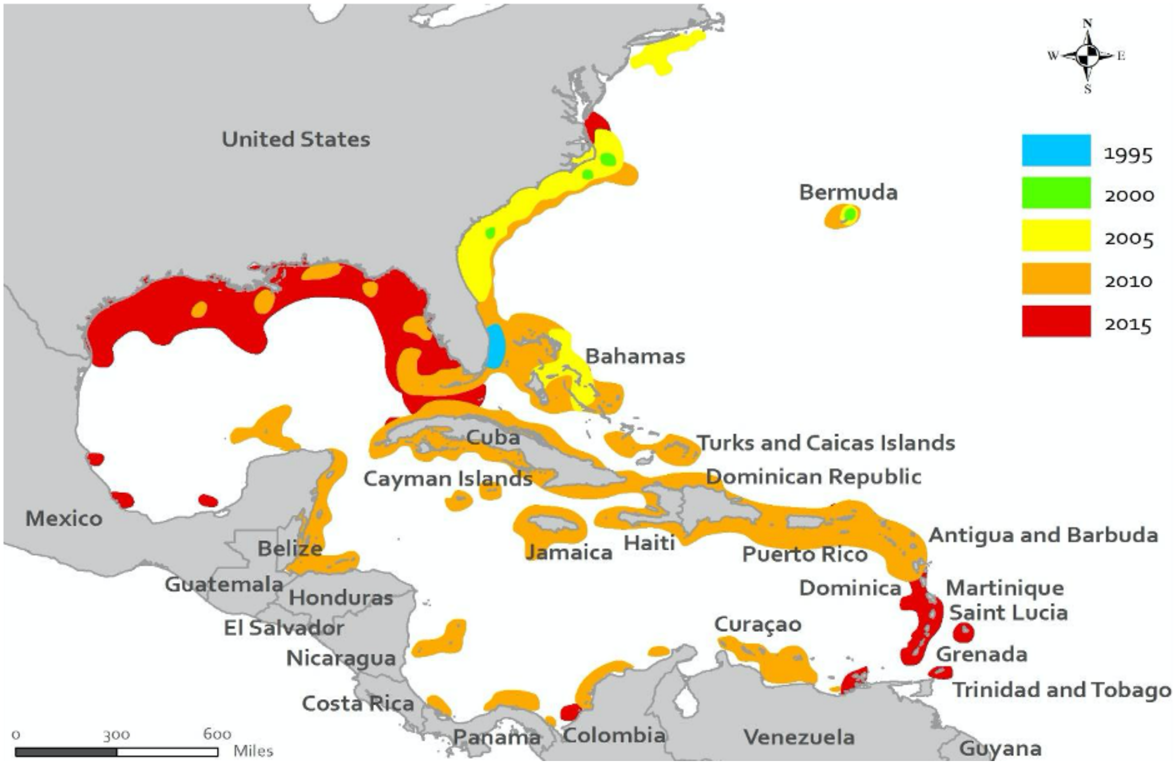


**Figure 2: Map of the Caribbean showing the advancement of lionfish in five year intervals, from 1995, when lionfish had only been observed in Florida, to 2015, by which time they had become widespread.**

A second and probably independent invasion of *P. miles* is underway in the Mediterranean Sea. After an initial report was made in Israel in 1991, no further reports were made for two decades. However since 2012, *P. miles* has been sighted at increasing frequency in Lebanon, Cyprus and Turkey [14]. This time-lag is typical of a biological invasion, and similar to the lag between the first sighting of a lionfish in Florida in 1985 and the rapid spread of lionfish across the Tropical Western Atlantic from 2000 onwards. Despite modelling projections suggesting that oceanographic conditions and habitat connectivity in the Mediterranean do not represent ideal conditions for the successful establishment of invasive *P. miles* populations [15], recently, several reports from Turkey and Cyprus show a rapid increase and westerly migration of the species towards the Aegean Sea, indicating that the region may indeed have become successfully established [14].

## Ecological and socio-economic threats

The lionfish is a reef predator with a generalist diet. In a study in Bacalar Chico Marine Reserve (BCMR), northern Belize in which 1023 lionfish were dissected and prey species were visually identified; three phyla (crustaceans, molluscs and fish), comprising 22 families [16] were recorded (Fig. 3). A study in the Mexican Caribbean which used genetic analysis of stomach contents identified 14 families of fishes from five orders, and three orders of crustaceans (Decapoda, Stomatopoda, Euphausiacea) [17]. Smaller lionfish primarily feed on crustaceans, shifting to a fish-dominated diet as their total length increases [16]. While lionfish diet is largely influenced by prey availability, lionfish have been seen to selectively target their prey, based on a strong preference for specific prey traits; small, shallow-bodied solitary fish with nocturnal, benthic habits appear to be most vulnerable [18] to the impacts of lionfish predation.

Lionfish are voracious predators. In experimental studies, they have been shown to cause a reduction in the abundance of small native coral-reef fishes that is 2.5 times greater than that caused by a similarly sized native piscivore in the Caribbean [19]. Their success as a predator can be attributed to two main traits:

**1. Predation strategy unique to the Caribbean**

Spreading their long, broad pectoral fins, lionfish corral prey into a confined space [20–22] and shoot a jet of water towards their prey, likely to distract or to orient their prey head-first towards the approaching predator [21]. Furthermore, the morphological structure of lionfish jaws is different to other ambush predators with similar prey, making it particularly fast moving; as the lionfish strikes and opens its mouth, it creates a powerful suction, enhancing its chance of success [22].

**2. Cryptic nature prevents detection/recognition by prey**

Lionfish are covered in stripes, a form of disruptive colouration that may conceal body shape and hinder its detection or recognition [23], or may allow lionfish to overcome prey fish ability to recognise them as a predator using visual cues [24]. This was determined during experiments with Indo-Pacific damselfish (from the lionfish's native range), during which the damselfish exhibited no predator avoidance response when exposed to either visual or chemical cues. The damselfish did respond to visual and/or chemical cues of other mesopredators. Therefore, lionfish may also possess some sort of chemical camouflage, which causes potential prey to label lionfish as non-threatening [24]. Similar tactics have been recorded in some predatory insects [25,26].

Experiments with Caribbean prey fish species indicate that prey fishes in the Atlantic likewise do not exhibit predator avoidance response when approached by lionfish [27,28]. Although this has been attributed to prey naivety, it is likely a result of the innate ability of lionfish to circumvent prey risk assessment, or a combination of both. Regardless, the lionfish is undoubtedly a highly effective predator.


**Figure 3: Stomach contents of lionfish caught during SEA's Placencia Lionfish Tournament, southern Belize (2014).**

Whilst the generalist diet of lionfish has facilitated their establishment in a wide range of habitats [4], their trait-based diet selection means that some species and families of prey are more threatened than others (Table 1). Uncontrolled populations of invasive lionfish reduce native fish abundance [29], recruitment [30] and species richness [19], with cascading effects through the food web. A model of ecosystem interactions on a Caribbean coral reef with and without lionfish showed that the invasion will have direct, negative impacts on small and intermediate carnivorous and omnivorous fish, and is expected to cause loss of large predators in the long term [31].

These ecological impacts likely have significant socio-economic impacts [32], particularly with respect to the expected medium- to long-term negative impacts of uncontrolled lionfish populations on populations of commercially important species such as snapper, grouper and lobster [31], which are essential to local economy and food security [33,34].

Moreover, envenomation (stings caused by lionfish spines) accidents present a health threat to fishers and tourists that practice underwater recreational activities [35]. The most common symptoms of untreated lionfish stings are localised pain, swelling, numbness and abdominal cramps, which can persist for over 24 hours [35]. In severe cases, a sting may temporarily reduce fishing success or ability to fish, leading to lost income for fishers. There have been no recorded fatalities resulting from a lionfish sting, and symptoms are significantly reduced or avoided by immersing the affected area in hot water within three hours of being stung [35]. Nevertheless, it is possible that the presence of a venomous species may repel tourists – of concern considering that tourism is the greatest contributor to Belize's GDP [36].

***Table 1:*** *Traits for vulnerability of native fish species to predation by invasive lionfish.*

| TRAIT | MORE VULNERABLE | LESS VULNERABLE |
|---|---|---|
| **Size** | Small, e.g. greenblotch parrotfish  | Large, e.g. graysby  |
| **Shape** | Shallow-bodied, e.g. clown wrasse  | Deep bodied, e.g. butterflyfish  |

| | | |
|---|---|---|
| **Aggregation size** | Solitary, e.g. Spanish hogfish  | Schooling, e.g. French grunt  |
| **Water column position** | Benthic fishes, e.g. masked goby  | Pelagic fishes, e.g. bar jack  |
| **Nocturnally active** | Yes, e.g. squirrelfish  | No, e.g. striped parrotfish  |
| **Cleaning behaviour** | No, e.g. masked goby  | Yes, e.g. cleaning goby  |

## Approaches to lionfish management

### Bounty program

Bounty programs encourage the harvest of invasive or problematic species by providing pre-determined financial incentives to individuals who provide evidence that they have successfully removed or collected a specified organism. For example, a recreational angling initiative that aimed to reduce the abundance of predatory pike-minnow (*Ptychocheilus oregonensis*) from Columbia and Snake Rivers, USA, by paying anglers USD $4 - $8 bounty for each individual that they captured has been highly successful, with a 40% reduction in predation on native juvenile salmonids [37,38].

In an effort to prevent lionfish establishment, after the first confirmed report of a lionfish in Turneffe Atoll in December 2008 [2], a bounty of BZD $50 was offered by the Belize Fisheries Department as a cash reward for every individual caught. By August 2009, the bounty program was discontinued due to the overwhelming numbers of lionfish being submitted [36].

### Fishery development

Belize's small-scale fishers across the entire Belize Barrier Reef System provide an ideal framework for year-round removal at sites across the length of the barrier reef system. However, not all sites are accessible to fishers, in particular deep reefs and no-take zones, leaving these areas unmanaged and vulnerable. The Belize Lionfish Management Plan (2009-2013) [39], recommended development of a fishery targeting lionfish as the most feasible and effective mechanism to achieve the necessary high and consistent removal rates to reduce population density [39], and modelling presented in Belize's National Lionfish Management Strategy (2019-2023) indicated that a commercial fishery landing 50 million tonnes of lionfish per year would provide the necessary level of removal for effective lionfish population suppression in areas accessible to fishers [36]. The development of a fishery is also recommended in regional lionfish control plans [32,40].

Outreach has been carried out in coastal communities countrywide since 2010, involving both safe-handling demonstrations for fishers and to encourage lionfish consumption [39,41]. In 2019, 76% of the general public had heard of lionfish and of those surveyed, 22% had tasted lionfish (Blue Ventures, funder report).

## Dive tourism

Dive operators and volunteer divers have the potential to complement professional lionfish survey and removal efforts and to monitor ecological trends more intensively across broader spatial and temporal scales [42]. Volunteer SCUBA divers are increasingly supporting efforts to address marine conservation issues [43,44]. Existing studies show that recreational SCUBA divers and volunteers can offer cost-effective and reliable assistance in monitoring coral reef ecosystems and recording elasmobranch sightings with the same level of accuracy as professional scientists [42,45–47]. The potential for volunteers to assist with monitoring the distribution of marine Invasive Alien Species (IAS), which are often patchily distributed, is considered particularly valuable [43].

However, as dive tourism is often concentrated in 'more appealing' and ecologically diverse areas, and fluctuates seasonally, it would most likely complement, rather than replace, existing lionfish monitoring activities. Moreover, the repeated monitoring of lionfish by citizen scientists requires intensive training of individuals and a regimented survey protocol, which may reduce the appeal of the diving experience, and hence the interest and motivations of volunteers [46,48]. Studies also suggest that volunteer divers may lose motivation in lionfish removals if they do not see a visible change in their density in the area they dive in, and dive operators may be deterred from encouraging divers to remove lionfish by concerns about diver's safety and the potential for venom-related injuries [49].

## Legal frameworks and licensing

As lionfish have spread across the Caribbean region, lionfish management plans have been developed as national responses to deal with the issue. While these plans have been in place since the onset of the invasion, few countries have established dedicated legislation for invasive species and lionfish control [32]. It is important to fill in the gaps in existing legal frameworks with amendments and special provisions, or to enact new legislation that can exclusively address the lionfish invasion. MPAs pose regulatory conflict as they usually prohibit fishing activities which include the culling of lionfish, though they are critical control locations given their high ecological value and typically high abundance of juvenile fish [49]. The use of special permits, licensing and amendments to legislation should be seen as effective tools to allow for the control of lionfish within MPA boundaries. Sustained action must be taken for evolving management strategies, developing new legislation and identifying ways to strengthen the prevention and control of invasive species.

## Lionfish tournaments

Over recent years, competitions to catch lionfish (commonly known as lionfish tournaments or derbies) have led to the removal of 4,000 lionfish from the Abaco Islands, Bahamas [50], 2,349 lionfish from the Gulf of Mexico [51], and well over 10,000 lionfish from across the Belize Barrier Reef Reserve System [63]. Where measured, tournament removals have led to a >60% reduction in lionfish densities within the tournament area [36], demonstrating the potential effectiveness of this form of population suppression. Since 2010, a number of companies and NGOs have organised lionfish tournaments in locations across Belize.

In 2014, the Southern Environmental Association (SEA) and Blue Ventures organised surveys before, during and after SEA's Placencia Lionfish Tournament to evaluate and improve the tournament's effectiveness. No significant differences in density, mean size of lionfish, or size distributions of lionfish before or after the tournament were detected, however teams were spread across nearby reefs, including within and outside of the reserve [36]. Population modelling indicates that even doubling the number of lionfish tournaments held each year in Belize would not have any significant impact on lionfish population density [36], due to their fast rate of reproduction and ability to quickly recolonise areas.

## Belize's marine protected area network

***"For marine protected areas to function as conservation areas, it's important that the biology and ecology be conserved to the highest level possible, and that now requires lionfish control."***

***– James Morris (2014) in Nature.***

Marine protected areas (MPAs); areas of the sea where activities are managed, and in some cases where fishing is prohibited, can be a valuable marine conservation tool when properly designed and enforced. Effective MPAs have been associated with increases in the size, density, biomass and diversity of marine species while the spill over of fish and larvae beyond the MPA boundaries can help to sustain surrounding populations of commercially important fish and invertebrate species [52]. Ironically, the protection afforded by marine reserves may have the same positive effects on populations of alien species [53] such as lionfish. The spill-over of larvae of invasive species beyond the reserve may counteract control efforts in surrounding areas.

## Description of the Belize Barrier Reef Reserve System

The Belize Barrier Reef extends 220 km from Sapodilla Cayes in the south to the Belize-Mexico border in the north, and forms the heart of the Mesoamerican Barrier Reef, the second longest reef in the world, shared by Mexico, Belize, Guatemala and Honduras. In 1996, seven of Belize's MPAs – collectively the Belize Barrier Reef Reserve System (BBRRS) was declared a UNESCO World Heritage Site due to its high level of biological diversity, ecological processes, natural beauty, and important and significant natural habitats for threatened species [64].

The Belize MPA network covers over 945,000 acres of marine environment and encompasses 14 areas: nine Marine Reserves (seven of which are IUCN classified), two Natural Monuments, two Wildlife Sanctuaries and one National Park (Fig. 4). The Fisheries Department has also established 11 protected Spawning Aggregation Sites (SI 161 of 2003) and a further 2 have seasonal protection for Nassau Grouper (SI 162 of 2003). The 14 MPAs in the network are managed by the Belize Fisheries Department (BFD) or Forest Department either directly or through co-management agreements with non-governmental organisations (Appendix I). Marine Reserves are established by the BFD as fisheries management tools. These reserves have specific zones defined for conservation, extractive and non-extractive use, with allowed uses primarily comprising sustainable fishing, tourism, research and education. Thanks to the long-standing protection and management of key species and habitats, MPAs ensure the preservation of valuable resources for future generations. Benefits of the marine reserve network have included:

- Increases in spawning stock biomass, providing greater replenishment;
- Spillover has enhanced local catches;
- Increase in predictability of catches;
- Insurance against uncertainty;
- Fewer problems around multi-species management;
- Greater equity among fishers; and
- Greater public understanding of the objectives of marine reserves

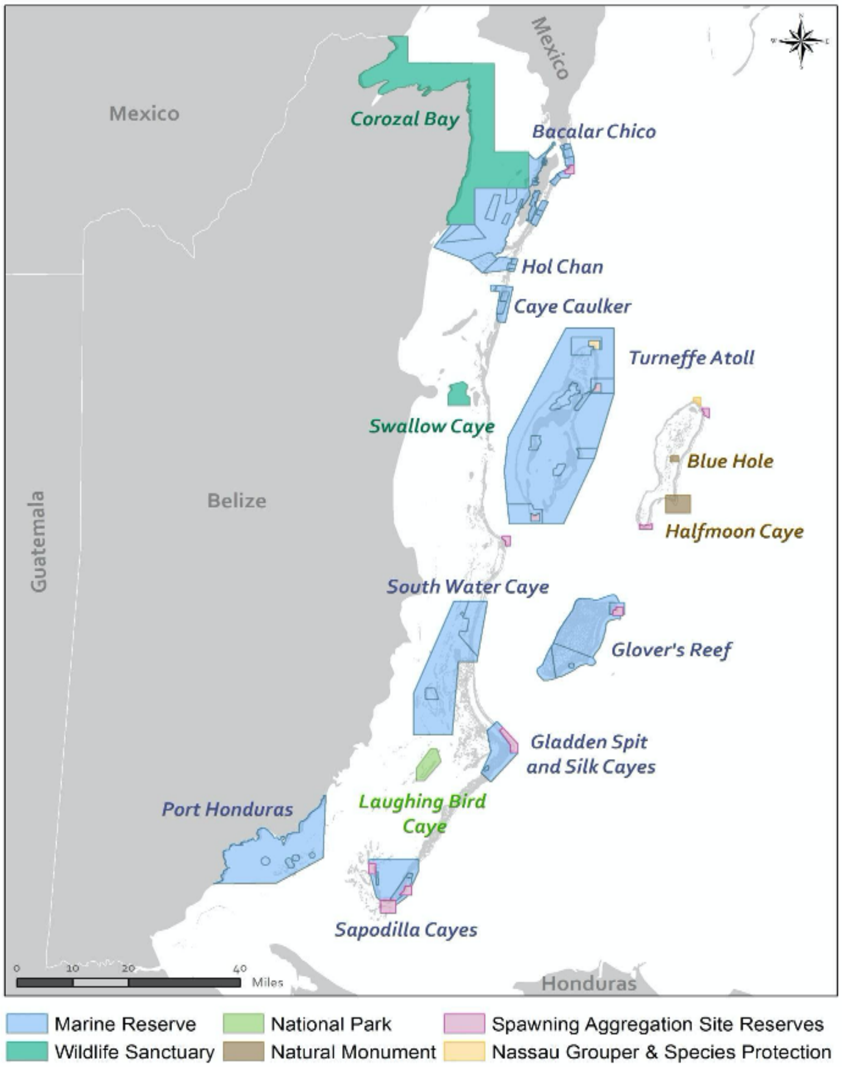


**Figure 4: A map of Belize's Marine Protected Area network**

## Importance of coral reefs for Belize's economy

It is estimated that 2,590 people actively work as fishers in Belize [36], with the total direct revenue of the fishing industry in 2011 estimated to be USD 22 million – 1.8% of national Gross Domestic Product [36] . The Belize fishing industry is dominated by queen conch (*Lobatus gigas*) and Caribbean spiny lobster (*Panulirus argus*), which together account for 95% of national fisheries landings [36] and generate over USD 13 million/year in revenue [36]. Both fisheries are considered to be fully- or over-exploited, with total reported landings steadily declining since the 1980s, despite increased fishing efforts [33]. Populations within protected areas show declining trends, and are unlikely to recover without significant human intervention [36]. Subsistence and artisanal fisheries for finfish, such as Nassau grouper (*Epinephelus striatus*) and mutton snapper (*Lutjanus analis*), provide not only a vital source of income but also important food security [36], however these resources are also recognised as being in decline [54]. Local and international management interventions, which have had some localised success, have included size limits, seasonal closures, managed access and quotas.

Many coastal communities are directly dependent upon healthy reefs as their primary source of income – San Pedro Town and Placencia, Belize's tourism hubs, attract divers and sport fishers. Sarteneja village, in Corozal District, is the largest fishing community in Belize, where over 80% of households are directly dependent upon fishing as their primary source of income [36]. Sartenejan fishing boats are active throughout the Belize Barrier Reef System [36], and the community's fishers are key stakeholders of eight of Belize's marine reserves. With such a large footprint across the entire BBRS and high dependency upon fishing, Sarteneja is particularly affected by depleted fish stocks.

## Status of reef health in Belize

Overall reef health, measured using the Reef Health Index developed by the Healthy Reefs Initiative was evaluated as 'Fair' in 2020, with Belize seeing a marginal improvement in three of the four indicators measured to evaluate reef health since 2018 [55]. Coral cover remains 'Fair' (17%), fleshy macroalgal cover is ranked as 'Poor' (19%) and herbivorous fish biomass achieved Belize's only 'Good' indicator (2744 g/100 $m^2$) [55]. However, commercial fish biomass remained 'Fair' (824 g/100 $m^2$) over the same period. With only 3% of Belize's territorial sea within fully protected zones in the MPA network, this highlights the need for more commercial fish protections to be enacted [41]. The BBRRS continues to face numerous threats, including coastal development, illegal fishing, coral bleaching, agricultural run-off and incomplete sewage treatment [55]. In recent years, the region has also seen a higher incidence of sargassum blooms, coral bleaching and disease which can be attributed to the effects of global climate breakdown. These stressors will reduce ecological functioning and overall resiliency on an already impaired reef system[65].

Despite these challenges, the BBRRS was removed from the list of World Heritage Sites in Danger in 2018 [66]. The BBRRS had previously been placed on the list in 2009, due to coastal activity leading to the destruction of mangrove and marine ecosystems. The World Heritage Committee recognised Belize's efforts to address and mitigate these conservation issues, which included a moratorium on oil exploration. This marks a major milestone in the conservation status of the BBRRS, but there is still a need to implement more effective Environmental Impact Assessment policy and processes [55].

## What does effective lionfish control look like?

The interconnectivity of lionfish populations, demonstrated by their rapid re-colonisation rates, means that management must take place at a wide geographic scale and be sustained in the long-term. With eradication no longer considered possible [56], strategies for control must instead focus on lionfish population suppression, to reduce negative impacts on reef communities. Experimental manipulation of lionfish densities on small patch reefs in the Bahamas has demonstrated that maintained lionfish population suppression does allow native fish populations to recover [57]. The necessary level of suppression is specific to individual reef sites and depends upon native fish community structure and sea surface temperature. The tipping point at which lionfish populations have a significant impact on native fish communities is called the site's **lionfish threshold density** (Fig. 5). That is, native fish populations can recover if the lionfish population is kept at or below the site-specific threshold density. Threshold density is affected by both the amount of standing prey biomass at the site, and the size structure of resident fishes, with smaller bodied fishes generating new biomass at faster rates than larger bodied individuals.

Calculating current and threshold densities for sites, and maintaining lionfish below threshold, presents the best opportunity for effective lionfish control. Due to resource limitations, sites should be prioritised based on social, economic and/or environmental importance. A strategic combination of fishery and market development, recreational culling by tourists, SCUBA divers, and MPA managers, and culling competitions, is likely to be the optimal approach to achieving this.

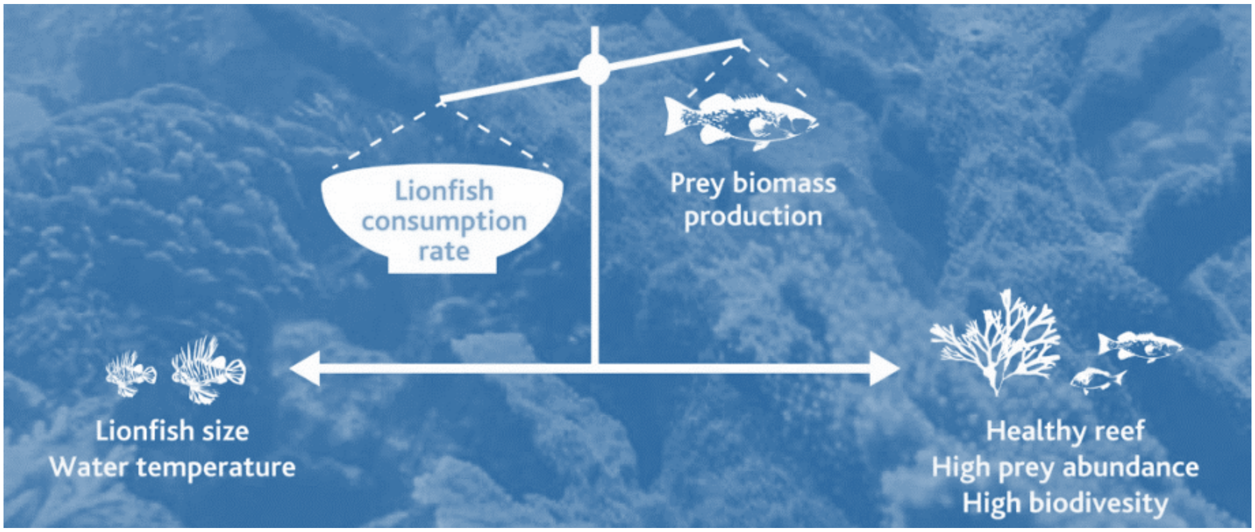


**Figure 5: A coral reef's lionfish threshold density is the tipping point between the rate at which lionfish consume prey (lionfish consumption rate) and the rate at which new prey biomass is created (prey biomass production).**

# Aims and objectives of study

The aim of this study was to establish a long-term lionfish monitoring approach, using a proven and standardized method, enabling effective monitoring and evaluation of conservation actions throughout the Belize MPA network.

**Objectives included:**

1. To assess lionfish population density, biomass and size structure in priority MPA areas
2. To assess prey fish, predator and competitor communities in priority MPAs
3. To establish lionfish threshold targets for site specific control

# Materials and methods

## Study design

Five MPAs were selected as being representative of the highly variable conditions and users of coral reefs across Belize, and ensuring inclusion of prioritised conservation areas that contain coral reefs. Caye Caulker Marine Reserve (CCMR), Bacalar Chico Marine Reserve (BCMR), Hol Chan Marine Reserve (HCMR) and South Water Caye Marine Reserve (SWCMR) are located along the main barrier of Belize Barrier Reef System, and Port Honduras Marine Reserve (PHMR) is located behind the main barrier. All five locations are multiple use marine reserves (MR) with demarcated zoning buoys indicating whether commercial fishing, sport fishing or other marine recreational activities such as snorkeling are permitted. For the purpose of this study, all zones were classified as either No Take Zone (NTZ), where no fishing is permitted, or General Use Zone (GUZ), where commercial fishing is regulated and all recreational activities permitted (Fig. 6). See National Lionfish Management Strategy (2019-2023), *Chapter 4: Case Study - Developing Lionfish Management Targets in Five Marine Reserves* for more information.

Survey sites were randomly selected by overlaying a numbered grid across a map of each MPA, populating this map with waypoints for known reef monitoring sites, haphazardly locating waypoints in grids without known reef monitoring sites, and ensuring that waypoints were distributed every ± 400 m. We selected lionfish survey sites by using a random number generator, paying attention to reef location to ensure that we balanced survey effort by reef type (backreef and forereef) and management regime (NTZ and GUZ).

## Site description

All forereef sites were spur and groove reefs, while backreef sites comprised continuous backreef (behind the reef crest), patch reef and fringing reefs around mangrove cayes. Surveys were restricted to depth ranges 1-5 m or 8-15 m, except for some shallow forereef sites in SWCMR where transects were located in a shallower depth band, 6-9 m. In PHMR, which is behind the main barrier, all sites were classified as backreef. A total of 176 belt transect surveys of the native prey fish community and 96 roving transect surveys of lionfish and native predators were conducted, at 50 sites across five marine reserves. Sites were also evenly balanced between management regime to allow for comparison. (Table 2)

***Table 2:*** *Number of survey sites in each marine reserve and zones (general use zone, GUZ and no-take zone, NTZ) within those reserves*.

| | | Management | | |
|---|---|---|---|---|
| **Reef Type** | **Region** | **GUZ** | **NTZ** | **Total Sites** |
| **Backreef** | **BCMR** | **4** | **3** | **7** |
| | **CCMR** | **2** | **2** | **4** |
| | **HCMR** | **3** | **3** | **6** |
| | **PHMR** | **3** | **5** | **8** |
| | **SWCMR** | **4** | **2** | **6** |
| ***Backreef Total*** | | ***16*** | ***15*** | ***31*** |
| **Forereef** | **BCMR** | **2** | **2** | **4** |
| | **CCMR** | **2** | **2** | **4** |
| | **HCMR** | **2** | **3** | **5** |
| | **SWCMR** | **3** | **3** | **6** |
| ***Forereef Total*** | | ***9*** | ***10*** | ***19*** |
| **Total Sites** | | **25** | **25** | **50** |

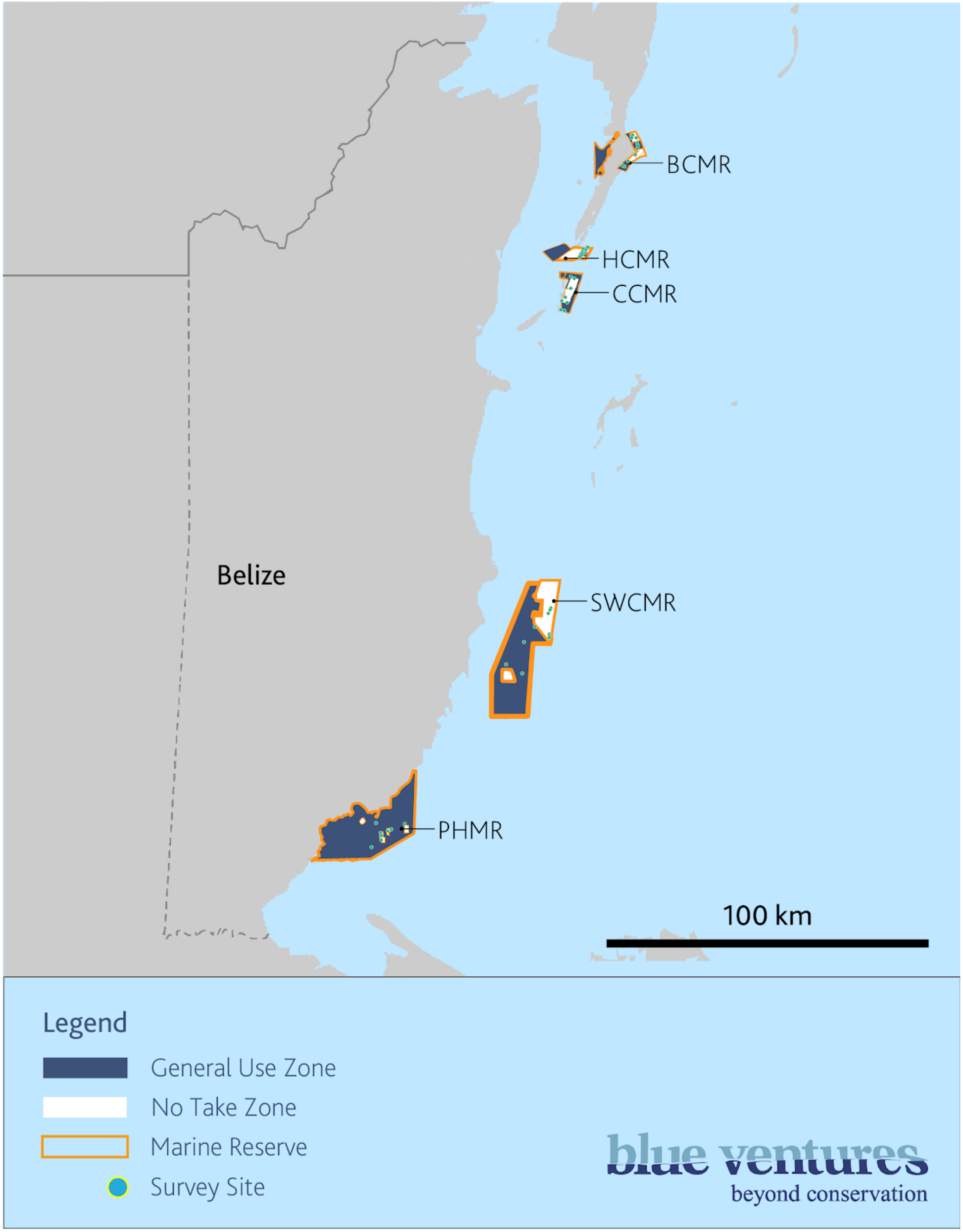


**Figure 6: Map of the five marine reserves and survey site, indicating if NTZ or GUZ**

## Data collection method

Field data was collected on lionfish and native fish communities between October and December 2015 using the Lionfish Focused Search method, a standard methodology for lionfish population and ecological impact monitoring [50,58]. All survey participants were trained in conducting the method and passed a test in estimating in-water fish size, within a week prior to data collection. To perform fish belt transects, the researcher additionally needed to have passed a REEF Fish Identification Level 3 test or higher within six months prior to data collection.

**Fish >30 (fish belt transect 50 m x 2 m)**

At each forereef site, two 50 m transect tapes were deployed parallel to one another and following the reef spur formation (Fig. 7). As the transect was being laid, one diver recorded all fish with a total length (TL) greater than 30 cm within 2 m of either side of the transect tape – identified to species level and tallied by TL. On backreef sites that represented patch reef habitat less than 50 m in diameter, the transect length matched the length of the patch reef. All actual transect lengths and widths were recorded on the underwater data sheet.

**Prey Fish (fish belt transect 10 m x 2 m)**

Along the same transect tape, a diver also gathered data on small-bodied reef fishes (i.e. <30 cm TL) for two subsections of the line (10 m long x 2 m wide each). For small patch reefs with truncated transects, these two subsections were made proportionately shorter. For prey fish transect belts, all fishes were identified to species level and tallied by size (TL) to the nearest cm. To perform these surveys, the researcher additionally needed to have passed REEF Fish Identification Level 3 test.

**Lionfish focused search (roving transect 50 m x 10 m)**

On each transect, a buddy pair of divers systematically swam the entire length of the transect using an S-shaped search pattern (Fig. 7), covering an area 10 m wide and searching in caves and crevices to record species, behaviour and estimate TL of lionfish and competing predators (e.g. grouper spp.) following the method of Green et al (2012). On patch reefs smaller than the transect area, actual dimensions of the patch were recorded and a full census performed. For full methods, see Appendix II.

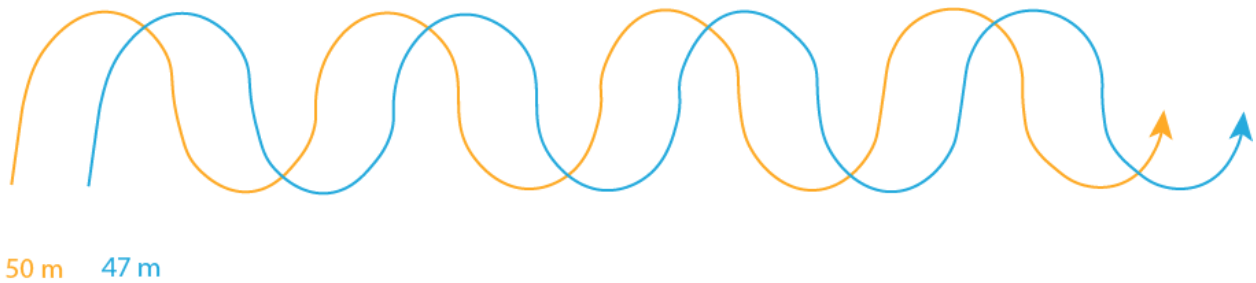


**Figure 7a: S-shaped search pattern by the leader (blue) and recorder (orange) along the transect.**

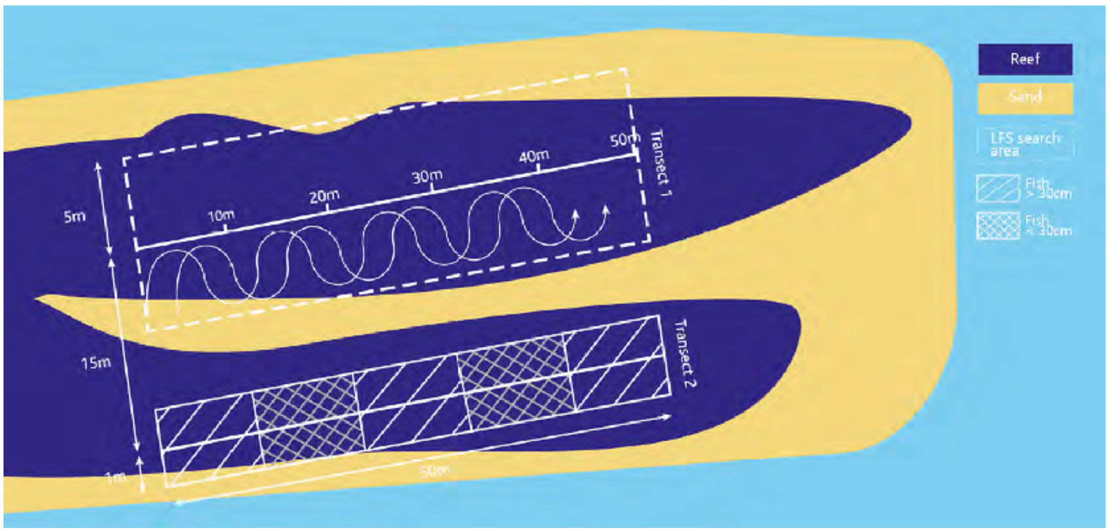


**Figure 7b: Illustration of an LFS transect layout at a survey site**

## Data analysis

### Population Status of Invasive Lionfish and Native Fishes

We converted visual estimates of fish length to weight by estimating the body mass (B) of each individual of fish species *i* using the allometric scaling function,

$$B = a_i L^{b_i}$$

where L is the TL of the individual of species *i* observed during a visual survey and $a_i$ and $b_i$ are constants specific to that species.

For lionfish, on continuous reef sites where two transects were performed, results of roving transects were combined to generate an estimate of lionfish density per site, as a larger survey area provides better estimates due to lionfish's clumped distribution [58].

Data on native fishes from belt transect surveys were analysed separately and associated to roving transects as matched data at the site level. All fish less than 14 cm TL (the maximum prey size reported for lionfish [57]) sighted on our visual belt transect surveys were categorized as potential lionfish prey. When calculating site biomass across all belt transects, observations of fish recorded as the same TL, were included only once, to reduce any risk of double counting the same species. Fishes were categorised into functional groupings as follows: small-bodied prey species (as identified a priori in studies of lionfish stomach contents); small-bodied non-prey species; large-bodied fishes considered ecologically similar to lionfish based on diet and body size (competitors); large-bodied non-predatory and non-competitive fishes; and large predatory fish (top carnivores). Refer to Appendix III for a detailed description of categories.

**Lionfish threshold densities**

An ecological model published by Green et al., (2014)[57] was applied to calculate site-specific lionfish threshold densities. The model uses field data including water temperature, prey species abundance and size, and lionfish body size distribution to estimate prey biomass production and lionfish biomass consumption rates, to predict the density at which lionfish populations begin to deplete the standing biomass of their prey on invaded marine habitats (i.e. the threshold density at which ecological impacts to their prey base of native fishes occur). The model was then re-run using reduced and increased lionfish average size (adjusted mean body size; 15 cm and 30 cm TL, respectively) to estimate threshold densities for possible future scenarios with different lionfish population size structures.

The model is set up to provide 1,000 predictions of threshold density for each survey site, and the $25^{th}$ percentile of these predictions was selected as the ecological threshold for that particular site. We chose to use the $25^{th}$ percentile instead of the median ($50^{th}$ percentile), as the model has only been tested in patch reefs and therefore choosing the $25^{th}$ percentile represents a more precautionary approach.

# Results

## Comparison of native fish community diversity between regions

The results show that BCMR and SWCMR observed the highest Species Richness (SR) from belt transects compared across regions (30 species and 31 species, respectively) and BCMR, HCMR and CCMR recorded the highest Shannon's Diversity Index (2.5, 2.4 and 2.4, respectively). Conversely, PHMR recorded the lowest Species Richness (SR) and Shannon's Diversity Index (H') of all five regions (Fig. 8).

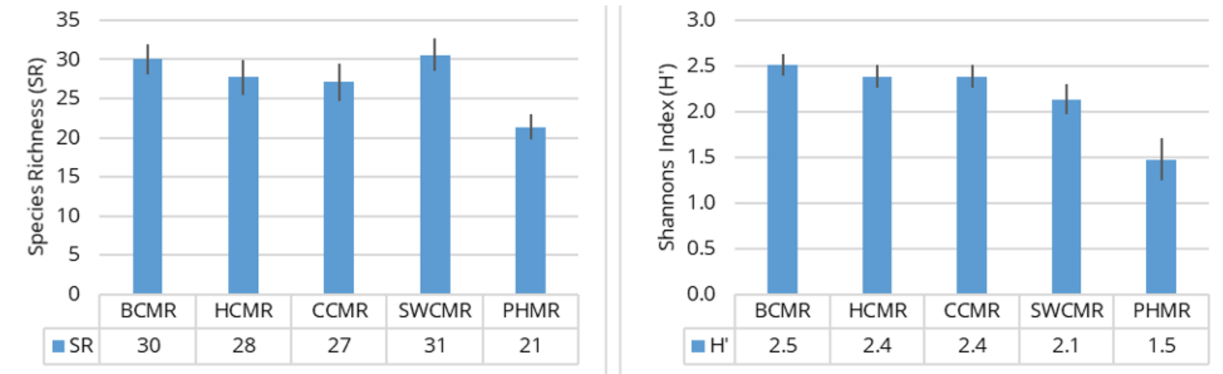


**Figure 8: Total Species Richness (SR) and Shannon's Diversity Index (H') with results presented by region.**

## Native reef community composition

Data collected from belt transects on community composition of reef fishes across regions reveals that large predators at HCMR and PHMR had the highest biomass. CCMR and HCMR recorded the highest biomass of large-bodied competitors (889 and 683 kg/ha). Small-bodied non-prey fish biomass remained low across all regions and BCMR and SWCMR recorded the lowest biomass for both large bodied competitors and non-competitors respectively (Fig. 9).

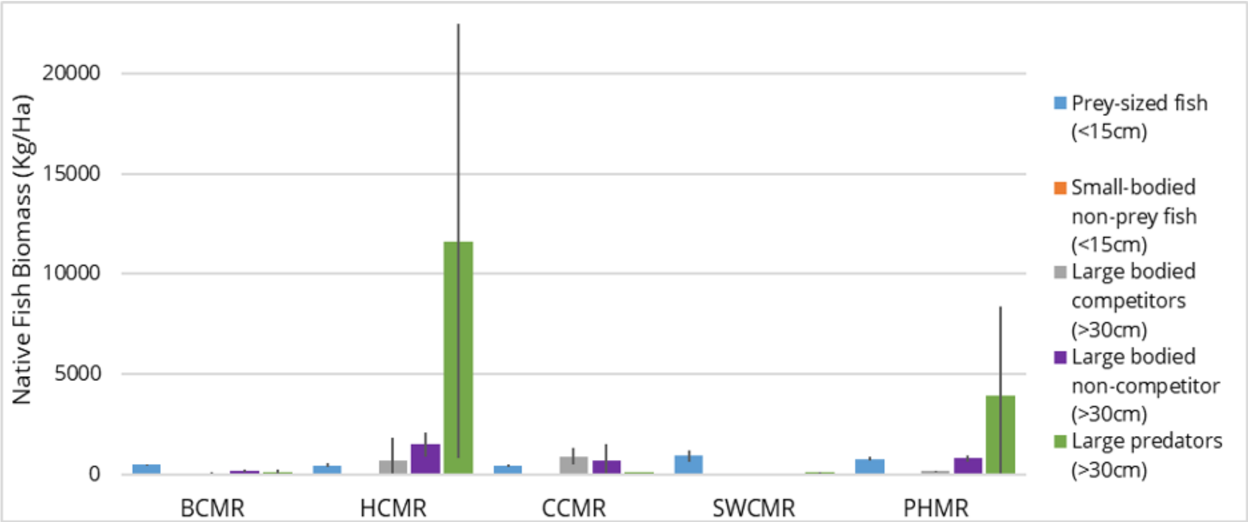


**Figure 9: Native fish biomass (Mean ± 95% confidence intervals) observed on belt transect surveys in each reserve (abbreviation list provided on page 1 of the report), by fish functional group.**

Each category was broken down into fish families. From the large-bodied competitor data (Fig. 10), snappers (Lutjanidae) feature highest in biomass across all regions followed by seabasses (Serranidae), which observed a higher biomass at CCMR and BCMR respectively. SWCMR had the lowest biomass of large-bodied competitors across all five regions. From the large-bodied non-competitor data (Fig. 11), "Other reef fish" dominated the surveys at HCMR and PHMR and parrotfish (Scaridae), constituted a large portion of the fish biomass across all surveys except SWCMR, with parrotfish making up the majority of non-competitors on surveys in CCMR.

The highest proportion of large predatory fishes were seen on surveys in HCMR and CCMR with rays featuring highest in biomass among surveys (Fig. 12).

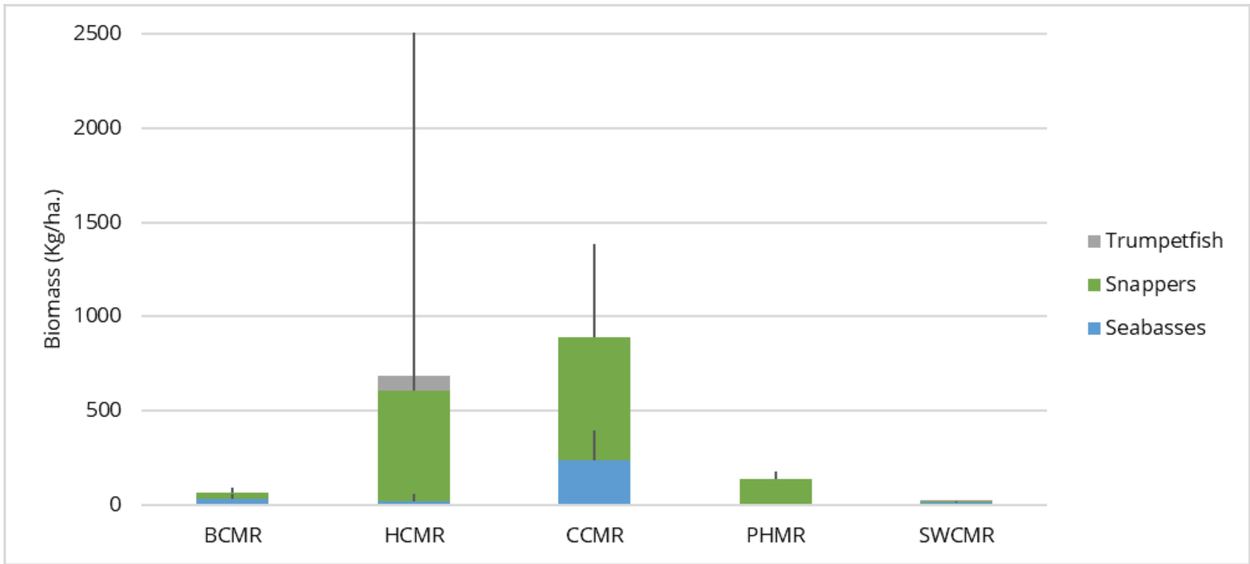


**Figure 10: Biomass of large bodied competitor fishes (mean ± 95% confidence intervals) with results presented by fish family and region.**

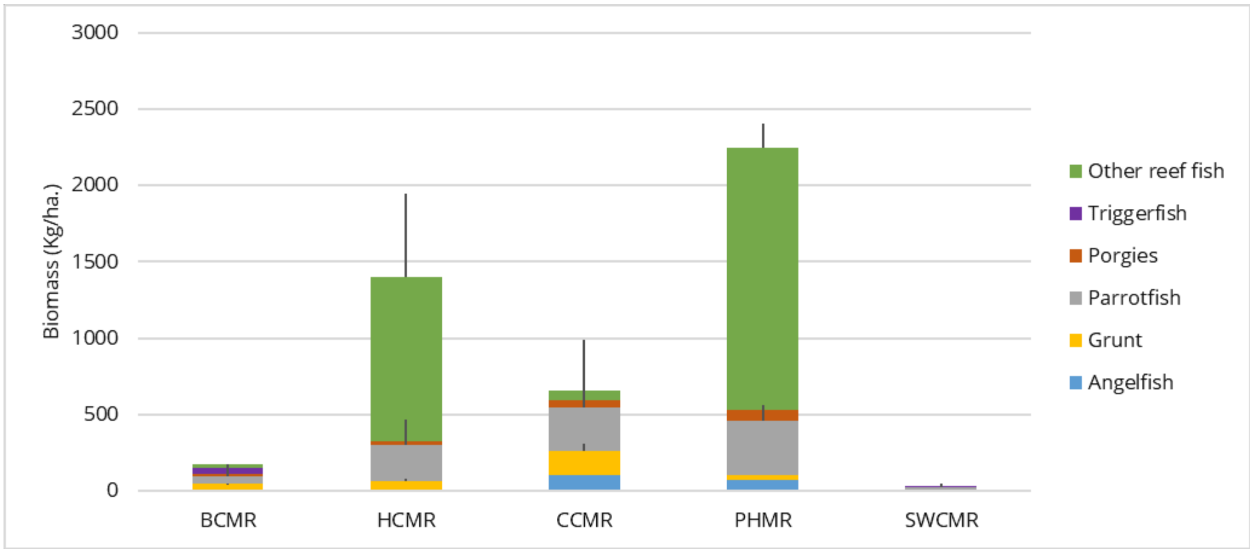


**Figure 11: Biomass of large bodied non-competitor fishes (mean ± 95% confidence intervals) with results presented by fish family and region.**

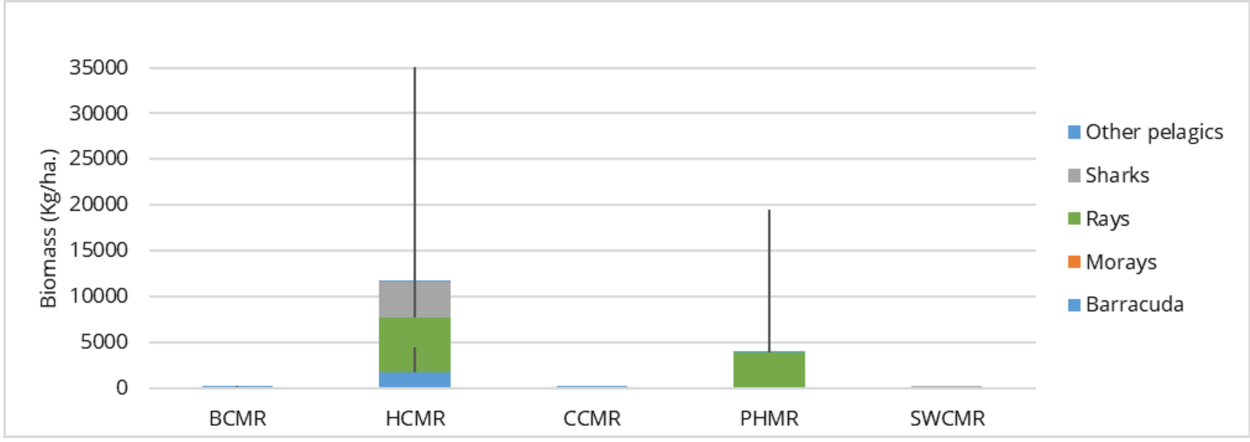


**Figure 12: Biomass of large predatory fish (mean ± 95% confidence intervals) with results presented by fish family and region.**

In all five regions, when fish categories were compared across management zone, NTZs were recorded to have higher native fish biomass than their GUZ counterparts. Large-bodied competitors featured highest in HCMR (1230 ± 703 kg/ha) and CCMR (1256 ± 969 kg/ha) NTZs, with CCMR recording the highest competitor biomass in its GUZ (522 ± 26 kg/ha). The same trend was observed with large-bodied non-competitors, with both HCMR and CCMR recording highest biomass accordingly (1751 ± 912; 1049 ± 979 kg/ha). Large predatory fish were observed highest in HCMR's NTZ (19102 ± 160 kg/ha) and GUZ (2829 ± 0 kg/ha) (Fig. 13).

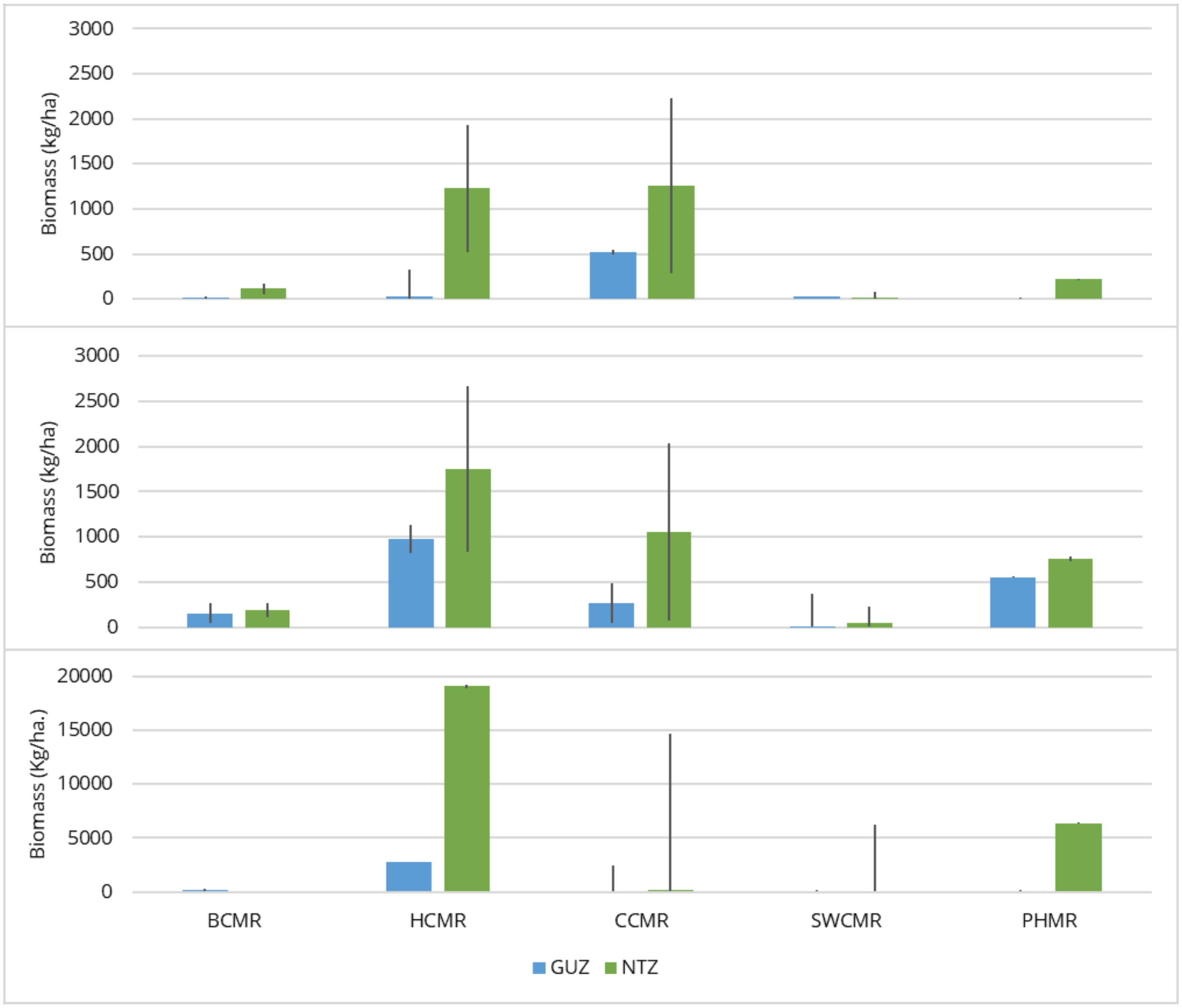


**Figure 13: Native fish biomass (mean ± 95% confidence intervals) with results presented by category a). large-bodied competitors b). large-bodied non-competitive fishes and c). large predators.**

## Caribbean Spiny Lobster

Biomass of Caribbean Spiny Lobster (*Panulirus argus*) was highest in HCMR (4.5 ± 2.7 kg/ha) in the NTZ and PHMR recorded the highest biomass (3.9 ± 1.9 kg/ha) amongst GUZ zones (Fig. 14). Lobster biomass was lowest in the NTZs of BCMR, HCMR AND CCMR (<1 kg/ha).

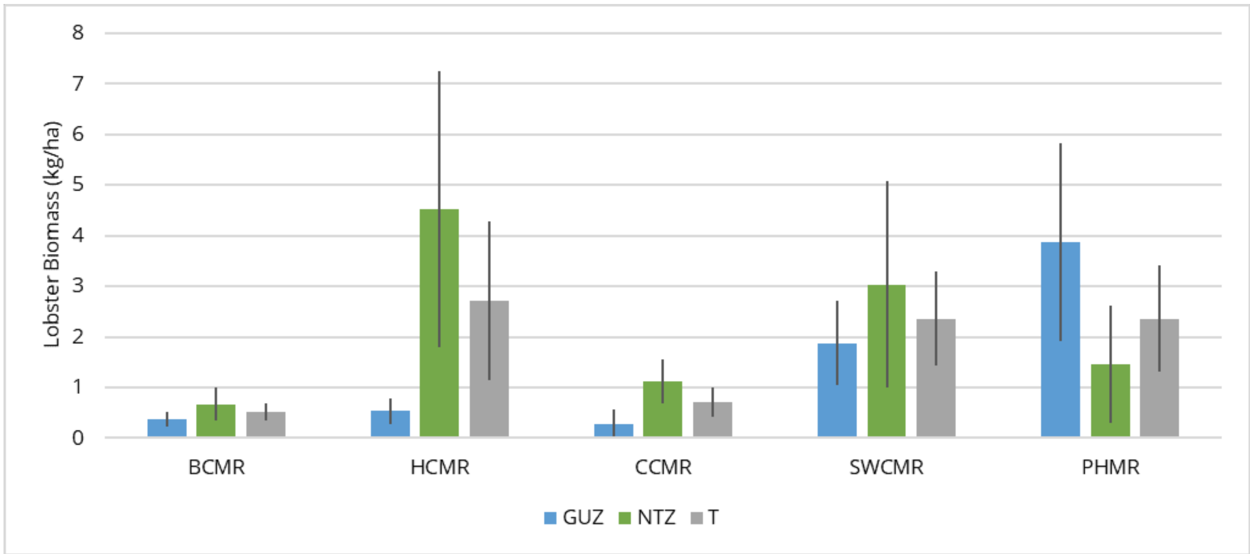


**Figure 14: Biomass of Caribbean spiny lobster, *Panulirus argus* (mean ± 95% confidence intervals) observed on belt transects in each marine reserve, within no-take zones (NTZ, blue bars), general use zones (GUZ, green bars) and total area (T, grey bars).**

## Prey fishes

In total 76 species of fish from 20 families were sighted that were within the size limits that could be accessed by lionfish predators across the system, with the composition of native prey fish community differing between each of the five regions (Appendix IV). Excluding surveys at 5-8m, prey biomass was significantly different between reef regions ($p = 0.019$; DF = 4; $F = 3.4$), with sites in SWCMR and PHMR having greater fish biomass than the other three regions (Fig. 15).

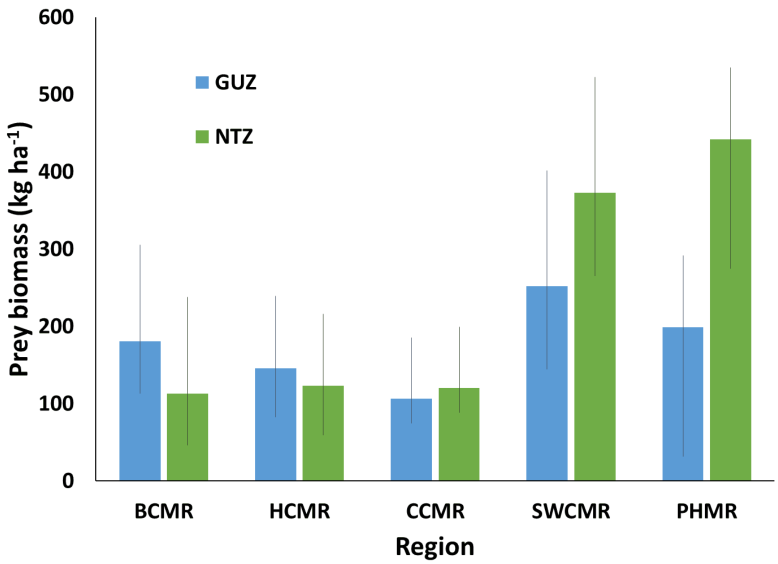


**Figure 15: Biomass of prey-sized native fishes (mean ± 95% confidence intervals) observed on belt transect surveys, for both NTZz and GUZs in each reserve.**

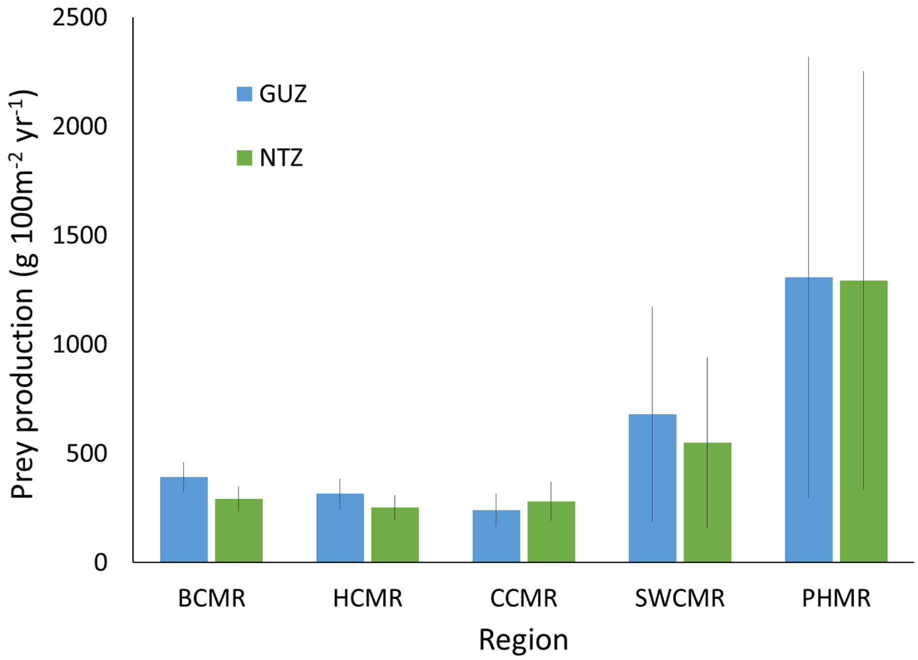


**Figure 16: Productivity of prey-sized native fishes (mean ± 95% confidence intervals), calculated using Metabolic Scaling theory with body mass estimates collected during belt transect surveys.**

## Lionfish population status

A total of 22 lionfish were sighted on visual surveys from 11 of the 50 coral reef sites that were studied in five coastal regions of Belize. The mean estimated TL of lionfish sighted was 21 ± 2 cm (SEM), with body sizes ranging from 8 to 32 cm TL (Fig. 17).

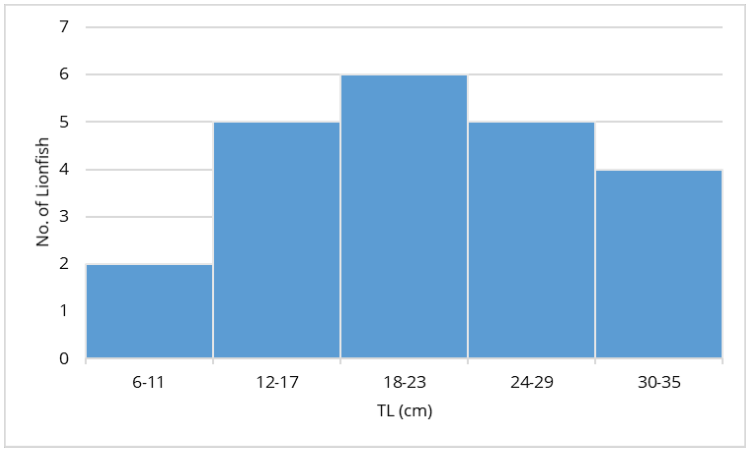


**Figure 17: Distribution of lionfish body sizes (total length [TL] to the nearest 1 cm; n=22) estimated visually during surveys across all five marine reserves off coastal Belize.**

Excluding surveys at 5-8 m, lionfish density was significantly different between reef regions ($p = 0.018$; DF = 4; F = 3.4), with sites in SWCMR having the highest densities. In contrast, lionfish were absent from our surveys in PHMR, and very low or zero at sites within CCMR and HCMR (Fig. 18). In SWCMR, lionfish density was greater in shallow, backreef sites (29 ± 20 ind.$ha^{-1}$) when compared with deep, forereef sites (2 ± 2 ind.$ha^{-1}$). Lionfish density did not differ significantly between depth bands ($p = 0.99$, DF = 1, F = 0.001) or protection status ($p = 0.13$, DF = 1, F = 2.37).

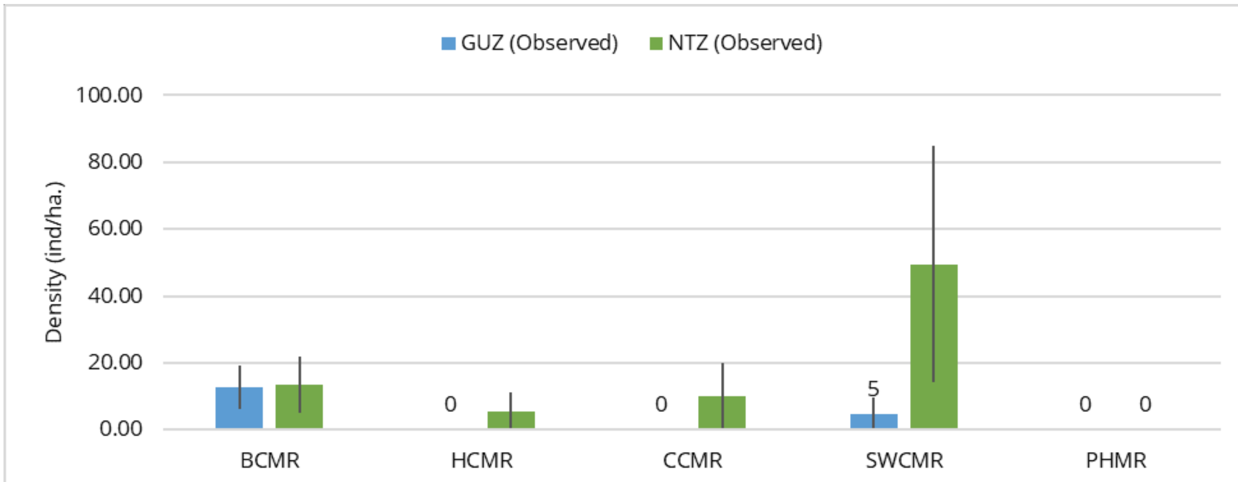


**Figure 18: Density of lionfish (mean ± 95% confidence intervals) inside no-take zones (NTZ) and general use zones (GUZ) of five marine reserves.**

## Lionfish threshold densities

Lionfish threshold density, predicted using the ecological model developed by Green et al. (2014), varied greatly across coral reef sites and regions (Appendix V). Threshold densities were highest (i.e. reefs can withstand the greatest density of invasive lionfish) within NTZs in PHMR and SWCMR. At the time of our surveys, lionfish densities were at or below threshold levels in nearly all study areas, except for coral reefs within the NTZs at SWCMR and HCMR where average densities exceed levels at which predation impacts are forecast to occur (Fig. 19). In total, 22% of surveyed sites exceeded the predicted threshold density, with 18% of these designated as NTZs (Fig. 20)

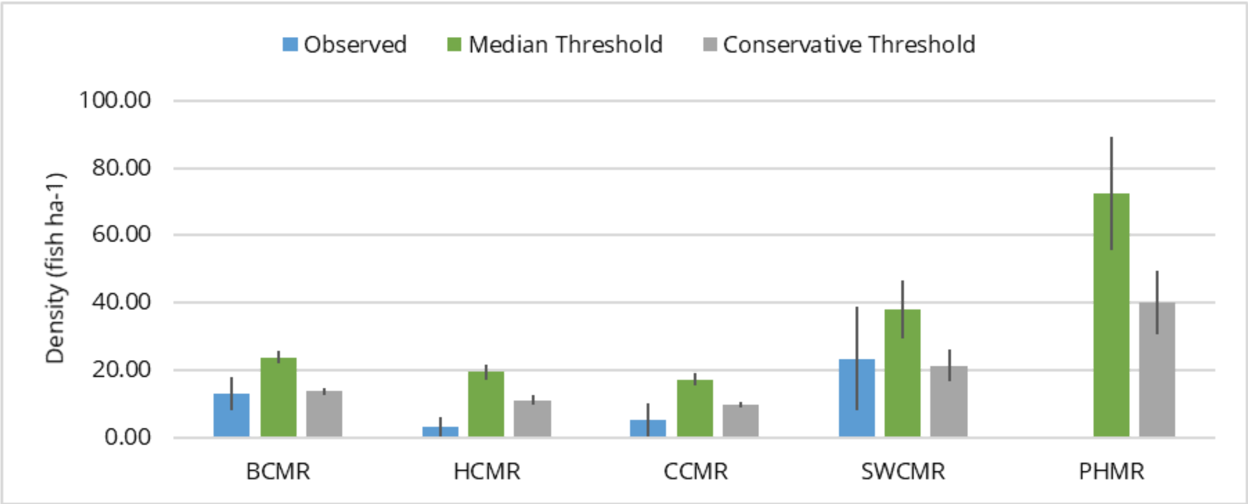


**Figure 19: Density of lionfish (mean ± 95% confidence intervals) in the five selected marine reserves (dark blue bars) alongside intermediate (light green bars) and conservative (grey bars) threshold densities (mean ± 95% confidence intervals).**

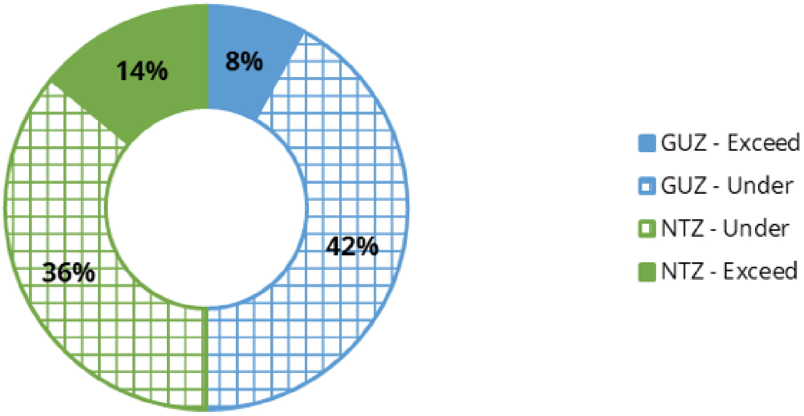


**Figure 20: The proportions of all NTZs (blue) and GUZs (green) exceeding (hatched) and below (solid) lionfish threshold densities.**

# Discussion

## General discussion of results

Lionfish are now a part of every tropical marine ecosystem throughout the Caribbean region, having colonised coastal mangroves, seagrass beds, coral reefs, continental slopes and human-made structures such as fish and lobster traps, piers and discarded debris. Basic data on lionfish populations is lacking from the majority of Belize's marine reserves, which has made it impossible to develop, implement or evaluate management targets and action plans. The findings in this study help to address this critical issue and present the most thorough population census to date for invasive lionfish and associated native fish communities in Belize. Having addressed the status of lionfish across five priority marine reserves, we have been able to develop site-specific threshold density estimates of lionfish within different management zones and provide a framework for effective population suppression within the BBRRS. Our results show that lionfish populations are generally low across all five regions, with no presence observed within the PHMR and very low or no observations on reefs within the CCMR and HCMR (Fig. 18). In SWCMR, lionfish density was greater in shallow, backreef sites versus deep, forereef sites. Excluding surveys at 5-8m, lionfish density was significantly different amongst regions, however there was no significant difference between depth bands or protection status. Lionfish were also observed at higher densities and as larger individuals within NTZs, which corresponded with the higher prey biomass observed within these zones (Fig. 18). Reefs can sustain larger numbers of lionfish if lionfish average TL is smaller [57], however with so few lionfish sighted across the system, it was not possible to evaluate how body size distributions varied with protection status or habitat type.

Lionfish feed on a wide range of juvenile fish and crustaceans which include important ecological and commercial species, and predation by lionfish can cause significant declines in the abundance of native fishes at different spatial and temporal scales [4,57]. Across all MPA regions, the composition of the native prey fish fauna varied between region and prey biomass was significantly different between reef regions (excluding surveys 5-8m) (Fig. 15). Sites in SWCMR and PHMR were shown to have greater prey fish biomass and productivity than the other three regions (Figs. 15 & 16). Prey biomass production is linked to both the amount of standing prey biomass at the site and the size structure of resident fish populations, with smaller bodied individuals generating new biomass at faster rates than larger bodied individuals [59]. When compared against protection status, prey biomass was higher in NTZs than the GUZ, and highest prey biomass was recorded in PHMR and SWCMR. These differences could be attributed to the fact that large-bodied competitors and lionfish were considerably less abundant at these locations and therefore have less of an impact on prey communities.

## Native fish community distribution

Native fish biomass across our surveys was highest within the NTZs of all five regions. The data suggests that these zones are effective tools for replenishing and conserving native biodiversity. Large-bodied competitors, which included a majority of snapper (Lutjanidae) and seabass (Serranidae) species, were highest within the NTZs of HCMR and CCMR. These reef-associated species, although recorded at size classes (>30cm) considered to be no longer vulnerable to predation by lionfish, are known to exploit the same ecological niche as lionfish, based on diet and body size and compete for similar resources (food and shelter) within the reefscape [29,58]. Given that these species contribute significantly to Belize's commercial fishery, it is important to monitor changes to the stock and identify areas of vulnerability. Selective predation by lionfish may also have repercussions for large-bodied non-competitors, which include parrotfish (Scaridae). Both herbivorous and commercial fishes have a body shape that is vulnerable to lionfish predation [18] and juveniles of at least some of these species may be prey for lionfish. A higher rate of lionfish-induced mortality on juvenile stages could impair herbivory, thereby reducing ecological functioning and overall resiliency of reef systems in the long term. Additionally, cascading impacts to large predatory fish such as barracuda and elasmobranchs – which are considered to be important keystone species in mediating marine food webs - could occur [60].

This study was designed to provide a 'snapshot' of the structure of lionfish and native fish communities in Belize's MPAs, and a baseline which MPA managers can use to evaluate management effectiveness. Further research is required to update the status of these indicators as well as expand the scope of this study to include other MPAs, improving existing knowledge on the status of the invasion and providing a better understanding of the spatial and temporal scales and drivers of native fish and lionfish community structure within Belizean MPAs.

## Establishing lionfish threshold targets

It has been demonstrated that effective lionfish control is achievable through population suppression to site-specific thresholds [57]. Therefore, determining lionfish suppression targets and strategies to meet those targets must form the core of any lionfish control strategy. The necessary level of suppression is unique to individual reef sites and depends upon native fish community structure and sea surface temperature. Our reef-specific model predictions use a size-based scaling relationship between fish size, production rate and lionfish predation mortality, supporting the evidence that lionfish predation has a stronger influence on prey population dynamics than recruitment and mortality via natural predation [57]. Lionfish threshold density is the tipping point between the rate at which lionfish consume prey and the rate at which new prey biomass is created [57]. The rate at which lionfish consume prey (lionfish consumption rate) increases with lionfish size and water temperature [61]. As lionfish body size increases, the density of lionfish that invaded coral reef fish communities can withstand decreases. In contrast, coral reef fish communities can tolerate higher densities of smaller bodied invasive lionfish predators before declines in standing biomass are forecasted to occur.

> **Therefore, if lionfish density at a coral reef site exceeds the site's predicted lionfish threshold density, it is expected that the biomass of prey fish will decrease over time. If lionfish density at a coral reef site is below its predicted threshold density, it is not expected that lionfish will have a significant impact on prey fish biomass [18,36,57].**

## Management implications

Effective management can only be achieved when the observed lionfish density is significantly below the target threshold density [57]. Threshold densities varied greatly across management zones and geographical regions, driven by differences in prey biomass production and inter-reef variation. Threshold densities were highest within PHMR, where reefs were predicted to be able to withstand the highest density of lionfish. In general, studies show that reefs within NTZs are predicted to be able to withstand a higher density of lionfish (i.e. have a higher threshold) compared with reefs in adjacent GUZs [36,57]. (Figure 18). Our results show that threshold densities were highest within the NTZs of PHMR and SWCMR, indicating that these regions are more resilient to the impacts of the invasion. Additionally, lionfish densities were at or below threshold levels in nearly all study areas, except for coral reefs within the NTZs at SWCMR and HCMR where average densities exceed levels at which predation impacts are forecasted to occur. In total, 22% of surveyed sites exceeded the predicted threshold density, with 18% of these designated as NTZs (Figure 20). This is an important result and suggests that the majority of reefs that were found to be ineffectively managed for lionfish occur within NTZs. This is a major problem, as NTZs will cease to function as fish replenishment zones that sustain biodiversity if lionfish populations are left unchecked.

This study backs up the assertions that assemblage-specific values of prey and lionfish biomass determine the severity of predation induced prey declines, and the level of control required to mitigate them [18]. Green et al. (2014) also found that morphological and behavioural traits predisposed certain prey species to be more vulnerable to the effects of lionfish predation. Juvenile wrasse and other small, shallow-bodied, solitary fishes found resting on or just above the reef are considered to be most vulnerable. PHMR and SWCMR are known to support large numbers of endemic reef fish, including the endangered social wrasse (*Halichoeres socialis*), which exhibits most of these preferred prey characteristics [62]. The probability of extinction is greatest for rare and endemic species that risk being selectively targeted by lionfish, therefore the Belize lionfish invasion, if not effectively controlled, may have serious implications for native biodiversity. Experimental manipulation of lionfish densities on small patch reefs in the Bahamas demonstrated that maintained lionfish control efforts does allow native fish populations to recover [57]. On reefs where lionfish were kept below threshold densities, native prey fish biomass increased by 50 - 70%.

Although our study was able to develop site-specific conservation targets to effectively suppress lionfish populations, there were several limitations. The predicted target estimates displayed high variability and large error due to the low abundance of lionfish recorded across surveys. Improved accuracy could be achieved with an increased sample size. Additionally, surveys only focused on coral reefs up to 18m depth. Further study needs to be undertaken to answer how thresholds could be adapted to non-reef environments, including mangrove and seagrass ecosystems. Shallow reefs are used by all stakeholders including commercial fishers who free dive to depths of 18m to access fishery resources. Deeper reef environments (>18 m), where lionfish are known to be larger and more abundant, are technically challenging to survey and may require resources beyond those available to a given protected area. Finally, it is important to note that for the purposes of this study, conservative estimate (25$^{th}$ percentile) of threshold density was used. Given that threshold will vary from reef to reef, model predictions can only be confidently applied at small scales, and cannot be considered applicable at national or regional scales.

# Conclusions and recommendations

The LFS method is a complex technical marine monitoring survey that requires advanced diving ability and excellent fish ID skills. There is also a need to perform a high level of replication, making these surveys expensive and time consuming. Data interpretation similarly can be complex & requires high technical scientific capacity. Within the Belize MPA network, it is unrealistic to complete these surveys annually, however a detailed population census is recommended every ~5 years, in order to be able to set appropriate ecological threshold targets for specific reef areas and management zones.

Through using this approach, MPA managers can identify whether lionfish management should be a priority, and/or which sites are most vulnerable to the impacts of lionfish and should be the focus of their efforts. For example, TIDE (which manages PHMR) could confidently *not* address lionfish in PHMR 2015-2020 as they knew they had extremely low actual densities and very high threshold densities, whereas BFD (manager of SWCMR) quickly responded to results by organizing a LF tournament that included NTZ areas. Finally, our study found that NTZs are most vulnerable to lionfish, yet these areas receive the least lionfish control, since no fishers or tour guides are permitted to operate within these zones. There is a need to establish sound guidelines for the implementation and continued support of lionfish culling activities within Belizean MPAs, to be able to effectively address the threat of the invasion and target vulnerable areas.

## National Biodiversity Monitoring Plan

The approach as outlined in this study for lionfish management in Belizean MPAs is aligned with existing priorities and objectives within the National Biodiversity Monitoring Program (NBMP), which serves as a tool to enable effective monitoring of biodiversity and protected areas and the implementation the National Biodiversity Strategy and Action Plan (NBSAP).

## Management action plan outline

There is a need to develop robust targets for lionfish control and management that aim to minimize the impacts of the invasion at local scales.

Green (2014)[57] outlines a general approach that can be characterized by three steps that can be applied across invasions:

1. Quantifying the impacts of the invader on native communities;
2. Identifying population thresholds of the invader that elicit community effects, and
3. Setting these thresholds as targets for control.

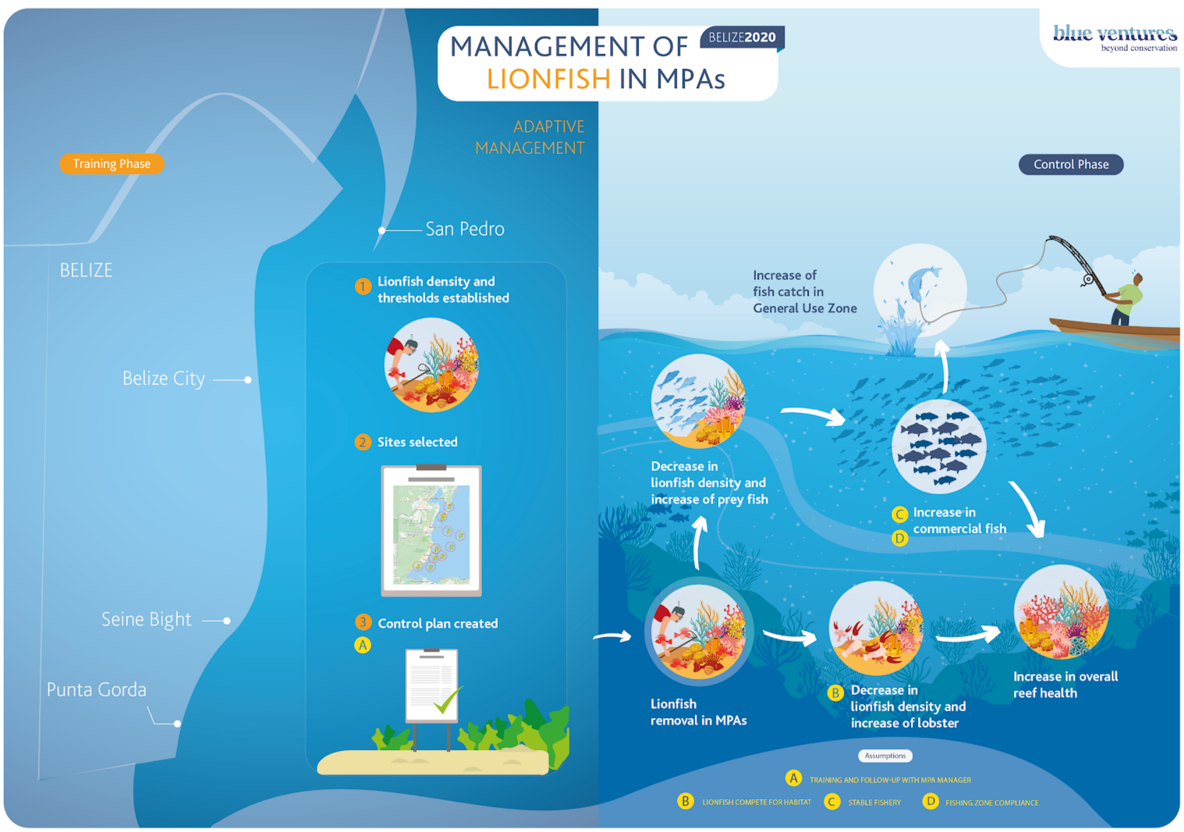


**Figure 21: The theory of change for management of lionfish in Belizean MPAs.**

## Key management steps

Establish key management objectives

- What is most important to the manager?
- What are the conservation targets?

Key questions and characterisation of the MPA

- Are there any known nursery sites (fish or invertebrate) in the MPA?
- Are there any endemic or endangered species directly threatened by lionfish in the MPA?

Identify resources

- Users: consider wealth, interest, permissions and access
- Who is legally permitted to cull lionfish in the NTZs of this reserve?
- How many people, affiliation, attributes (e.g. visitor/resident, SCUBA/non-SCUBA), level of interest in culling activities

Establish ecological threshold targets – create specific conservation targets for sites assessed and an average target for the reserve by management zone.

Identify priorities and develop control plan with reserve manager.

Using the steps outlined above to create removal targets for adaptive management will result in a more efficient allocation of limited resources to management. Lionfish then need only be controlled below levels which cause unacceptable ecological change. This is an important benefit for conservation practitioners seeking to allocate resources in a way that sustains sufficient invasive species control over the long term, in priority habitats [57].

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# Appendices

## Appendix I - Table of Belize protected areas & management designation

| PROTECTED AREA | MGMT./CO-MGMT | AREA (ACRES) | IUCN CATEGORY - WHS |
|---|---|---|---|
| **Bacalar Chico Marine Reserve * and National Park** | Fisheries Dept. | 15,766 | II (National Park) |
| **Blue Hole Natural Monument** | Forest Dept./BAS | 1,023 | II (Natural Monument) |
| **Caye Caulker Marine Reserve *** | Fisheries Dept./FAMRACC | 9,670 | |
| **Corozal Bay Wildlife Sanctuary** | Forest Dept./SACD | 180,509 | |
| **Gladden Spit and Silk Cayes Marine Reserve** | Fisheries Dept./ SEA | 25,978 | |
| **Glover's Reef Marine Reserve** | Fisheries Dept. | 86,653 | IV (Habitat/Species Management Area) |
| **Half Moon Caye Natural Monument** | Forest Dept./BAS | 9,771 | II (Natural Monument) |
| **Hol Chan Marine Reserve *** | Fisheries Dept. | 102,400 | |
| **Laughing Bird Caye National Park** | Forest Dept./SEA | 10,119 | II (National Park) |
| **Port Honduras Marine Reserve *** | Fisheries Dept./TIDE | 100,000 | |
| **Sapodilla Caye Marine Reserve** | Fisheries Dept./SEA | 38,594 | IV (Habitat/Species Management Area) |
| **South Water Caye Marine Reserve *** | Fisheries Dept. | 117,875 | IV (Habitat/Species Management Area) |
| **Swallow Caye Wildlife Sanctuary** | Forest Dept./FOSC | 8,972 | |
| **Turneffe Atoll Marine Reserve** | Fisheries Dept./TASA | 325,412 | |

## Appendix II - Lionfish Focused Search Method

Lionfish Focused Search Method 2016.pdf can be found here.

## Appendix III - Species and size classes included in each of the four categories considered in the native fish community analysis

| CATEGORY | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| **Large-bodied competitive fishes ecologically similar to lionfish based on diet and body size. (Figure 9: 'Large-bodied competitors') Only individuals >30cm TL considered in analysis** | Aulostomidae | *Aulostomus maculatus* | piscivore |
| | Lutjanidae | *Lutjanus analis* | carnivore |
| | Lutjanidae | *Lutjanus apodus* | carnivore |
| | Lutjanidae | *Lutjanus cyanopterus* | carnivore |
| | Lutjanidae | *Lutjanus griseus* | carnivore |
| | Lutjanidae | *Lutjanus jocu* | carnivore |
| | Lutjanidae | *Lutjanus mahogoni* | carnivore |
| | Scorpaenidae | *Scorpaena plumieri* | piscivore |
| | Serranidae | *Cephalopholis fulva* | piscivore |
| | Serranidae | *Epinephelus adscensionis* | piscivore |
| | Serranidae | *Epinephelus guttatus* | piscivore |
| | Serranidae | *Epinephelus striatus* | piscivore |
| | Serranidae | *Mycteroperca bonaci* | piscivore |
| | Serranidae | *Mycteroperca interstitialis* | piscivore |
| | Serranidae | *Mycteroperca tigris* | piscivore |
| | Serranidae | *Mycteroperca venenosa* | piscivore |

| CATEGORY | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| **Large-bodied non-predatory fishes (Figure 9: ‘Large-bodied non-competitors’). Only individuals >30cm TL considered in analysis** | Acanthuridae | *Acanthurus bahianus* | herbivore |
| | Acanthuridae | *Acanthurus chirurgus* | herbivore |
| | Balistidae | *Canthidermis sufflamen* | invertivore |
| | Echeneidae | *Echeneis naucrates* | omnivore |
| | Ephippidae | *Chaetodipterus faber* | omnivore |
| | Haemulidae | *Anisotremus surinamensis* | invertivore |
| | Haemulidae | *Anisotremus virginicus* | invertivore |
| | Haemulidae | *Haemulon album* | invertivore |
| | Haemulidae | *Haemulon carbonarium* | invertivore |
| | Haemulidae | *Haemulon flavolineatum* | invertivore |
| | Haemulidae | *Haemulon parra* | invertivore |
| | Haemulidae | *Haemulon plumierii* | invertivore |
| | Haemulidae | *Haemulon sciurus* | invertivore |
| | Holocentridae | *Holocentrus adscensionis* | invertivore |
| | Holocentridae | *Holocentrus rufus* | invertivore |
| | Holocentridae | *Myripristis jacobus* | invertivore |
| | Holocentridae | *Neoniphon marianus* | invertivore |
| | Holocentridae | *Sargocentron vexillarium* | invertivore |
| | Labridae | *Bodianus rufus* | invertivore |

| | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| | Labridae | *Halichoeres garnoti* | invertivore |
| | Lutjanidae | *Ocyurus chrysurus* | planktivore |
| | Monacanthidae | *Aluterus schoepfii* | herbivore |
| | Monacanthidae | *Aluterus scriptus* | omnivore |
| | Mullidae | *Mulloidichthys martinicus* | invertivore |
| | Mullidae | *Pseudupeneus maculatus* | invertivore |
| | Ostraciidae | *Lactophrys triqueter* | invertivore |
| | Pomacanthidae | *Centropyge argi* | herbivore |
| | Pomacanthidae | *Holacanthus ciliaris* | invertivore |
| | Pomacanthidae | *Pomacanthus arcuatus* | omnivore |
| | Pomacanthidae | *Pomacanthus paru* | omnivore |
| | Scaridae | *Scarus coeruleus* | herbivore |
| | Scaridae | *Scarus iserti* | herbivore |
| | Scaridae | *Scarus taeniopterus* | herbivore |
| | Scaridae | *Scarus vetula* | herbivore |
| | Scaridae | *Sparisoma aurofrenatum* | herbivore |
| | Scaridae | *Sparisoma rubripinne* | herbivore |
| | Scaridae | *Sparisoma viride* | herbivore |
| | Sparidae | *Calamus bajonado* | invertivore |
| | Sparidae | *Calamus calamus* | invertivore |

| CATEGORY | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| **Small-bodied lionfish prey species identified from stomach contents (Figure 9: 'prey sized fish'). Only individuals <15 cm TL considered in the analysis** | Apogonidae | *Apogon planifrons* | invertivore |
| | Apogonidae | *Apogon townsendi* | invertivore |
| | Apogonidae | *Phaeoptyx pigmentaria* | invertivore |
| | Atherinidae | *Atherinomorus sp.* | planktivore |
| | Aulostomidae | *Aulostomus maculatus* | carnivore |
| | Chaenopsidae | *Acanthemblemaria aspera* | planktivore |
| | Chaenopsidae | *Lucayablennius zingaro* | planktivore |
| | Gobiidae | *Coryphopterus bol* | omnivore |
| | Gobiidae | *Coryphopterus eidolon* | omnivore |
| | Gobiidae | *Coryphopterus glaucofraenum* | omnivore |
| | Gobiidae | *Coryphopterus hyalinus* | planktivore |
| | Gobiidae | *Coryphopterus personatus* | planktivore |
| | Gobiidae | *Gnatholepis thompsoni* | omnivore |
| | Gobiidae | *Lythrypnus spilus* | invertivore |
| | Gobiidae | *Priolepis hipoliti* | invertivore |
| | Grammatidae | *Gramma loreto* | invertivore |
| | Holocentridae | *Sargocentron coruscum* | invertivore |
| | Inermiidae | *Inermia vittata* | planktivore |
| | Labridae | *Bodianus rufus* | invertivore |

| | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| | Labridae | *Clepticus parrae* | planktivore |
| | Labridae | *Halichoeres bivittatus* | invertivore |
| | Labridae | *Halichoeres garnoti* | invertivore |
| | Labridae | *Halichoeres maculipinna* | invertivore |
| | Labridae | *Thalassoma bifasciatum* | planktivore |
| | Labrisomidae | *Labrisomus haitiensis* | invertivore |
| | Labrisomidae | *Malacoctenus boehlkei* | invertivore |
| | Monacanthidae | *Monacanthus tuckeri* | omnivore |
| | Mullidae | *Pseudupeneus maculatus* | invertivore |
| | Pomacentridae | *Chromis cyanea* | planktivore |
| | Pomacentridae | *Chromis multilineata* | planktivore |
| | Pomacentridae | *Stegastes partitus* | herbivore |
| | Pomacentridae | *Stegastes variabilis* | herbivore |
| | Scaridae | *Sparisoma aurofrenatum* | herbivore |
| | Serranidae | *Cephalopholis cruentata* | carnivore |
| | Serranidae | *Epinephelus striatus* | carnivore |
| | Serranidae | *Hypoplectrus spp.* | carnivore |
| | Serranidae | *Liopropoma rubre* | carnivore |
| | Serranidae | *Serranus tabacarius* | carnivore |
| | Serranidae | *Serranus tigrinus* | carnivore |
| | Synodontidae | *Synodus intermedius* | piscivore |
| | Synodontidae | *Synodus saurus* | piscivore |
| | Synodontidae | *Synodus synodus* | piscivore |

| CATEGORY | FAMILY | SPECIES | FUNCTIONAL GROUP |
|---|---|---|---|
| **Small-bodied non-prey species (Figure 9: 'Small-bodied non-prey fish'). All individuals <15 cm TL** | Gobiidae | *Elacatinus chancei* | invertivore |
| | Gobiidae | *Elacatinus evelynae* | invertivore |
| | Gobiidae | *Elacatinus genie* | invertivore |
| | Gobiidae | *Elacatinus horsti* | invertivore |

## Appendix IV - Relative ranked abundance of native prey fish species

Diversity of native prey-sized (i.e. <14cm total length) fish species sighted on transect surveys within five marine reserves. Numbers indicate the relative ranked abundance of species in each region, where 1=most abundant.

| Family | Species | Common Name | BCMR | CCMR | HCMR | PHMR | SWCMR |
|---|---|---|---|---|---|---|---|
| **Acanthuridae** | *Acanthurus bahianus* | Ocean Surgeonfish | 10 | 13 | 5 | | 13 |
| **Acanthuridae** | *Acanthurus chirurgus* | Doctorfish | | | | | 43 |
| **Acanthuridae** | *Acanthurus coeruleus* | Blue Tang | 2 | 5 | 2 | | 16 |
| **Carangidae** | *Carangoides ruber* | Bar Jack | 16 | | | | |
| **Chaenopsidae** | *Acanthemblemaria aspera* | Roughhead Blenny | | | 33 | | |
| **Chaenopsidae** | *Acanthemblemaria maria* | Secretary Blenny | 36 | | 35 | | |
| **Chaenopsidae** | *Acanthemblemaria spinosa* | Spinyhead Blenny | | | | | 54 |
| **Chaetodontidae** | *Chaetodon capistratus* | Foureye Butterflyfish | 24 | 12 | 21 | 6 | 20 |
| **Chaetodontidae** | *Chaetodon ocellatus* | Spotfin Butterflyfish | 34 | | | | |

| Family | Species | Common Name | BCMR | CCMR | HCMR | PHMR | SWCMR |
|---|---|---|---|---|---|---|---|
| **Chaetodontidae** | *Chaetodon striatus* | Banded Butterflyfish | 8 | | | | 38 |
| **Ginglymostomatidae** | *Ginglymostoma cirratum* | Nurse Shark | | | 22 | | |
| **Gobiidae** | *Coryphopterus dicrus* | Colon Goby | | | | 26 | 47 |
| **Gobiidae** | *Coryphopterus eidolon* | Pallid Goby | | | | | 52 |
| **Gobiidae** | *Coryphopterus glaucofraenum* | Bridled Goby | | 22 | 32 | | 40 |
| **Gobiidae** | *Coryphopterus personatus* | Masked Goby | 32 | 20 | | 17 | 18 |
| **Gobiidae** | *Elacatinus dilepis* | Orangesided Goby | | | 34 | | 51 |
| **Gobiidae** | *Elacatinus evelynae* | Sharknose Goby | 38 | | | | |
| **Gobiidae** | *Elacatinus lobeli* | Caribbean Neon Goby | | | | | 35 |
| **Gobiidae** | *Gnatholepis thompsoni* | Goldspot Goby | 37 | | | | |
| **Haemulidae** | *Anisotremus surinamensis* | Black Margate | 35 | | | | |
| **Haemulidae** | *Anisotremus virginicus* | Porkfish | | | | 7 | 49 |
| **Haemulidae** | *Haemulon aurolineatum* | Tomtate | | | | 1 | |
| **Haemulidae** | *Haemulon chrysargyreum* | Smallmouth Grunt | 33 | | | | |
| **Haemulidae** | *Haemulon flavolineatum* | French Grunt | 3 | 7 | 10 | 2 | 2 |
| **Haemulidae** | *Haemulon parra* | Sailors Choice | 22 | | | | |
| **Haemulidae** | *Haemulon plumierii* | White Grunt | 13 | | | 9 | 11 |

| Family | Species | Common Name | BCMR | CCMR | HCMR | PHMR | SWCMR |
|---|---|---|---|---|---|---|---|
| **Haemulidae** | *Haemulon sciurus* | Bluestriped Grunt | 11 | | | | |
| **Holocentridae** | *Holocentrus adscensionis* | Squirrelfish | | | | | 45 |
| **Holocentridae** | *Holocentrus rufus* | Longspine Squirrelfish | | | 24 | | |
| **Holocentridae** | *Sargocentron coruscum* | Reef Squirrelfish | | | | | 23 |
| **Holocentridae** | *Sargocentron vexillarium* | Dusky Squirrelfish | 29 | | | | 41 |
| **Labridae** | *Bodianus rufus* | Spanish Hogfish | | 17 | 31 | | |
| **Labridae** | *Clepticus parrae* | Creole Wrasse | | | | | 1 |
| **Labridae** | *Halichoeres bivittatus* | Slippery Dick | 6 | 2 | 4 | 3 | 14 |
| **Labridae** | *Halichoeres cyanocephalus* | Yellowcheek Wrasse | | | | | 39 |
| **Labridae** | *Halichoeres garnoti* | Yellowhead Wrasse | 12 | 3 | 12 | 16 | 4 |
| **Labridae** | *Halichoeres maculipinna* | Clown Wrasse | 14 | 19 | | | 44 |
| **Labridae** | *Halichoeres poeyi* | Blackear Wrasse | | | 27 | | |
| **Labridae** | *Halichoeres radiatus* | Puddingwife | | | 20 | | |
| **Labridae** | *Halichoeres socialis* | Social Wrasse | | | | 14 | 22 |
| **Labridae** | *Lachnolaimus maximus* | Hogfish | | | | | 31 |
| **Labridae** | *Thalassoma bifasciatum* | Bluehead Wrasse | 9 | 9 | 6 | | 28 |
| **Lutjanidae** | *Lutjanus apodus* | Schoolmaster | 4 | | 1 | 4 | 10 |
| **Lutjanidae** | *Ocyurus chrysurus* | Yellowtail Snapper | 20 | | | 13 | |
| **Monacanthidae** | *Cantherhines pullus* | Orangespotted Filefish | 26 | | | | 46 |

| Family | Species | Common Name | BCMR | CCMR | HCMR | PHMR | SWCMR |
|---|---|---|---|---|---|---|---|
| **Mullidae** | *Pseudupeneus maculatus* | Spotted Goatfish | | | | | 25 |
| **Myliobatidae** | *Aetobatus narinari* | Spotted Eagle Ray | | | 30 | 19 | |
| **Pempheridae** | *Pempheris schomburgkii* | Glassy Sweeper | 27 | | 19 | | |
| **Pomacanthidae** | *Holacanthus tricolor* | Rock Beauty | | | 16 | | 32 |
| **Pomacentridae** | *Abudefduf saxatilis* | Sergeant Major | 23 | | 3 | 5 | 34 |
| **Pomacentridae** | *Chromis cyanea* | Blue Chromis | 31 | | 23 | | 8 |
| **Pomacentridae** | *Chromis multilineata* | Brown Chromis | | | 13 | | |
| **Pomacentridae** | *Microspathodon chrysurus* | Yellowtail Damselfish | 25 | 14 | 9 | 12 | 27 |
| **Pomacentridae** | *Stegastes diencaeus* | Longfin Damselfish | 5 | 4 | 11 | | 17 |
| **Pomacentridae** | *Stegastes dorsopunicans* | Dusky Damselfish | 17 | 15 | 7 | 10 | 7 |
| **Pomacentridae** | *Stegastes leucostictus* | Beaugregory | 30 | 21 | 14 | 22 | 37 |
| **Pomacentridae** | *Stegastes partitus* | Bicolor Damselfish | | 8 | 25 | 20 | 30 |
| **Pomacentridae** | *Stegastes planifrons* | Threespot Damselfish | 28 | 6 | 28 | 18 | 12 |
| **Scaridae** | *Scarus iserti* | Striped Parrotfish | 1 | 1 | 8 | 8 | 3 |
| **Scaridae** | *Scarus taeniopterus* | Princess Parrotfish | 15 | | | 21 | 9 |
| **Scaridae** | *Sparisoma atomarium* | Greenblotch Parrotfish | | | | | 53 |
| **Scaridae** | *Sparisoma aurofrenatum* | Redband Parrotfish | 7 | 10 | 18 | | 5 |
| **Scaridae** | *Sparisoma chrysopterum* | Redtail Parrotfish | | | | | 21 |

| Family | Species | Common Name | BCMR | CCMR | HCMR | PHMR | SWCMR |
|---|---|---|---|---|---|---|---|
| **Scaridae** | *Sparisoma rubripinne* | Yellowtail Parrotfish | | | 15 | | 26 |
| **Scaridae** | *Sparisoma viride* | Stoplight Parrotfish | 19 | 11 | 17 | | 24 |
| **Sciaenidae** | *Odontoscion dentex* | Reef Croaker | | | | | 19 |
| **Scorpaenidae** | *Pterois volitans* | Lionfish | | | | | 36 |
| **Serranidae** | *Cephalopholis cruentata* | Graysby | 21 | | | 15 | 6 |
| **Serranidae** | *Epinephelus guttatus* | Red Hind | 18 | | | | |
| **Serranidae** | *Hypoplectrus guttavarius* | Shy Hamlet | | | | 24 | |
| **Serranidae** | *Hypoplectrus nigricans* | Black Hamlet | | 18 | | 23 | 42 |
| **Serranidae** | *Hypoplectrus puella* | Barred Hamlet | | | | 11 | 29 |
| **Serranidae** | *Hypoplectrus randallorum* | Tan Hamlet | | | | | 50 |
| **Serranidae** | *Serranus tigrinus* | Harlequin Bass | | 16 | | 25 | 33 |
| **Sparidae** | *Calamus calamus* | Saucereye Porgy | | | | | 15 |
| **Sphyraenidae** | *Sphyraena barracuda* | Barracuda | | | 26 | | |
| **Tripterygiidae** | *Enneanectes boehlkei* | Roughhead Triplefin | | 23 | 29 | | 48 |

## Appendix V - Lionfish threshold densities per site

| | DENSITY (INDIVIDUALS/HA) | |
|---|---|---|
| **REGION** | **OBSERVED** | **THRESHOLD** |
| **BCMR** | 12.99 | 13.66 |
| **HCMR** | 3.03 | 11.09 |
| **CCMR** | 5.00 | 9.69 |
| **SWCMR** | 23.40 | 21.34 |
| **PHMR** | 0.00 | 40.10 |

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