Rev Fish Biol Fisheries
https://doi.org/10.1007/s11160-021-09660-0

ORIGINAL RESEARCH

Trying to collapse a population for conservation: commercial trade of a marine invasive species by artisanal fishers

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Received: 2 April 2020 / Accepted: 27 April 2021

Abstract Implementing new and effective control strategies to reduce populations of invasive species is needed to offset their negative impacts worldwide. The spread of Indo-Pacific lionfish (*Pterois* sp.) through much of the western Atlantic has been one of the most publicized marine invasions globally, and is considered a major biodiversity threat whose longer-term impacts are still uncertain. Marine managers have explored several strategies to control lionfish, such as fishing tournaments (derbies) and commercial fisheries. Commercial fisheries for invasive species are controversial because they could create perverse incentives to maintain these populations, and they have never been demonstrated to successfully control target populations. We analyzed the development and impacts of an opportunistic fishing operation aimed at commercializing invasive lionfish in the Mexican Caribbean. We examined official lionfish landings and compared them to catches from lionfish derbies and lionfish densities from locations in the state of Quintana Roo, Mexico. We found that commercial fishers, particularly from one fishing cooperative on Cozumel Island, were effective at catching lionfish, with landings peaking at 20,000 individuals in 2014. This number is comparable to the number of lionfish caught in derbies across

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11160-021-09660-0.

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the entire Caribbean in the same year. Ecological survey data suggest a ~ 60% reduction in lionfish density on Cozumel reefs over two years (2013–2015), matching the peak landings in the lionfish fishing operation. However, the fishery's apparent success as a control tool during the time window analyzed seemed to trigger its own demise: a decline in landings was followed by evaporating market interest and loss of economic viability. If fisheries are to be established and used as management strategies to control future invasions, managers must develop strategic collaboration plans with commercial fishing partners.

Keywords Marine invasions · Invasive species management · Lionfish invasion · Artisanal fisheries · Coral reef conservation

Introduction

As the globalization of travel and trade continues apace, so has the rate of species introductions (Hulme 2009; Levine and D'Antonio 2003; Westphal et al. 2008). Although the role of introduced and invasive species in native species extinction has been disputed (Bellard et al. 2016; Didham et al. 2005; Gurevitch and Padilla 2004), non-native species can and do threaten local biodiversity and human livelihoods (e.g., Bradshaw et al. 2016; Katsanevakis et al. 2014; Simberloff et al. 2013; Vilà et al. 2011). However, there is increasing awareness of benefits from non-native species. In some cases, they can provide food and habitat for native species, functional replacements for extinct taxa, or the basis of new provisioning (e.g., food, fiber and fuel) and regulating (e.g., pollination, climate regulation, water purification) services (Pejchar and Mooney 2009; Schlaepfer et al. 2011). For example, in southern Africa, invasive *Acacia* and *Pinus* species are now used for thatching, timber, and firewood by local communities (de Wit et al. 2001). Similarly, although the introduction of Nile perch (*Lates niloticus*) to Lake Victoria caused the extinction of many species of endemic cichlids (Miller 1989), it has become the focus of a valuable capture fishery with a large export market, whose overexploitation is causing concern (Matsuishi et al. 2006; Mkumbo and Marshall 2015).

To date, there seems to be few positive consequences associated with the introduction of Indo-Pacific lionfish (*Pterois* sp.) to the western Atlantic. In the past couple of decades, this predatory fish has become widely distributed across the Wider Caribbean Region (Morris and Whitfield 2009; Schofield 2009, 2010). The spread of lionfish in the Atlantic has been one of the most publicized marine invasions globally, and is considered one of the most important threats to biodiversity in the region (Sutherland et al. 2010, 2017). Multiple studies have assessed the short-term ecological impacts of lionfish predation, such as reduced native fish recruitment, local biodiversity loss, local species extirpation, as well as non-consumptive effects, such as behavioral shifts and trophic niche prey shifts (Albins and Hixon 2008; Arias-Gonzalez et al. 2011; Côté et al. 2013; Green et al. 2012a; Green et al. 2014; Ingeman 2016; Kindinger and Albins 2017; Malpica-Cruz et al. 2019; reviewed by Côté and Smith 2018). Potential socioeconomic repercussions of the lionfish invasion have also been examined. However, the predicted socioeconomic impacts, such as fisheries declines (Albins and Hixon 2013) loss of ecosystem services (Johnston et al. 2015), and loss of reef-related tourism (Malpica-Cruz et al. 2017) have not yet come to pass (Côté and Smith 2018).

The uncertainty surrounding the longer-term impacts of the lionfish invasion has prompted interventions from governments and management agencies. Collaborative efforts have been implemented across the Caribbean involving the general public, non-governmental organizations, researchers and government agencies. The most effective method to capture lionfish is by spearing them individually (Dahl and Patterson 2017, but see Harris et al. 2020b). The success of this low-tech method is the basis of the most common lionfish control strategy to date: lionfish derbies (Malpica-Cruz et al. 2016). These are sport-fishing tournaments focused on removing as many lionfish as possible through targeted spearfishing. Given their popularity and support from local

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communities, recreational divers and fishers, derbies have had positive and lasting impacts locally. For example, Green et al. (2017) found that annual derbies in some locations can reduce lionfish biomass down to a level expected to stem the decline of native reef fish species. However, these efforts and their likely ecological benefits are limited to shallow areas within recreational diving limits (< 30 m depth; Andradi-Brown et al. 2017a, b). Derbies and similar campaigns aimed at removing invasive species also provide economic benefits to local communities and help to promote conservation awareness (Nuñez et al. 2012; Pasko and Goldberg 2014; Trotta 2014).

Commercial harvest has also been proposed as a strategy to alleviate the impacts of invasive lionfish (Albins and Hixon 2013; Morris et al. 2010; Morris and Whitfield 2009; Chapman et al. 2016). This approach has been adopted to control various invasive species, both on land and in aquatic ecosystems (Pasko and Goldberg 2014). However, there is a debate about whether commercial markets are really a win–win solution to the problem of biotic invasions (reviewed in detail by Nuñez et al. 2012; Pasko and Goldberg 2014; Gibbs et al. 2015). A major concern is that local communities may become dependent on the economic benefits of invasive species exploitation to the point of aiming for sustainable harvest (Nuñez et al. 2012; Pasko and Goldberg 2014). Additionally, commercial harvest may not be cost-effective at low invader population densities and additional incentives or governmental support may be needed to sustain such programs to the point of eradication (Nugent and Choquenot 2004; Pasko and Goldberg 2014). Nevertheless, the idea has received widespread support as a form of lionfish control. For example, the US National Oceanic and Atmospheric Administration spearheaded a "Eat Lionfish" campaign in 2010 (Williams 2010), and various initiatives have been considered, developed or implemented to create lionfish markets in the Caribbean region (e.g., Aruba: Blakeway et al. 2020; Belize: Chapman et al. 2016). In line with general concerns voiced about the commercial harvest of invasive species, there is a risk that, if not implemented properly, the goal of any lionfish fishery might shift from conservation to purely economic benefits (Aguilar-Perera 2013; Carrillo-Flota and Aguilar-Perera 2017; Chapman et al. 2016; Côté and Smith 2018). In addition, from an ecosystem perspective, a long-term, sustainable lionfish stock in the Caribbean could further destabilize food webs and jeopardize biodiversity (Arias-Gonzalez et al. 2011). However, until now, these concerns have been hypothetical because there is no published empirical information on the size, value or ecological effectiveness of any commercial lionfish harvest in the invaded range [but see Chapman's et al. (2016) report on exploring market-based approaches to lionfish management in Belize].

The goal of this study was to analyze the development and impacts of a commercial fishing operation aimed at controlling invasive lionfish in the Mexican Caribbean. This operation started with a bounty program established by a coalition of university, government, and non-governmental organizations in response to fears that lionfish would negatively impact commercial fisheries in the Mexican Caribbean (Albins and Hixon 2013; Rodriguez et al. 2014). The Cozumel Cooperative was the first fishing cooperative to take advantage of the program, which originally paid fishers for each dead lionfish produced. After the first year when lionfish was found to be edible and marketable as a 'sustainable' seafood option, the program connected buyers with fishing organizations, and the commercial fishing operation rapidly expanded; the Cozumel Cooperative was well-positioned to take advantage of the new market, although other fishing cooperatives also participated. We assessed the limited data available and discuss lionfish population status, limitations, local economic effects, and potential conservation impacts. To our knowledge, this is the first report of a commercial fishing operation for a marine invasive fish species. We discuss this information in light of additional large-scale initiatives that have been established to control and manage the lionfish invasion.

Methods

Fisheries data

The lionfish fishing operation is not officially recognized as a fishery under Mexican law. It does, however, involve the four main components of any fishery (i.e., a targeted fish stock, a fishing fleet, a harvest and a market, Charles 2000). We therefore refer to it as a lionfish fishery for simplicity. It is important also to note that the Mexican National

Commission of Fisheries and Aquaculture (CONAPESCA), which manages fisheries in national waters, has a mandate aiming for maximum economic benefit of fishing without compromising the natural capital (CONAPESCA 2001). CONAPESCA does not consider invasive lionfish part of the country's natural capital. This specification opens the way for unregulated fishing of lionfish within Mexican waters, without regards to sustainability, as long as the marine environment is not harmed.

We obtained lionfish landings from official catch statistics collected by the Mexican fisheries ministry (CONAPESCA) in the Caribbean state of Quintana Roo. Across Quintana Roo, lionfish is captured using different methods but spearing while free-diving or using SCUBA dominates. To our knowledge, this is the only state in Mexico where lionfish is fished on a commercial scale. We analyzed reports from December 2011 (the start of lionfish records) to December 2017. The data reported by fishers include landing and capture location, fishing permit holder name, month, year, common name of species captured, landing weight of whole fish (kg), and price per kg of whole fish. Beyond the recognized flaws of official fisheries data in Mexico (Cisneros-Montemayor et al. 2013), it is important to note that reporting lionfish to CONAPESCA is voluntary, not mandatory, because lionfish is not currently listed as a fishery resource in the Fisheries National Chart—the list of species for which an established fishery exists within Mexican territorial waters. The data we report here therefore undoubtedly underestimate true landings.

We contextualized the fisheries landings data with unstructured interviews and focus groups with local managers (n = 5) from the National Commission of Natural Protected Areas (CONANP-Cozumel) and with fishers (n = 20) from fishing cooperatives from across the Mexican Caribbean state of Quintana Roo (e.g., Puerto Morelos, Isla Mujeres, Cozumel and Chetumal) between 2012 and 2016. Fishing cooperatives are autonomous unions of fishers that hold fishing permits and rights to access designated fishing areas and comply with federally mandated quotas and closures. We also spoke with chefs (n = 4), restaurant owners (n = 3) and potential or current lionfish retailers in the local, national and international market (n = 3). The goal of these interviews was to document different aspects of lionfish management actions implemented by park managers, and regular fishing operations as well as those aimed at capturing, processing, and selling lionfish to local, national and international markets (e.g., fishing gear used, targeted species, landing and selling prices, processing infrastructure, products marketability, supply and demand levels, etc.).

Lionfish derby data

To compare lionfish fisheries landings to lionfish captured during derbies, we compiled information on regional lionfish derbies held across the tropical northwestern Atlantic, Gulf of Mexico and Caribbean from 2010 to 2015 reported by Malpica-Cruz et al. (2016). From this published dataset we calculated the total number of lionfish caught during derbies. We also extracted specific lionfish numbers caught during derbies held around Cozumel during the time period coinciding with the commercial fishery.

Lionfish surveys

Underwater SCUBA surveys were conducted by teams of six trained local fishers, members of the non-governmental organization, Comunidad y Biodiversidad, A.C. (COBI) and CONANP to assess lionfish density at three reef locations in Cozumel (Punta Sur, Barracuda and Cordillera Norte), specifically in the Cozumel Island Flora and Fauna Protected Area in June 2013, 2014 and 2015, i.e. years that match our landings data. The Cozumel Island Wilderness Protected Area is an area under protection but where the Cozumel Cooperative has fishing rights. Surveyed sites were chosen based on accessibility as well as to represent the larger area where the fishing cooperative operates. Surveys consisted of 12–14 transects, 30 m long by 4 m wide, at depths of 10–25 m, conducted during daylight hours (09.00–16.00). To account for the likelihood of lower detection levels due to culling-induced behavioral shifts (Côté et al. 2014) and lower activity levels during daylight hours (Cure et al. 2012) divers carefully searched for lionfish in crevices and overhangs following the lionfish-focused survey protocol of (Green et al. 2012b), recording number and size (total length to the nearest cm) of all lionfish encountered.

We also examined trends in lionfish abundance from the publicly available database of the Reef Environmental Education Foundation (http://www.

reef.org, accessed October 2020). This non-governmental organization collates fish species survey data from recreational divers trained in reef fish identification. We extracted the proportion of surveys in which lionfish were sighted as an index of lionfish abundance for three adjacent areas: Cozumel Island (REEF area 5402), the mainland coast just north of Cozumel (REEF area 5401—Cabo Catoche (21.5° N) to Puerto Morelos), and the mainland coast just south of Cozumel (REEF area 5403—Puerto Morelos to 20° N), including Playa del Carmen.

Data analysis

To compare fishery and derby landings we estimated total number of lionfish captured by fishers reported in the official catch statistics by transforming landed wet weight to number of individuals. Interviews with fishers in Cozumel revealed that they aim to capture lionfish weighing ~ 500 g, as smaller fish are not deemed commercially valuable (Cozumel Cooperative president, pers. comm.). Therefore, we used the known total length (TL)–wet weight relationship for individual lionfish reported for Quintana Roo locations by Sabido-Itzá et al. (2016a, b) to calculate the number of lionfish if all lionfish were 36 cm TL (~ 482 g, close to the targeted weight reported by the Cozumel fishing cooperative). We bounded this estimate by calculating the number of lionfish if individuals were all smaller (33 cm, ~ 363 g) or larger (39 cm, ~ 625 g), thus producing a range of likely number of lionfish captured. The TL values used were supported by the landed values and lionfish weights reported by members of the Cozumel Cooperative.

We used abundance data derived from transects from the three reef locations in Cozumel to calculate average lionfish density per location (lionfish per hectare). We ran a linear mixed-effects model (lmm) with location as random effect to explore the trend in lionfish density over time (with year as a continuous variable) using the lme4 package in R (Bates et al. 2015):

$$\begin{aligned} &\log(\mathit{lionfish\ density}_i) \sim N\left(\mu_i, \sigma^2\right) \\ &\log(\mathit{lionfish\ density}) = \mathit{Year}_i + \mathit{Location}_i \qquad (1) \\ &\mathit{Location}_i \sim N\left(0, \sigma^2\right) \end{aligned}$$

Lionfish density data were log-transformed prior to analysis to linearize any exponential trend in abundance over time. We added a constant (i.e. 1, which represents 0.8% of the overall mean, and 1.2% of the smallest non-zero density values) to all density values prior to log transformation. After data transformation, visual diagnostics confirmed that model assumptions were met (i.e., heteroscedasticity, normality and influential observations; Harrison et al. 2018; Zuur et al. 2010). All data manipulation and statistical analysis were done in R (R Core Team 2016); packages from the tidyverse were used for data wrangling and plotting (i.e., ggplot, dplyr and tidyr; Wickham et al. 2019).

Results

Lionfish fisheries and derbies: quantitative analysis

Official government landings data indicate that five major lionfish landing locations exist along the Quintana Roo coast. Of these, the island of Cozumel was by far the most important landing site in terms of landed weight, with 30 times more catch than the next most important landing site (Table 1, Fig. 1); over 90% of all lionfish landed in Mexico's lionfish fishery were landed at Cozumel. Cozumel also had the most consistent lionfish fishing operation among the Quintana Roo landing sites, with continuous landings from 2011 to 2017 while other sites had at most four years of landings data (Online Resource 1). Because Cozumel dominated lionfish landings and because of the consistency of reporting at this location, we focus primarily on Cozumel's landings data in subsequent analyses and discussion.

The estimated number of lionfish captured in Cozumel shows a steadily increasing trend from 2011 to 2014, peaking around 20,000 individual lionfish (Fig. 2, Online Resource 1). The same temporal pattern is seen for the number of lionfish caught in derbies across the Wider Caribbean Region between 2011 and 2014 (Fig. 2). In 2014, i.e. the peak year for both fishery landings and derby kills, as many lionfish were captured by the Cozumel fishery alone as were caught in derbies across the entire Caribbean region (Fig. 2). From 2014 to 2017 Cozumel landings steadily decreased back to 2012 levels (Fig. 2). The total number of lionfish captured during derbies in Cozumel represents only 9% of the total number of

Table 1 Total landed weight and mean landed price by landing site reported by Fishers' Cooperatives to the Mexican National Commission of Fisheries and Aquaculture (CONAPESCA) from late 2011 to late 2017

Landing site	Landed weight (kg)	Mean landed price ($ USD)* ± SD
Isla Mujeres	556	3.52 ± 0.83
Puerto Morelos	1289	2.41 ± 0.80
Cozumel	35,328	3.63 ± 1.22
Punta Allen	1160	2.36 ± 0.28
Chetumal	155	3.31 ± 3.18

*Based on exchange rate of $18.00 MX per $1 US

Landed price reported is whole per kg

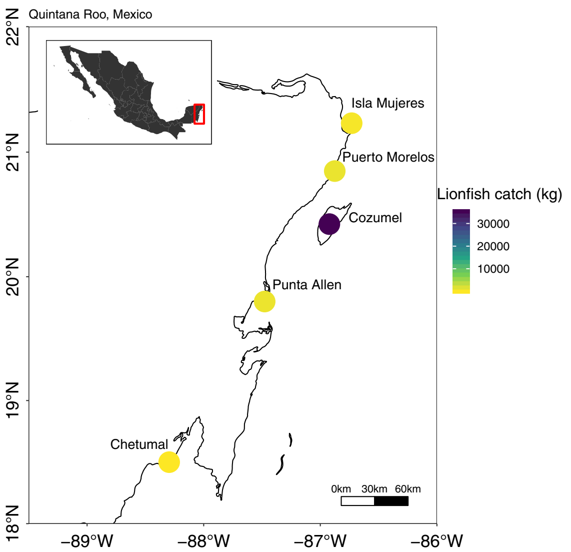


Fig. 1 Landed weight of lionfish captured in fishing concession zones by artisanal fishers from late 2011 to late 2017. Landing locations along the Quintana Roo coast of the Mexican Caribbean are shown

estimated lionfish captured by the Cozumel fishery. There were no more lionfish derbies in Cozumel after 2014 (B. Quiroga, pers. obs.). While smaller culling events may have occurred (e.g. by dive centers) after derbies stopped, these are infrequent, and carrying spears/slings is forbidden within the marine park, where the majority of diving tours take place (Cozumel park managers pers. comm.).

Unfortunately, there was no information available to estimate effort, and therefore catch per unit of effort (CPUE), for Cozumel or elsewhere. Our interviews indicated that fishers in the Cozumel Cooperative captured lionfish mostly while fishing for lobster. It is therefore difficult to estimate the time they allocated to capture lionfish exclusively. Nevertheless, during the 6-year span analyzed, the numbers of vessels (15 panga boats), fishers (75 active fishers), and fishing days throughout the year remained constant.

The mean landed price of lionfish per kg was variable among and within landing locations, with the highest price reported in Cozumel and the lowest in Punta Allen (Table 1). Cozumel showed relative price stability from 2011 to 2015 (Fig. 3). However, median prices steadily increased after 2015 (Fig. 3), concurrent with the observed reduction in lionfish landings (Fig. 2). Price variability also increased over time (Fig. 3). In our interviews, several fishers as well as local authorities said that, as price and demand for lionfish increased, fishers dedicated more effort to catching lionfish, even as total catch declined. Our interviews also revealed that lionfish is traded whole and as fillet, but the official reports only list whole fish prices.

Lionfish fisheries: qualitative analysis

Interviews and meetings with managers and fishers suggest a complex scenario regarding the management of the lionfish invasion through a commercial fishery in Quintana Roo. At the onset of the invasion in the Mexican Caribbean (ca. 2009–2010), the government implemented lionfish derbies within protected areas through CONANP (Cozumel Reefs National Parks Director, CONANP, pers. comm.). The main goal of these initiatives was to show that lionfish could be fished as well as to find markets for lionfish. Interviews with fishers suggest that, at the time of interviews, the only government agency directly involved in the lionfish issues was CONANP, whose mandate is to

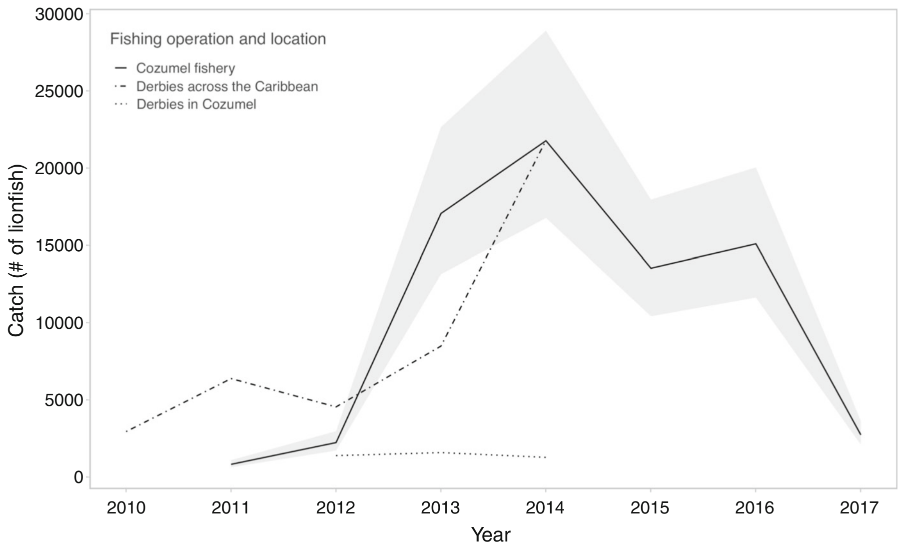
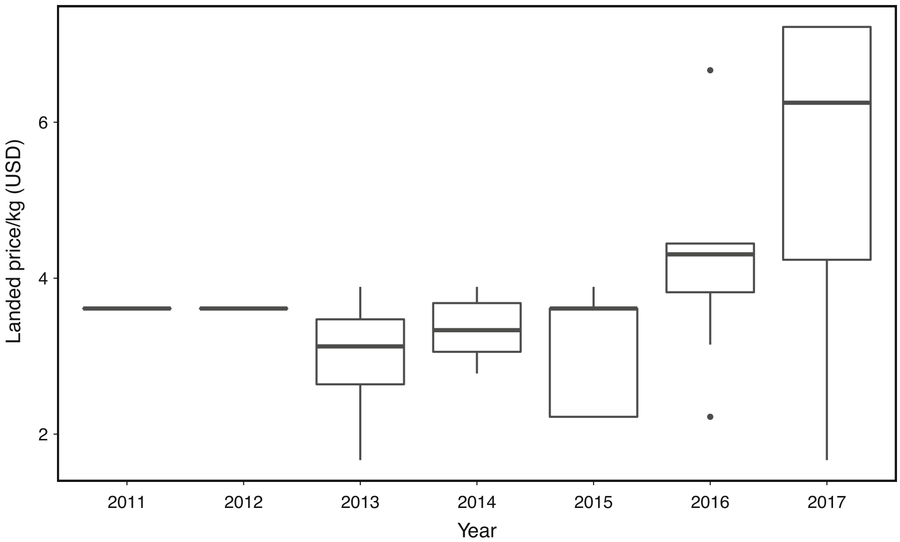


Fig. 2 Total estimated number of lionfish captured (based on landed weight; see Methods for details) reported by the Cozumel Cooperative, in Cozumel, Mexico, from 2011 to 2017. The solid line shows estimates based on length–weight conversions for lionfish averaging 36 cm TL; grey area represent a likely estimate of lionfish numbers captured based on average lionfish sizes of 39 cm TL (upper bound) and 33 cm TL (lower bound). The dashed-dotted line shows the total number of lionfish captured each year during derbies organized across the Wider Caribbean Region from 2010 to 2014. The dotted line represents number of lionfish captured at derbies organized at Cozumel from 2012 to 2014; there were no derbies after 2014

Fig. 3 Yearly price per kg of whole lionfish landed in Cozumel from 2011 to 2017. Lower boundary of box indicates the 25th percentile, the black line within the box marks the median, and the upper boundary indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles, respectively. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles



manage natural protected areas. Therefore, there was no unified government support for control and management.

Chefs, restaurant owners and other national and international retailers indicated that demand for lionfish existed and increased over the period analyzed. Fishers in Cozumel became aware of this demand and addressed it by increasing fishing effort ("as the demand and price of lionfish went up, we dedicated more time fishing it", Cozumel Cooperative, pers. comm.). However, fishers also indicated that as demand increased and they were unable to meet supply agreements, buyers became disinterested. Prospective and current buyers and restaurant owners corroborated this statement. They also indicated that two key aspects were needed to keep interest in a product: (1) steady volumes, and (2) proper fish/fillet sizes. These two aspects were seemingly not fulfilled by fishers during 2015–2016.

Ecological surveys

Ecological surveys of three sites in Cozumel showed a decrease in lionfish density over 3 years coinciding with the peak in fisheries landings. Diving teams surveyed 114 transects in Cozumel from 2013 to 2015, totaling a coral reef area of 13,680 m^2. The size of lionfish in underwater surveys ranged in total length from 2 to 40 cm (mean ± 1SD: 15.20 cm ± 8.63 cm) (Fig. 4). Note that it would be unwise to assume that the size frequency distribution of lionfish in these surveys is indicative of the sizes of fish captured in the fishing operation as fishers likely targeted the larger (i.e. the most profitable) lionfish. Lionfish density was generally lower at Barracuda than at Punta Sur and Cordillera Norte (Fig. 5). However, lionfish density varied among years (Table 2, Fig. 6), and the pattern of change was similar across the three sites (Fig. 5). We found a negative association between lionfish density and years ($\beta_1 = -0.90$, 95% CI -1.43 to -0.37, Fig. 6, Table 2), with a ~ 60% (95% CI 31 to 76%) reduction in lionfish density, on average, per year across sites, which represents roughly 55 fewer lionfish per hectare per year (Figs. 5 and 6).

Additionally, recreational diving surveys in Cozumel and at mainland adjacent areas had a similar pattern of rapid increase in the proportion of surveys on which lionfish were recorded, from 2008 to 2011 (Fig. 7). However, while all three areas showed a decline in the relative frequency of occurrence of lionfish from 2011 to 2014, the trajectory of decline continued from 2014 onward for Cozumel but not for the other two areas, which experienced peak abundances in 2015 (mainland south of Cozumel) and 2017 (mainland north of Cozumel). Cozumel comprised the majority of survey effort among the three areas. Also, lionfish removal in the two mainland areas was largely limited to recreational divers and—compared to Cozumel—smaller lionfish fishery operations corresponding to the landing sites at Isla Mujeres and Puerto Morelos (Fig. 1).

Discussion

Between 2011 and 2017, lionfish was captured across the coast of Quintana Roo and landed in at least five locations. The largest lionfish landings by weight were recorded in Cozumel, where over 90% of Mexico's commercial lionfish was landed. The reported data are likely an underestimate of the actual volume of lionfish caught, because reporting for this unofficial fishery was voluntary rather than mandatory. Nevertheless, the lionfish landings in Cozumel alone were comparable to or higher than the reported numbers of lionfish captured in derbies across the entire Caribbean region over the same time period (Malpica-Cruz et al. 2016). Lionfish landings increased continuously from

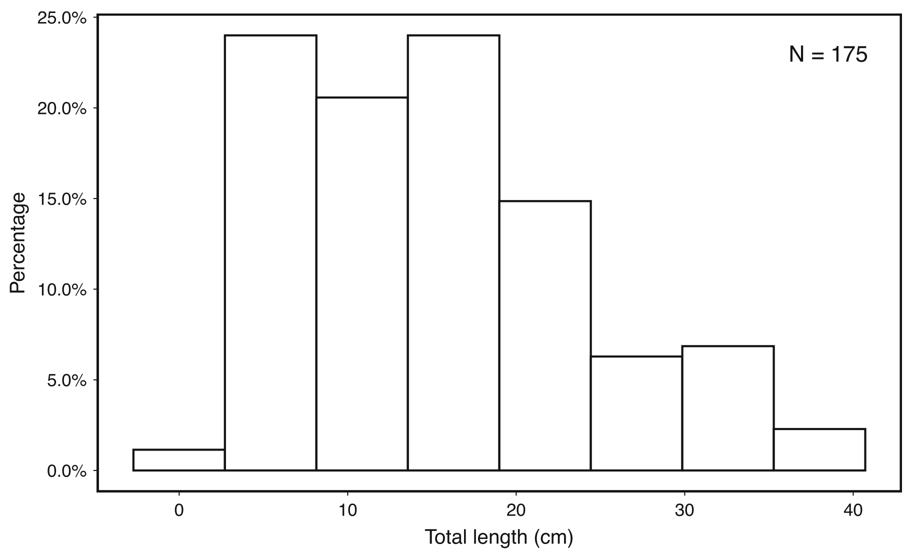


Fig. 4 Relative frequencies of lionfish total length, from underwater surveys on reefs off Cozumel, Mexico, from 2013 to 2015

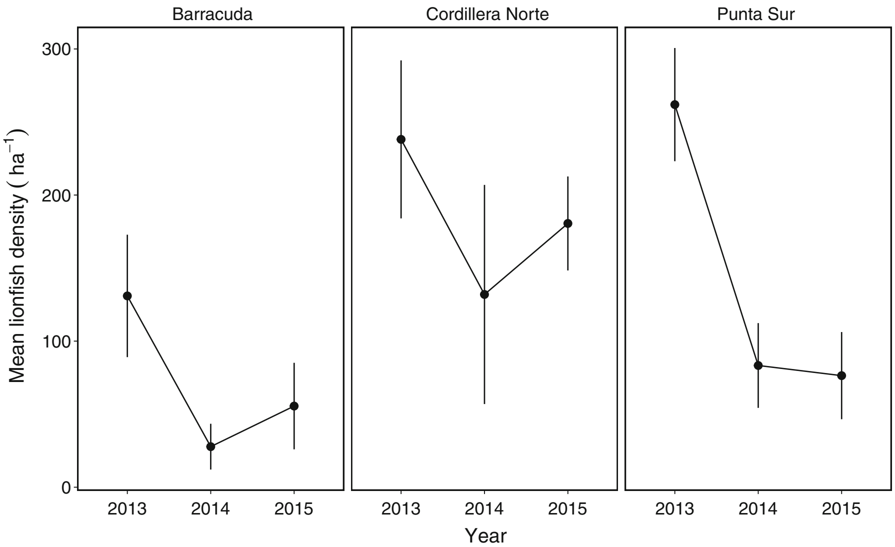


Fig. 5 Mean density of lionfish (number of lionfish per hectare) over time at three locations surveyed from 2013 to 2015 in Cozumel, Mexico. Vertical bars represent standard errors

Table 2 Linear mixed-effects model estimates of lionfish density (individuals ha^{-1}) over time from 2013 to 2015 (fixed effect) at three locations in Cozumel, Mexico. Lionfish density data were transformed (constant + 1 value added to all values) and logged prior to analysis

	Estimate	Std. error	*t* value	*p* value
Intercept	1809.63	546.15	3.31	0.001
Year	− 0.90	0.27	-3.31	0.001

2011 and peaked in 2014, followed by a steep decline. The decline in landings after 2014 coincided with a reduction in lionfish density on Cozumel reefs and a steady increase in landed price, both of which could be a response to sustained, or perhaps increasing, fishing effort. These findings show that government and community action, here through fishing and derbies, might contribute to controlling an invader that has sparked ecological and socioeconomic concerns.

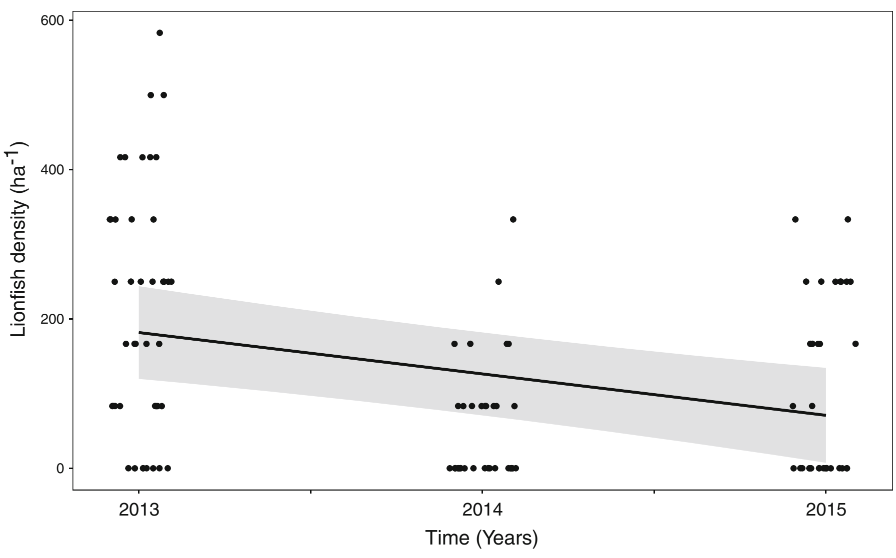


Fig. 6 Linear mixed-effects model visualization presenting our model estimate (solid line) with confidence intervals (95%; grey shaded area) of lionfish density observed in the three years of the study

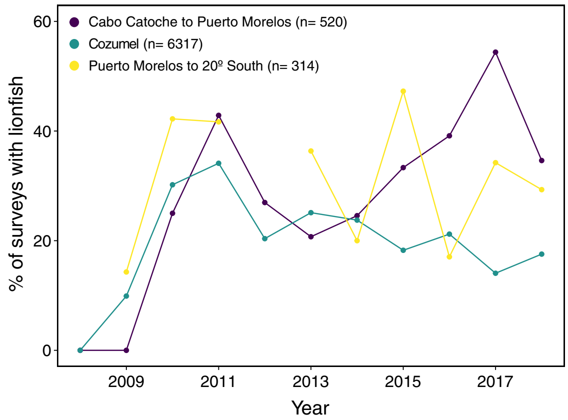


Fig. 7 Trajectories of proportions of surveys where lionfish was recorded in three areas of Quintana Roo: Cozumel Island, the mainland coast just north of Cozumel (Cabo Catoche, ~ 21.5° N, to Puerto Morelos), and the mainland coast just south of Cozumel (Puerto Morelos to 20° N)

Local economic benefits

Fishers and managers in Cozumel quickly found a suitable market, i.e. restaurants and national/international buyers, to commercialize their product (Cozumel Cooperative, pers. comm.). This is a key point in the apparent success achieved by this fishing cooperative. Failing to find the right market could have been a barrier to the development of this fishery, as has been reported in similar commercial fishing efforts targeting lionfish in Belize (Chapman et al. 2016). This allowed Mexican fishers to profit from fishing invasive lionfish right from the start and further expand their market. Cozumel presented large landed volumes, likely as a result of a thoroughly organized fishing operation, stemming from the vision and willingness of fishing cooperative leaders to explore new economic opportunities. Additionally, technical assistance by local park managers and concerned NGOs helped in making this new venture a reality. Chapman et al. (2016) also noted that succeeding in these important initial steps was critical in overcoming the barriers to the development of a lionfish fishery.

The harvest of lionfish offered economic opportunities to local communities in Mexico. Many species historically targeted in the Caribbean region have declined substantially (Paddack et al. 2009). For example, several commercially important predatory species, such as groupers and snappers, have become scarcer and smaller over time or with increasing human population size (Graham et al. 2008; Sadovy de Mitcheson et al. 2013; Stallings 2009; Valdivia et al. 2017), which has likely reduced profits to local fishers. In addition, seasonal fishery closures, which are needed to allow reproduction and recruitment of harvested species, may have a seasonal impact on the revenues of artisanal fishers. Therefore, exploiting a new species with little regulation and of comparable landed value to that of other regularly harvested fish species in the region (e.g., grouper ~ \$3.5 USD per kg; Cozumel Cooperative pers. comm.) was a welcomed opportunity. However, the economic value of lionfish was and remains less attractive than that of the main targeted marine resource in the region: lobster (~ \$15 USD per kg; Cozumel Cooperative pers. comm.), which means that it is less likely that fishers would target lionfish throughout the open lobster season. Moreover, the variability observed in landed price of lionfish (Fig. 3) suggests that there is not a stable market and demand fluctuates. Informal interviews with fishers from elsewhere than Cozumel also indicate little motivation to capture lionfish given the extra care needed to handle it and—unlike in Cozumel—generally little financial incentive to do so. More studies focusing on economic aspects of the lionfish fishery are needed to truly evaluate its potential economic benefits, if any.

The collapse of a fishery

After a few years of growth in the lionfish fishery in Cozumel, a collapse of lionfish numbers on the reef appears to have led to a financial collapse of the incipient fishery. A fishery is only sustained as long as it is profitable. In fact, when targeted native fish populations have collapsed elsewhere (e.g., Atlantic cod *Gadus morhua*, Pacific sardine *Sardinops sagax* in the Northeast Pacific, among others), the fishery often ceased to be commercially viable before the populations were extirpated (Clark 1990; Finlayson and McKay 2000). An inherent contradiction arises when suggesting fishing as a means to control a targeted species: fishing may reduce population size, but the fishery will likely become unprofitable at very low population levels (Fryxell et al. 2017). The demand for lionfish in Cozumel steadily increased during the years of the fishery, up to the point when supply could not meet the demand, which drove prices high and buyers became disinterested (Cozumel Cooperative pers.

comm; A. Quintana unpublished data). Reports from the Cozumel Cooperative indicate that the lionfish fishery continues at present, but the fishery's apparent success as an ecological control has prevented fishers from meeting demand from buyers. Even sourcing lionfish from other cooperatives has not helped, as landings outside of Cozumel were inconsistent and considerably lower (Online Resource 1) and most fishers elsewhere do not target lionfish as efficiently as Cozumel fishers do (see below). Chapman et al. (2016) reported that similar demand issues are preventing the successful implementation of a lionfish fishery in Belize. This poses a challenge going forward. Fishers now have a vested economic interest in the fishery, but maintaining market interest and the fishery in the long term is at odds with the goals of extirpation, presenting a dilemma for fishers and conservationists alike as experts had predicted could occur (Morris and Whitfield 2009, Nuñez et al. 2012).

There are several characteristics of the Cozumel Cooperative that may have contributed to its large lionfish landings (30 times larger than the other cooperatives) and thus made this fishery effective at removing lionfish. Founded in 1960, the Cozumel Cooperative is one of the oldest in the Mexican Caribbean. They hold exclusive territorial use rights for fishing (TURF, locally named "concession") for lobster in three protected areas (the Sian Ka´an Biosphere Reserve, the Cozumel Island Wilderness Protected Area and the Cozumel Reefs National Parks), which has forced them to collaborate with CONANP to regulate their fishing. Additionally, unlike most fishers in Quintana Roo who are restricted to free-diving for lobster due to fishing regulations, Cozumel cooperative fishers use SCUBA and dive to 60 m or deeper. This has allowed them to target lionfish more effectively than free-diving fishers (Gress et al. 2018). Lastly, it is the cooperative with the most advanced processing capacity, i.e. a dedicated facility, which they claim allows them to meet food safety certifications and access the international market for lionfish.

Implementing other market incentives to sustain the lionfish control efforts in Cozumel could be evaluated. For example, a scheme akin to an ecolabel standard (Tlusty 2012) could be devised, with a focus not on guaranteeing the sustainability of the targeted fishery—the usual use of such a tool—but on promoting the sustainability of the local ecosystem by controlling the invasive species. Such is the focus of the Silverfin™ Group, which promotes invasive Asian carp as a quality food in national (i.e. USA) and international markets (http://www.cantbeatemeatem.us/ accessed, November 2020). A local sales guide that make recommendations to consumers locally and worldwide (Roheim 2009) has already been implemented by CONANP in the region (S. Fulton, pers. obs.), emulating renowned sustainable seafood guides (i.e., Ocean Wise and Monterey Bay Aquarium), which already list lionfish as a recommended seafood alternative to consume. All around the Caribbean, tourists could be offered lionfish as a "conservation delicacy", thus assigning a premium value that could help to sustain some fishing effort on the lionfish despite low population levels. Finally, establishing a Product System Committee focused on supporting the commercialization phase could mitigate barriers to commercialization. This would ensure that all levels of the production system, from fishers to retailers, agree upon supply and demand levels. These strategies should be implemented as long as conservation goals to control the lionfish populations are maintained.

Did the fishery impact lionfish populations?

A limitation of our dataset and modeling efforts is that we cannot conclusively connect the reduction in lionfish density on Cozumel reefs solely to fisheries activities because derbies and other lionfish harvesting programs were concurrent. However, there are multiple lines of evidence suggesting a causal link between the fishery and the population decline. First, Cozumel fishers exerted extremely high fishing pressure on lionfish. The local fishery landed as many or more lionfish as the number caught in derbies implemented across the whole Caribbean region over the same period (Fig. 2). Second, the onset of decline in the lionfish population observed at the three monitoring sites in 2013 coincided with the peak in reported landings nearby in 2014 (Figs. 2 and 3). Derbies could have contributed to lionfish decline in Cozumel as they started as early as 2010. However, they caught steady but small numbers of lionfish through 2014 ($\sim$ 1500 to 2500 individuals; Fig. 2), that represented no more than 9% of the catches of the commercial venture. In contrast, the regular presence of lionfish on nearby Mexican Caribbean reefs (i.e. mainland areas along the coast of Quintana Roo and Banco Chinchorro), where few to no control measures were implemented, suggest that lionfish were well established in the region through 2018 (Fig. 7; Sabido-Itzá and García-Rivas 2019; Sabido-Itzá et al. 2016a, b). Third, fishery-independent observations (i.e., by dive shop owners, tourists and by some of the authors) support a marked decrease in the prevalence of lionfish starting in 2014, at least within recreational diving limits inside reefs of the Cozumel Reefs National Park. Surveys made by recreational divers at Cozumel and adjacent mainland areas supports this trajectory of decline of lionfish abundance at Cozumel reefs from 2014 onward (Fig. 7). This perceived decrease in abundance could be the result of behavioral shifts by lionfish which, as a reaction to culling, have reduced activity and lower detectability (Côté et al. 2014). However, little culling takes place in areas where diving tours occur. The low abundance of lionfish around Cozumel post-2014 was confirmed by Gress et al. (2018), who found no lionfish on shallow (< 15 m deep) reefs and only two individuals on mesophotic (55 m deep) reefs, indicating the lack of a deep-water refuge from Cozumel fishers who are the only ones to harvest lionfish at these depths. These observations appear to support our ecological evidence that lionfish populations had declined substantially by 2014 in Quintana Roo, and that fishing pressure from the Cozumel fishery probably played at least some part in this decline. Further studies should assess lionfish population status, particularly the presence of lionfish in deep refuges as reported elsewhere (e.g. Andradi-Brown et al. 2017a, b).

Processes other than the fishery could have driven lionfish population declines, but these seems unlikely in Cozumel. Benkwitt et al. (2017), for example, suggested a suite of natural causes for lionfish population declines in The Bahamas. Interestingly, populations losses in The Bahamas were observed only on small and medium-sized reefs, while lionfish abundance on larger reefs did not change over time. While natural causes (e.g., larval or recruitment limitation, storms, etc.) could have contributed to the declining trend in Cozumel, the magnitude of the decline we observed (i.e. ~ 60% per year) was far greater than that reported by Benkwitt et al. (2017; 16.6% per year), perhaps owing to the Cozumel fishery. An increase in lionfish mortality due to native fish predation could account for lower lionfish density. This process was suggested for one island of The Bahamas (Mumby et al. 2011) but a regional analysis found no relationship between the abundance of native predators (i.e., groupers) and lionfish density (Hackerott et al. 2013). Despite some reports of direct consumption of lionfish by groupers based on stomach content analysis (Maljković et al. 2008; Smith 2019), the low predation rates observed are unlikely to control lionfish population. In addition, direct (e.g., competition for space, Ellis and Faletti 2016; competition for prey, Curtis et al. 2017) and indirect non-consumptive (e.g., fear) effects by groupers (Smith 2019) can affect lionfish demography. Nevertheless, the abundance of native predators in Cozumel is very low (Kramer et al. 2015; Gress et al. 2018), probably too low to account for the lionfish decline observed. Intraspecific competition (Benkwitt 2013) and cannibalism (Dahl et al. 2018) could also impact lionfish population dynamics, although these mechanisms have been observed only at very high lionfish densities. Finally, on reefs off Florida in the northern Gulf of Mexico, Harris et al. (2020a, b) reported large lionfish population declines (77–79%) and commercial CPUE declines (50%), likely associated with an ulcerative skin disease outbreak between 2017 and 2018. However, members of the Cozumel cooperative indicate they have not observed lionfish with evident ulcers during the fishery and up to August 2020. Further studies are needed to assess whether this disease has since reached Cozumel and its impacts on the lionfish population.

Regardless of the main driver of population change, the ~ 60% decline in lionfish density per year observed on Cozumel reefs is striking. Barbour et al. (2011) estimated that an annual exploitation rate between 35 and 65% would be required to curb the lionfish population and affect recruitment. Our results suggest that the strategies implemented by park managers, divers and, likely most importantly, by the fishing cooperative in Cozumel might have achieved this ambitious goal, at least in the time window analyzed. It is expected that this reduction should benefit many of the species inhabiting the local coral reef ecosystem (e.g. Green et al. 2014). Indeed, ecosystem-modeling efforts have suggested that a well-developed lionfish fishery—even with low levels of harvest—could increase biomass of reef fish by releasing them from predation and competition by lionfish (Chagaris et al. 2017). However, the ecological effect of lionfish on reef fish biomass and diversity in the Mexican Caribbean is still a matter of debate; on reefs in Belize, there is some evidence that lionfish have had little impact (Hackerott et al. 2017). Unfortunately, there are no available data to assess the effects of lionfish predation to date in the Mexican Caribbean, although monitoring surveys implemented now might still reveal community-level ecological changes as lionfish either continue to decline or rebound following a relaxation of fishing pressure.

The observed decline in the lionfish fishery after 2014 led to a downturn in fisher willingness to participate, which could allow the lionfish population to bounce back (Barbour et al. 2011). The extent to which lionfish populations can do so is unclear and likely depends on what initially drove the declines. For example, the localized lionfish declines reported recently in other invaded areas (Benkwitt et al. 2017; Harris et al. 2020a) appear to stem from natural causes, which might offer a more persistent regulation of lionfish numbers than market-driven fishing pressure. Therefore managers are advised to continue implementing control programs locally, as it is possible that additional and persistent impacts have yet to manifest, particularly in the southern Caribbean (Côté and Smith 2018). A balance should be explored to incentivize the continuing participation of both fishers and market buyers in the face of fluctuations in the lionfish population.

Implications for management

The apparent lack of management and coordination between government agencies, and value chain links observed for this opportunistic fishery could be considered representative of Mexico's fisheries administration (Espinoza-Tenorio et al. 2011). While there is hardly a single solution to fisheries problems and let alone the lionfish invasion problem, the program and initiative assessed here—while not perfect—illustrate ways to face them through a collaborative approach among government agencies, NGOs, and fishers. The concerns surrounding a fully established fishery to control or eradicate invasive species are clear, and focus mainly on the clashing goals of profitability and conservation (Nuñez et al. 2012). This issue was raised by Aguilar-Perera (2013) for the lionfish invasion in the Mexican Caribbean. However, in the specific context of an invasion with great potential for ecological damage, such as the lionfish invasion, this concern downplays the negative long-term ecological and socioeconomic impacts. The goals of the fishery need to be clear from the start. An invasive species fishery may be designed to collapse but during its boom years it can generate a financial dependence that can lead to fishers and managers to call for sustainability. It is therefore imperative to include a strategy to prevent such reliance within any invasive control program based on commercialization. Pasko and Goldberg (2014), for example, suggest that such a strategy could be to aim at restoring native grouper populations for future harvest.

Finally, we believe that lionfish fishing should not be developed as a single, stand-alone fishery, which is contrary to a suggestion made by Chapman et al. (2016). Our results suggest that the incipient lionfish fishing operation in the Mexican Caribbean was only viable and yielded the observed economic and potentially lionfish population control benefits by being developed within a previously established fishery (i.e., for spiny lobster) where lionfish was an alternative target. Small-scale fisheries in the developing world are generally multi-specific (Pérez-España et al. 2006), and this makes incorporating a new species like lionfish relatively easy. Indeed, in Cozumel and other locations in Quintana Roo and across the Caribbean, fishers already dive to capture lobster, their main source of income, using spearguns or slings. In many of these locations, including Cozumel, lobster fishers can use the same gear to capture lionfish. Therefore, fishers do not need to invest in additional gear, or become financially dependent on exploiting a new resource. Should the lionfish fishery be deemed a conservation success in the long term, the original goals must be continually remembered and revisited, incorporating feedback from fishers, managers and researchers. If fisheries are to be established and used as management strategies to control future invasions, clear conservation goals must come first (Nuñez et al. 2012; Pasko and Goldberg 2014).

Acknowledgements We greatly acknowledge the fishing cooperatives of Quintana Roo, particularly the Cozumel Cooperative (Sociedad Cooperativa de Producción Pesquera Cozumel), for their leadership in lionfish control efforts; CONANP, particularly the Cozumel Reefs National Parks Office for their support and regional leadership to control lionfish.

Funding L. Malpica-Cruz was supported during fieldwork in 2014 by a research grant from the International Development Research Center from Canada (Award #107473–99906075-043), and a research grant from the Rufford Foundation (#15373–1). Support for ecological and fisheries data collection was provided by the Summit Foundation, MARFund (#RG-OAK-COBI-2017), The Oak Foundation (#OCAY-13–569), and the Inter-American Foundation (#ME-517) to COBI, A.C.

Availability of data and materials We used two sources of data in this paper. The first is qualitative data from interviews, which were firstly reported on internal reports by the non-governmental organization, Comunidad y Biodiversidad A.C. (COBI), and are available upon request to: sfulton@cobi.org.mx. The second is ecological data on the status of the lionfish population in Cozumel, and lionfish fisheries landings reported by commercial fishers to the Mexican Fisheries Ministry (CONAPESCA). These two datasets are available for download at https://doi.org/10.6084/m9.figshare.13208102.v1.

Code availability R scripts for statistical analyses made are available for download at https://doi.org/10.6084/m9.figshare.13208102.v1.

Declarations

Conflict of interest The first author, L. Malpica-Cruz, declares no conflict of interest. L. Malpica-Cruz conceived of the article, performed data analysis and wrote the first draft. A. Quintana, J.A. Zepeda-Domínguez and I.M. Côté also declare no conflict of interest. S. Fulton works for the non-governmental organization, Comunidad y Biodiversidad A.C. (COBI), which has worked with the Cozumel Cooperative on the commercial lionfish fishery; they provided ecological and interview data, and contextual information to interpret the program results. L. Tamayo and J.A. Canto Noh work for the Sociedad Cooperativa de Producción Pesquera Cozumel (Cozumel Cooperative), which participated in the commercial lionfish fishery. They provided fisheries-dependent ecological data and contextual insights about the fishery's outcomes. B. Quiroga works for the National Commission of Natural Protected Areas (CONANP). All authors listed revised the manuscript for critical intellectual content; edited the manuscript; approve of the final manuscript form; and agree to be accountable for this work.

Ethics statement The Mexican-based institutions participating in this study—Universidad Autonoma de Baja California (UABC: L. Malpica-Cruz) and Comunidad y Biodiversidad A.C (COBI: S. Fulton) are not required to receive approval from ethics committees and/or develop ethics protocols for studies involving research with humans. However, before the start of interviews or focus groups all participants gave informed consent to provide information for this study. Authors took reasonable precautions (e.g., using an encrypted hard drive; not recording names with audio files or quotations; monitoring subjects to assess whether questions were causing emotional distress) to ensure well-being and confidentiality for all of the participants.

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