Coral Reefs
https://doi.org/10.1007/s00338-021-02132-8

NOTE

Ecological impacts of an invasive mesopredator do not differ from those of a native mesopredator: lionfish in Caribbean Panama

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Received: 12 September 2020 / Accepted: 10 June 2021

Abstract The impacts of invasive lionfish (*Pterois volitans/miles*) on native coral reef populations in the Western Atlantic Ocean and Caribbean Sea can be enormous. However, how much lionfish differ from native predators and whether their effects outweigh the abundant mesopredators that occupy many reefs invite continued examination. Here, we present empirical evidence from Caribbean Panama and beyond suggesting that lionfish are less abundant than native mesopredators. Furthermore, we show that their direct impacts on survivorship and size distributions of one native prey species are similar to those of a native mesopredator. These results support calls for lionfish management that considers evolving local ecological and social dynamics, including prey community composition, the roles of native mesopredators, and regional goals for conservation and fisheries. Recognition of regional context creates the potential for synergies between conservation actions aimed both at the invasion and other consequential problems such as overexploitation and climate change.

Keywords Indo-pacific lionfish · *Pterois volitans* · *Pterois miles* · Invasive species · Naiveté · Coral reefs · Social–ecological systems · Predation

Introduction

The ecological impacts of invasive species can have major economic, social, and cultural consequences (Pejchar and Mooney 2009). However, the effects of invasive species are not uniformly negative, and there is increasing attention to how the impact and function of invasive species can vary geographically (Davis et al. 2011; Lockwood and Robinson 2014; Doherty and Ritchie 2016). For example, in certain localities invasive plants can have null or positive effects on nesting native birds (Gleditsch and Carlo 2014). More generally, invasive species can offer novel socioeconomic opportunities (resource extraction, tourism; Pejchar and Mooney 2009). Quantifying the ecological and social significance of invasive species in different locations can facilitate an understanding of trade-offs between costly removals of invaders versus a more complex characterization of what it means to accept novel species in social–ecological systems riddled by "wicked problems" (Rittel and Webber 1973).

On coral reefs, there are few examples of successful invasions by vertebrate predators. A conspicuous exception is the introduction of Indo-Pacific lionfishes (*Pterois volitans* and *P. miles*) to the Atlantic in the 1980s and their rapid spread in the 2000s. Invasive lionfish are voracious generalist predators with venomous spines that act as a built-in defense against native predators (Côté et al. 2013). Exponential increases in invasive lionfish abundance in some areas have raised serious conservation concerns for native prey communities (e.g., Ingeman 2016). The

Topic Editor Alastair Harborne

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vulnerability of native communities to lionfish is likely compounded by a long history of overexploitation of apex predators. As in many ecosystems (Ritchie and Johnson 2009), the loss of apex predators on Caribbean reefs has caused an increase in the abundance of smaller predators such as small groupers and snappers (Stallings 2009). This increase in smaller predators, also known as mesopredators, threatens the abundance and biodiversity of coral reef fishes (Stier et al. 2017). The lionfish invasion may exacerbate these mesopredator threats given that lionfish can play a similar trophic role to native mesopredators (Albins 2013; Ellis and Faletti 2016; Curtis et al. 2017). For these reasons and others, there is a growing appreciation that the impacts of lionfish on native coral reef communities are likely to be heavily context-dependent, and mediated by the abundance, influences, and naiveté of native predators, competitors, and prey (Anton et al. 2016; Ingeman et al. 2017). However, there is an incomplete understanding of how lionfish abundance varies relative to native mesopredator abundance, and of the relative impacts of lionfish and native mesopredators on native prey species.

Here, we provide evidence from Caribbean Panama and beyond that lionfish are less abundant than native mesopredators and that lionfish impacts on one common prey species are indistinguishable from a native mesopredator. Our results provide support for the view that management of invasive lionfish may be succeeding in some places and that continuation of control efforts requires nuanced consideration in relation to specific conservation goals and in relation to other environmental concerns.

Methods

Observational surveys

We conducted two types of flashlight-assisted visual surveys at three different sites near Bocas del Toro, Panama (Punta Caracol, Casa Blanca, Casa Verde), in January 2015. First, we counted lionfish, native predators, and potential prey for these predators on 24 patch reefs. Two divers counted all non-cryptic fishes on each patch reef, which primarily consisted of the corals *Orbicella* spp. and *Agaricia* spp. Following surveys, divers measured the area of the reef approximated by the product of its maximum width and length in meters, compared their fish observations, and scored a predator species as present on a patch reef if at least one diver detected it. For prey, we averaged the counts of individuals ≤ 5 cm TL across divers. Patch reefs averaged 1-2 m^2 in area (range: 0.3–3.3 m^2), and those we surveyed were generally 2–10 m apart from one another. All surveys were conducted during the day, and flashlights were used to look inside dark crevices.

Second, we conducted timed roving diver surveys of lionfish and two types of native mesopredator, the graysby *Cephalopholis cruentata* and hamlets *Hypoplectrus* spp., at each site. In these surveys (which did not focus on individual patch reefs but rather the full matrix of habitat at each site), teams of three divers swam for 20 min each ~ 1 m above the substrate and along consistent depth contours of 4 m and 8 m. Counts focused on the mesopredators sighted directly below each diver and were summed within a team of divers to compare predator abundances (Table S1).

We conducted three analyses to quantify whether native mesopredators were more common than invasive lionfish. First, we tested the hypothesis that invasive and native mesopredators occupied an equal proportion of reefs by analyzing a generalized linear mixed model (logit link, binomial distribution) of occurrence as a function of predator type (native or invasive), with site as a random effect. Second, we tested the hypothesis that native and invasive mesopredators differed in conditional density (i.e., density when present). Because not all mesopredator species were present at all sites, we pooled all native mesopredators together and compared the conditional density of native mesopredators to lionfish using a Student's *t*-test. Third, we tested the hypothesis that invasive and native mesopredators were equally abundant during the timed surveys at the three sites by comparing mesopredator abundance across observer teams using a one-way ANOVA with survey sites as the replicates.

In the patch reef surveys, one prey species, the masked goby *Coryphopterus personatus*, was conspicuously more abundant than other prey species, forming large shoals above individual reefs where we observed multiple predator species stalking and striking them. To test the hypothesis that the masked goby was more abundant than all other prey species summed together, we analyzed a generalized linear mixed model of log-transformed densities to compare these two groups, using site as a random effect.

Because our predator surveys in Panama reflect a snapshot in time from one region, we also analyzed observational data from the Reef Environmental Education Foundation (www.reef.org) database, collected during surveys conducted across eight regions in the Caribbean and Western Atlantic in the six years leading up to our study 2010–2015. The REEF database compiles information from volunteer divers who use a roving diver technique to count all fishes observed during a dive, as well as metadata including location, date, time, and habitat. Expert density is a weighted average index based on the frequency of observations by expert REEF divers in different abundance categories (1, 2–10, 11–100, > 100 individuals). A dive without any reported sighting of a fish species is interpreted as 0 individuals for that dive. We used a Welch's two-sample *t*-test to compare expert densities of lionfish and graysby, treating regional means from 2010 to 2015 as replicates (Table S2).

Experimental test of lionfish and native mesopredator impacts

In January–February 2015, we conducted a laboratory experiment to test whether the direct effects of lionfish on native masked gobies differed from the effects of the native graysby, in Bocas del Toro, Panama, at the Smithsonian Tropical Research Institute.[1] We focused on this prey species because it was highly abundant and we observed lionfish and native mesopredators feeding voraciously on these gobies in the field. The experiment consisted of three trials, each of which included four treatments within replicate aquaria: empty control (10 gobies only), non-mesopredator control (1 parrotfish *Scarus iseri* with 10 gobies); native mesopredator (1 graysby with 10 gobies); and invasive predator (1 lionfish with 10 gobies; see Table S3 for sample sizes by trial). The laboratory experiment matched observed mesopredator densities, as when a graysby or lionfish was present on a patch reef at our study sites, it was uncommon to observe more than one. We collected fish from nearby reefs and allowed them to acclimate to the laboratory for $\geq$ 24 h prior to initiating experiments. We standardized mesopredator satiation by ensuring that individuals did not feed for $\geq$ 24 prior to inclusion in the feeding trials.

Each aquaria contained a single PVC tube (15 cm long, 2.5 cm diameter) to provide structure. At 1200 on the day of each trial, we introduced the mesopredators or parrotfish to aquaria. Trials began at 1630 when we introduced gobies to the aquaria (haphazardly with respect to goby size). We note that lionfish activity peaks during twilight periods in both their native and non-native ranges (Green et al. 2011; Cure et al. 2012; McCallister et al. 2018, but see Morris and Akins 2009). At 1830, we removed mesopredators/parrotfish from the experimental aquaria and placed them in larger holding tanks until the subsequent trial. We collected, counted, and measured (SL mm) surviving gobies from each tank the following morning.

To test the hypothesis that lionfish influenced the overall and size-selectivity of mortality of gobies differently than native mesopredators, we conducted nonparametric Kruskal–Wallis tests with proportion mortality or size of surviving gobies as the response variable and predator treatment as the predictor variable. Nonparametric tests were necessary because of the extreme differences in data distribution in the control treatments (very low mortality) and the mesopredator treatments (higher mortality). We pooled data across three temporal trials and across empty control and non-predator control treatments, as the differences between lionfish, graysby, and control treatments during each trial, and results for empty control and non-predator control treatments, were qualitatively similar. Because in some treatments there were an abundance of replicates without any predation, while in the mesopredator treatments approximately half of the fish were eaten, the data violated assumptions of normality and homogeneity of variance for parametric statistics. We used a Wilcox post hoc test to determine if response variables differed significantly between the native and invasive mesopredator treatments. All analyses were performed using R software (R Core Team 2020).

Results and discussion

We encountered significantly fewer lionfish than native mesopredators in Caribbean Panama, on both the patch reefs (occurrence: Fig. 1a; glmer $Z = 2.356$, $p = 0.019$; conditional density: Fig. 1b; *t*-test, = 2.803, $p = 0.015$) and during timed mesopredator survey counts (Fig. 1c; ANOVA, $F = 8.877$, $p = 0.016$). On average, native mesopredators occupied $> 2 \times$ as many patch reefs as lionfish (range: 1–fourfold differences), their conditional densities were ~ 50% greater, and they were 30–40 times more abundant during timed counts (Table S1). Relatively low occurrence, density, and abundance of lionfish in our study may reflect successful efforts to cull lionfish via fishing derbies (Malpica-Cruz et al. 2016; Green et al. 2017), effective biotic control by the native fish assemblage (Ellis and Faletti 2016), and/or a tapering of the invasion wave (Benkwitt et al. 2017). We do not have data to speak directly to lionfish control efforts in Caribbean Panama, though anecdotal evidence[2] and reports in conference proceedings suggest that derbies and fisheries by Ngobe indigenous people have reduced lionfish densities in this region (Fehr et al. 2012; ICRI 2014).

Our local finding in Caribbean Panama appears to generalize: comparison of graysby and lionfish densities across eight regions in the Western Atlantic and Caribbean suggests that graysby densities are ~ 20% higher on average (Fig. 1d; Welch's $t = 2.44$, df = 11.25, $p = 0.033$). These results are consistent with observations from several other studies in the western Caribbean (Elise et al. 2014; Hackerott et al. 2017; Peiffer et al. 2017), which have described much lower lionfish abundance than in locations farther north and east (Green et al. 2012). These geographic

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[1] https://stri.si.edu/facility/bocas-del-toro

[2] http://www.tropicalcc.org/lionfish-control-management

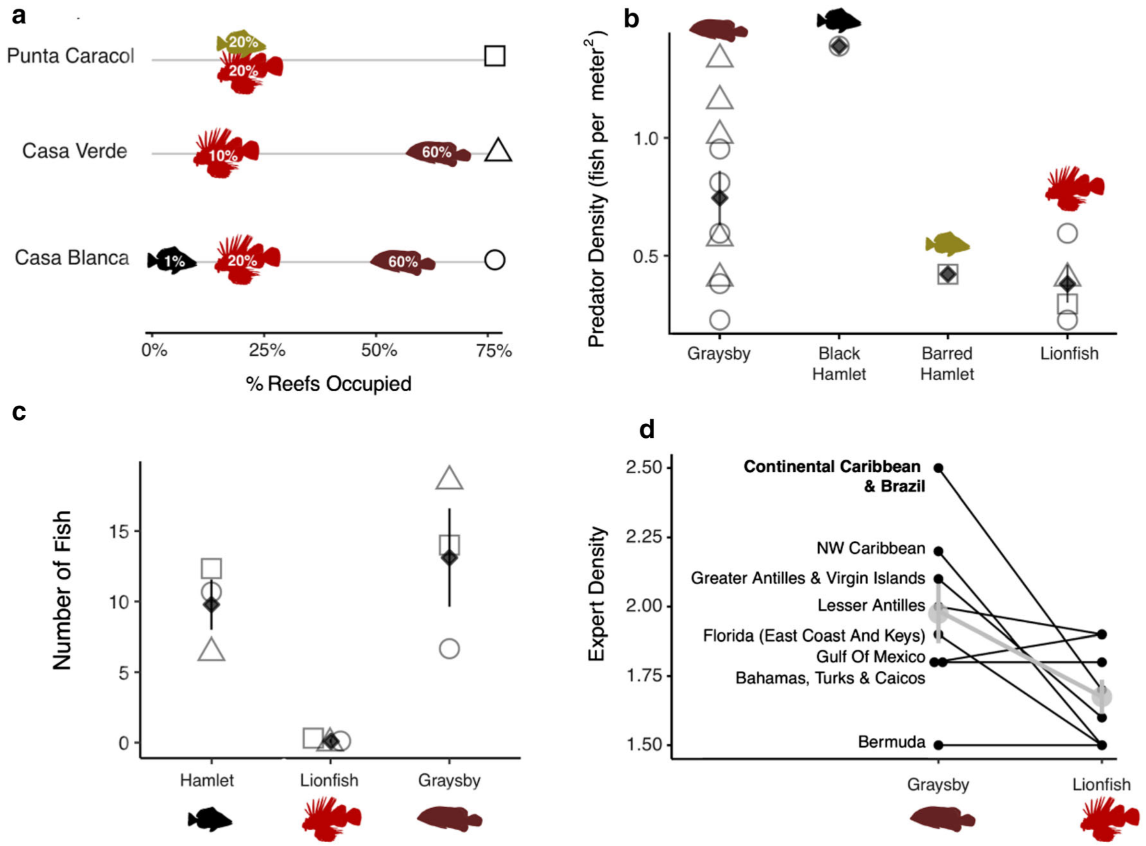

Fig. 1 Comparison of **a** the percentage of patch reefs (Punta Caracol: $n = 5$; Casa Blanca: $n = 11$; Casa Verde: $n = 8$) occupied by native mesopredators (graysby *Cephalopholis cruentata* and hamlets *Hypoplectrus puella*, *H. nigricans*) and Indo-Pacific lionfish (*Pterois volitans* and *P. miles*), **b** the density of native mesopredators and lionfish when present on those patch reefs, **c** the number of native mesopredators and lionfish observed on timed, roving diver surveys, and **d** the expert densities (derived from the REEF database) of one native mesopredator (the graysby) and lionfish across eight regions in the Caribbean and Western Atlantic from 2010 to 2015. Panels **a**-**c** focus on three sites in Caribbean Panama (Punta Caracol, squares; Casa Verde, triangles; Casa Blanca, circles) surveyed in 2015. Filled symbols in **b**-**d** reflect means ± 1SE across sites/regions

differences may imply disparities in lionfish control efforts, carrying capacities, or ecological interactions (Ingeman et al. 2017). One hypothesis associated with disparities in ecological interactions is that lionfish prefer patch reef habitats or show higher growth, survival, and immigration on patch reefs, compared to contiguous reef habitats. We note that the highest density of lionfish recorded in the invaded range comes from artificial reefs in the northeastern Gulf of Mexico (Dahl and Patterson 2014) and that many studies in the northeastern Caribbean have focused on patch reef habitats (e.g., Green et al. 2011; Albins 2013; Ingeman 2016). While we do not have information about the characteristics of the reef matrix at each of the REEF study sites (Fig. 1d), our own observations from Caribbean Panama are consistent with the hypothesis that habitat configuration (cf. Sandin and Pacala 2005; White et al. 2011) plays a role in lionfish population dynamics: invasive lionfish were less common than native mesopredators on the patch reefs we surveyed (Figs. 1ab), but they were even less common and rarely observed at all on roving diver surveys across contiguous reef habitat (Fig. 1c).

Our results demonstrate that lionfish are less common than native mesopredators in Caribbean Panama and beyond, but it is possible that lionfish impacts on native prey are greater (Albins 2013; Ellis and Faletti 2016). We tested this hypothesis using the masked goby as a focal prey species, which occurred in shoals of 10–100 s of individuals with densities $\geq$ tenfold those of all other prey species combined ($t = 13.365$, $p < 0.001$; Fig. S1).

Goby mortality was higher in the invasive and native mesopredator treatments compared to the control (K-W $\chi^2 = 17.73$, $p = 0.001$). While all gobies survived in the control treatments, on average ~ 50% of them survived the 2-h experimental trials in both the invasive lionfish and native graysby treatments (Fig. 2a), mortality rates that were statistically indistinguishable (Wilcox post hoc test = 81.5, $p = 0.66$). Furthermore, the size selectivity of predation by invasive and native mesopredators did not differ from each other or from the control treatment (K-W

$\chi^2 = 2.56$, $p = 0.28$; Fig. 2b). Though replication was limited with our experimental design, we found strong congruence in outcomes across trials, giving little reason to suspect that more replication would lead to different inferences. Furthermore, these results are consistent with a recent meta-analysis of field experiments (Stier et al. 2017), which found that the effect of lionfish predation on native prey communities is consistently negative and strong, but statistically identical to predation effects induced by native mesopredators.

In contrast to our findings, the one direct, field-based experimental test of native mesopredator and lionfish impacts on native prey mortality (in the Bahamas) demonstrates that lionfish effects are stronger than native mesopredators for many species (Albins 2013). This difference could result from several factors. For instance, lionfish and native mesopredators may exhibit geographically distinct effects on native prey communities because of the higher lionfish densities in the Bahamas compared to Panama (Fig. 1d; Green et al. 2014) or due to enhanced biotic resistance closer to the equator (Freestone et al. 2013 but see Anton et al. 2019). In addition, vulnerability of gobies to lionfish predation may be low; Albins (2013, Table 1) shows weak or positive impacts of lionfish on three of the five gobies examined in that study. Similarly, separate experimental evidence suggests that two species of Caribbean gobies (*Coryphopterus glaucofraenum* and *Gnatholepis thompsoni*), including one congener of the masked goby, show a moderate level of recognition of lionfish as a predation threat (Marsh-Hunkin et al. 2013). While prey naiveté toward lionfish has been shown to be an important ecological mechanism behind the invasion success of lionfish in the Caribbean and the eastern Mediterranean (Côté et al. 2013; Anton et al. 2016; Haines and Côté 2019; D'Agostino et al. 2020), this mechanism does not appear to be a strong factor for gobies and it is possible that past co-evolutionary history between the *Coryphopterus* genus and the *Pterois* genus has dampened the impact of naiveté.

Alternatively, our findings may contrast with the longer and broader field study undertaken by Albins (2013) due to the short-term nature, confined laboratory environment, restricted time of day, and singular prey species we employed for predation trials. While there are several inferential advantages of a field experiment, additional field- and lab-based experimental studies in different geographies and with different prey species will clarify the relative influences of invasive lionfish and native mesopredators on native prey. Strong effects of lionfish are less likely in locations with low densities of invasive lionfish—as in the present study (Fig. 1)—but also where there is a high standing biomass of fishes and larger size classes of fishes (Ingeman et al. 2017). Additional experimental work to understand how these factors interact to influence lionfish impacts on native communities will allow for more targeted, effective control efforts (cf. Green et al. 2014). Inconsistency of results across prey species, studies, and regions is not without precedent in the study of invasive species and emphasizes the need to evaluate how short-term impacts of invaders over small geographic areas scale to entire ecosystems in the medium to long terms after an initial invasion wave (Lockwood and Robinson 2014).

No matter their relative influence, in absolute terms both native mesopredators and invasive lionfish drive shifts in the abundance and biodiversity of Western Atlantic and Caribbean coral reef fish communities (Stier et al. 2017). These effects are partially a result of disproportionately high fishing rates of apex predators that have allowed for mesopredator release (Stallings 2009), a widespread phenomenon on coral reefs and in other ecosystems (Ritchie and Johnson 2009). It remains an open question whether lionfish are exacerbating widespread mesopredator release in the Western Atlantic and Caribbean by adding another highly abundant species to this guild, or if they are competing and partially or wholly replacing contemporary functional roles of native mesopredators. No matter where reality lies, emerging studies showing the potential for native apex predators to inhibit lionfish (Mumby et al. 2011; Diller et al. 2014; Ellis and Faletti 2016) suggest that restoration of native apex predators may offer significant promise to address mesopredator release and the lionfish invasion simultaneously (Doherty and Ritchie 2016). However, additional research on the interactions between lionfish and native predators is needed to understand the context under which native predators may mediate the effects of lionfish (Hackerott et al. 2013).

The evidence synthesized here embraces recent calls for critical examination of claims about the consequences of invasive taxa more generally (Davis et al. 2011). Our study also underscores the role time and spatial scale play in shaping the impacts of species introductions (Lockwood and Robinson 2014) and suggests that geographic differences and trends in lionfish impacts are evolving. Given that in Caribbean Panama lionfish are uncommon compared to native mesopredators and have similar effects on at least one of the most common native prey species, current management practices to control lionfish may be considered quite effective. Alternatively, given the generally low relative abundance of lionfish, they may be well thought of as leverage points to address "wicked problems" such as climate change and overexploitation (Rittel and Webber 1973) also affecting coral reefs in the region. For example, the social and economic opportunities provided by the emergence of lionfish as a new source of food, livelihoods, and tourism remain largely unexamined (but

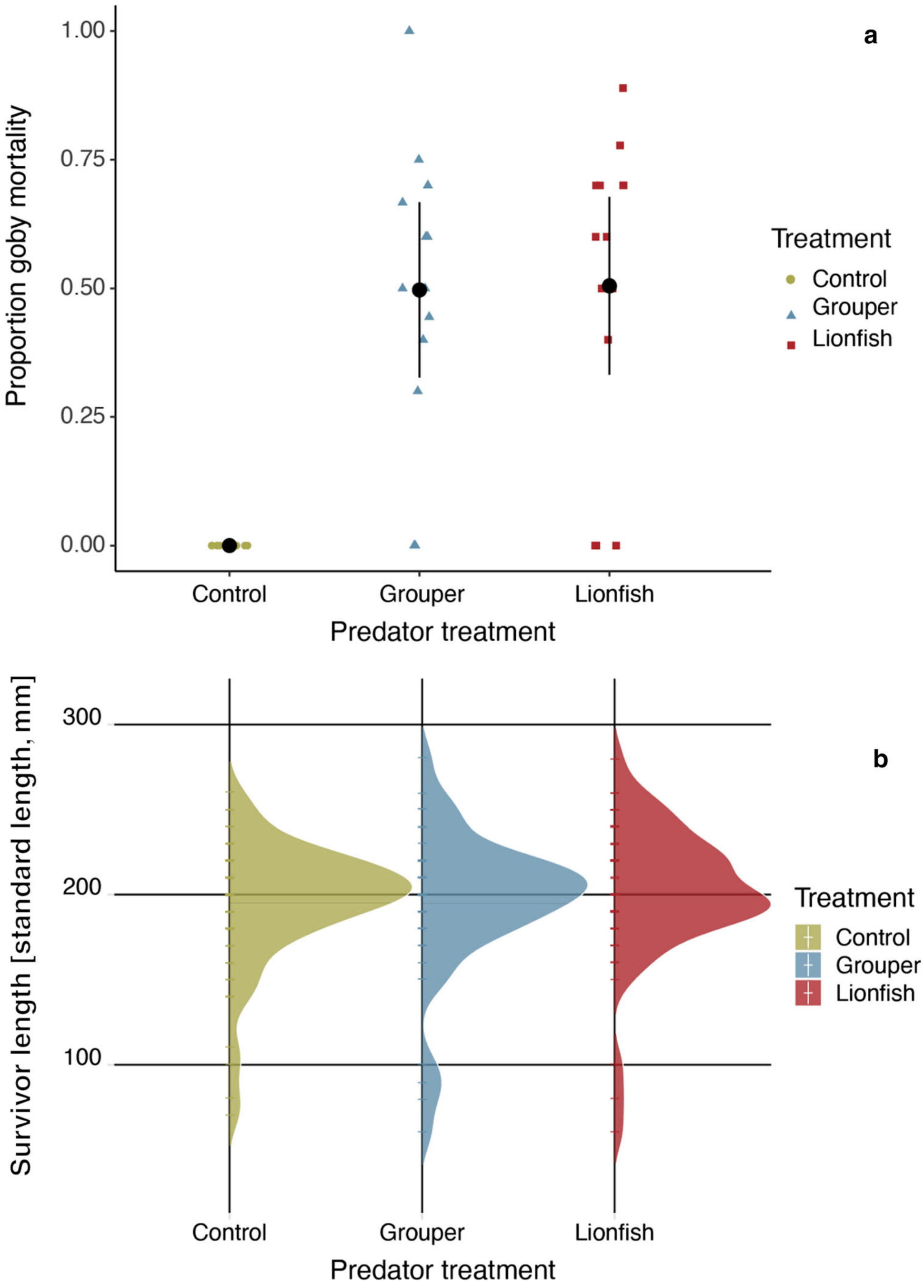

Fig. 2 The **a** mortality and **b** size distribution of native prey (*Coryphopterus personatus*) exposed to native mesopredator (graysby), invasive mesopredator (lionfish), and control treatments in mesocosm experiments. In **a**, black points and error bars represent mean proportional mortality ± 95% CI, and colored triangles represent results from individual replicate aquaria for each treatment. In **b**, density plots show the smoothed distribution of the points along the numeric axis of survivor length and hash marks on *x*-axis reflect size of individual survivors from each treatment, pooled across trials and aquaria. The peaks of the density plots are at the locations where there is the highest concentration of points

see Chapman et al. 2016), but could be important in areas where the status of fisheries is poor, food security is low, and vulnerability to climate change is high (Siegel et al. 2019). On the other hand, if lionfish depress densities of native herbivores that graze algae sufficiently, they may aggravate the challenges already faced by corals due to fishery removals (Bellwood and Goatley 2017), which would inspire a redoubling of control efforts where local economies are heavily dependent on reef-based tourism. We encourage future efforts to build a place-based understanding of the ecological, economic, and social links to lionfish in Panama and throughout their introduced range.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-021-02132-8.

Acknowledgements Craig Layman, John Bruno, Kurt Ingeman, Blake Feist, Joe Curtis, Julian Olden, Melissa Poe, and four anonymous reviewers provided helpful comments on earlier versions of this manuscript. We also gratefully acknowledge the entire 3 Seas XXX and XXXI classes for their work on this study, as well as Sebastian,

Fufo, Abuelo, Aqualounge, and all the odd-numbered breeding hamlets that got away.

Declarations

Conflict of interest The authors declare that they do not have conflict of interest.

Ethical statement We certify that this article was prepared as part of our official duties. The article is thus in the public domain and cannot be copyrighted.

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