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Density dependence mediates the ecological impact of an invasive fish

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Abstract

Aim: The way in which habitat heterogeneity and predator density affect predator–prey dynamics, space use and prey risk are understudied aspects of foraging ecology, particularly for invasive species. Likewise, how an invasive species' impact scales with its abundance is poorly understood. We used a model invasive species—lionfish (*Pterois volitans*)—to understand emergent multiple predator effects and influences of habitat heterogeneity on consumption rate and prey mortality risk.

Location: Florida, USA.

Methods: We considered effects of both predator and prey abundance on density-dependent impact. We used functional response methodology to quantify the per-capita effect of *P. volitans*, assessing concomitant influences of prey refuge (3 levels) and predator density (3 levels) on predator–prey space use and predation efficiency across increasing prey densities (7 levels). We then assessed intraspecific interaction outcomes by comparing observed per-capita effects with predicted estimates based on consumption rates of individual predators. This allowed us to detect the presence of emergent multiple predator effects (MPEs) and tease apart density-dependent impacts.

Results: Lionfish predatory impact was mediated by predator and prey density but unaffected by refugia. Despite incongruent patch preferences between predators and their prey, predator impacts were context-independent. We also detected non-linear scaling of impact with increasing predator abundance. Pairs of lionfish had the greatest per-capita effect, whose cumulative impact on prey matched that expected of independently foraging predators. At the highest predator density (four fish), antagonistic multiple predator effects precipitated prey risk reduction, in which we observed the lowest per-capita effect. Across predator abundances, prey mortality rates were inversely density-dependent.

Main conclusions: Quantifying non-independent consumptive effects of multiple conspecific predators across levels of prey abundance can inform better prediction and understanding of invasive species' density-dependent effects. Additionally, consideration of heterogeneity-mediated FRs and predator–prey spatial distributions

may facilitate more precise and realistic predictions of invader impact across their invaded range.

1 | INTRODUCTION

Fundamental to our understanding of predator–prey interactions is a predator's functional response (FR), modelling resource consumption as a function of its density (Holling, 1959). Considerable research has sought to understand a predator's FR. However, the effect of predator density on consumption remains an understudied aspect of FR research, particularly for marine predators (Stier & White, 2014). Predator density provides more advanced insight into FRs (Kratina, Vos, Bateman, & Anholt, 2009), whose effects on prey are often nonlinear. In the presence of conspecifics, predators may alter their behaviour through emergent multiple predator effects (MPEs) (Sih, Englund, & Wooster, 1998). While consumption rates are assumed to increase proportionally with predator abundance, MPEs may precipitate differences in interaction strengths—and prey risk—relative to effects expected for independently foraging predators. Conspecifics can facilitate or hinder consumption rates—total or per-capita—through cooperative hunting and competition, respectively (Abrams & Ginzburg, 2000; Beddington, 1975). The former may increase per-capita predation rates (Major, 1978), whereas antagonisms among predators may dilute total and per-capita impacts. In turn, these effects have important implications for prey population persistence.

While MPEs neatly differentiate resource use between single and multiple predator conditions (Mofu et al., 2019), they are often determined at a single prey density (e.g. Porter-Whitaker, Rehage, Liston, & Loftus, 2012). However, non-independent effects of multiple predators may covary with prey abundance (Abrams & Ginzburg, 2000). As prey density increases, predator encounter rates with prey often increase (Mols et al., 2004) which may increase total but decrease per-capita prey mortality risk (Gregory & Courchamp, 2010). FRs provide an efficient way to deconstruct MPEs, the magnitude of which can be used to quantify community outcomes and prey population stability (Juliano, 2001). While they are seldom integrated in MPE studies, this approach can provide meaningful insights into predator–predator and predator–prey interactions (Wasserman et al., 2016).

Predation can negatively affect prey populations directly through consumption, while its risk can play a significant role in shaping prey habitat use. Habitat heterogeneity may lessen predator impact by increasing interference for limited resources (Hassell, 1978) and creating prey refuge (Beukers & Jones, 1998; Cuthbert et al., 2020). Mediating effects of heterogeneity on both predator impact and prey risk may be further influenced by predator and prey

abundance (Buxton, Cuthbert, Dalu, Nyamukondiwa, & Wasserman, 2020; Nachman, 2006). In turn, spatial arrangements of predators and their prey—which are affected by habitat heterogeneity—have significant implications for a predator's FR (Vucic-Pestic, Birkhofer, Rall, Scheu, & Bröse, 2010). More broadly, consideration of habitat heterogeneity can address the population FR of multiple predators by describing per-capita impact as a function of their effects across multiple patches (Ives et al., 1999). Ultimately, this permits better understanding of predator–prey population dynamics (Ives et al., 1999).

Predators and prey have opposing interests, the conflict between which underpins the predator–prey space race, a "game" in which both occupy a habitat containing multiple patches of variable risk (Sih, 2005). While competing foraging theories make consistent predictions about refuge-seeking behaviour of prey, they make opposing predictions of predator foraging behaviour in response to heterogeneity in resource distribution. For example, optimal foraging theory predicts that predators should aggregate in high-refuge habitats harbouring the most prey (reviewed in Lima, 2002; Sih, 1984) while the predator–prey space race predicts that predators should aggregate in patches where prey are most vulnerable, irrespective of density (Sih, 2005).

Prey abundance, predator density and habitat heterogeneity collectively influence prey mortality. Understanding how such factors alter conspecific interaction strengths is important for invasive species—high-impact non-indigenous species that can alter ecological patterns or processes (Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). Invasive species often have profound negative effects on native community richness, diversity and evenness, the direction and strength of which may be governed by their abundance (Bradley et al., 2019). Impact assessments have historically assumed a proportional increase in per-capita effect with abundance (Parker et al., 1999). However, the often nonlinear relationship between an invasive species' abundance, per-capita effect and impact underlines the need for more tailored impact estimates with increasing predator abundance (Bradley et al., 2019; Sofaer, Jarnevich, & Pearse, 2018; Wasserman et al., 2016). Despite their importance, abundance–impact relationships are poorly characterized for most invasive species (but see Latzka, Hansen, Kornis, & Vander Zanden, 2016). FRs that incorporate emergent MPEs offer one way to clarify invasive species' density-dependent impacts, though such studies are seldom conducted (but see Wasserman et al., 2016).

Predator–prey space use is an important component of community dynamics (Sih, 2005). It is also an important consideration for invasive species, whose ecological impacts are often

context-dependent and differ between habitats (Ricciardi et al., 2013). However, few studies have assessed predator–prey space use of invasive species and its implications on predator per-capita impact (Jackson et al., 2017). Ultimately, knowledge of density- and habitat-mediated impacts can more reliably generalize and predict invasive species' impacts, which has proven difficult (Blackburn et al., 2014).

Herein, we combined two approaches of quantifying invasive species' impacts, assessing their feeding rate both across prey densities and as a function of increasing predator density, across multiple habitat patches. Furthermore, we sought to understand the ranked importance of these individual drivers under controlled experimental conditions. We assessed these effects in a notorious invasive fish, lionfish (*Pterois volitans*). Lionfish have spread widely across the western Atlantic Ocean following their initial introduction off Florida's east coast in the 1980s (Schofield, 2010) and provide an ideal model to assess interactive effects of habitat, predator density and prey abundance on per-capita impact. Lionfish are often observed in groups and appear to alter their hunting behaviour based upon conspecific density (Benkwitt 2015), providing a ripe avenue to quantify conspecific MPEs using a FR approach.

The present study aimed to determine whether: (a) predator abundance mediates total and per-capita consumption rates; (b) multiple predator effects can be predicted by summing per-capita impacts of independent predators; (c) lionfish predatory impacts differ by habitat type and availability of refugia; (d) prey mortality risk is mediated by refuge availability and predator density; (e) lionfish preferentially forage in patches of high prey density or high prey risk; and (f) predator patch use is contingent on or irrespective of prey patch use.

2 | METHODS

This study took place between February and June 2018. Lionfish (N = 39, mean total length (TL) ± SE = 215.7 ± 9.2 mm) were collected in southern Florida (30 m average depth) by scuba divers. Fish were transported to Florida Gulf Coast University's Vester Marine and Environmental Research Field Station (Bonita Springs, Florida) in live wells or coolers. Due to the capture depth, the majority of fish (>75%) were vented (16-g hypodermic needle inserted into the body wall at a 45° angle). Several fish (N = 10) were field-collected by Dynasty Marine Associates to provide an inclusive size range, which were housed collectively with the aforementioned fishes. Their prey, live pink shrimp (*Penaeus duorarum*) ($\overline{x}$ = 4 cm, range 2–7 cm), were purchased from a local vendor. Shrimp were chosen given the importance of crustaceans in lionfish diets across ontogeny (reviewed in Chagaris et al., 2017).

All fish underwent a week-long quarantine period following capture, held communally in fibreglass tanks (757 L). After one week, fish were transferred to recirculating tank systems (1,135 L: 34 ppt, 24°C, pH 8.2, dissolved oxygen near saturation) within the field station's semi-enclosed aquaculture cage. Fish were subject to a natural photoperiod (12 ± 1.5-hr daylight). Water quality was maintained with UV sterilizers, charcoal filters, biofilters and weekly 20% water changes. Water heaters (Aqua Logic® model #TIL5) maintained temperatures at 24°C (±0.5°C). Lionfish underwent a three-week acclimation period prior to trials and fed ad libitum live and frozen baitfish (*Atheriniformes* spp., *Harengula* spp., *Gambusia affinis*, *P. duorarum* and *Sardinops sagax*).
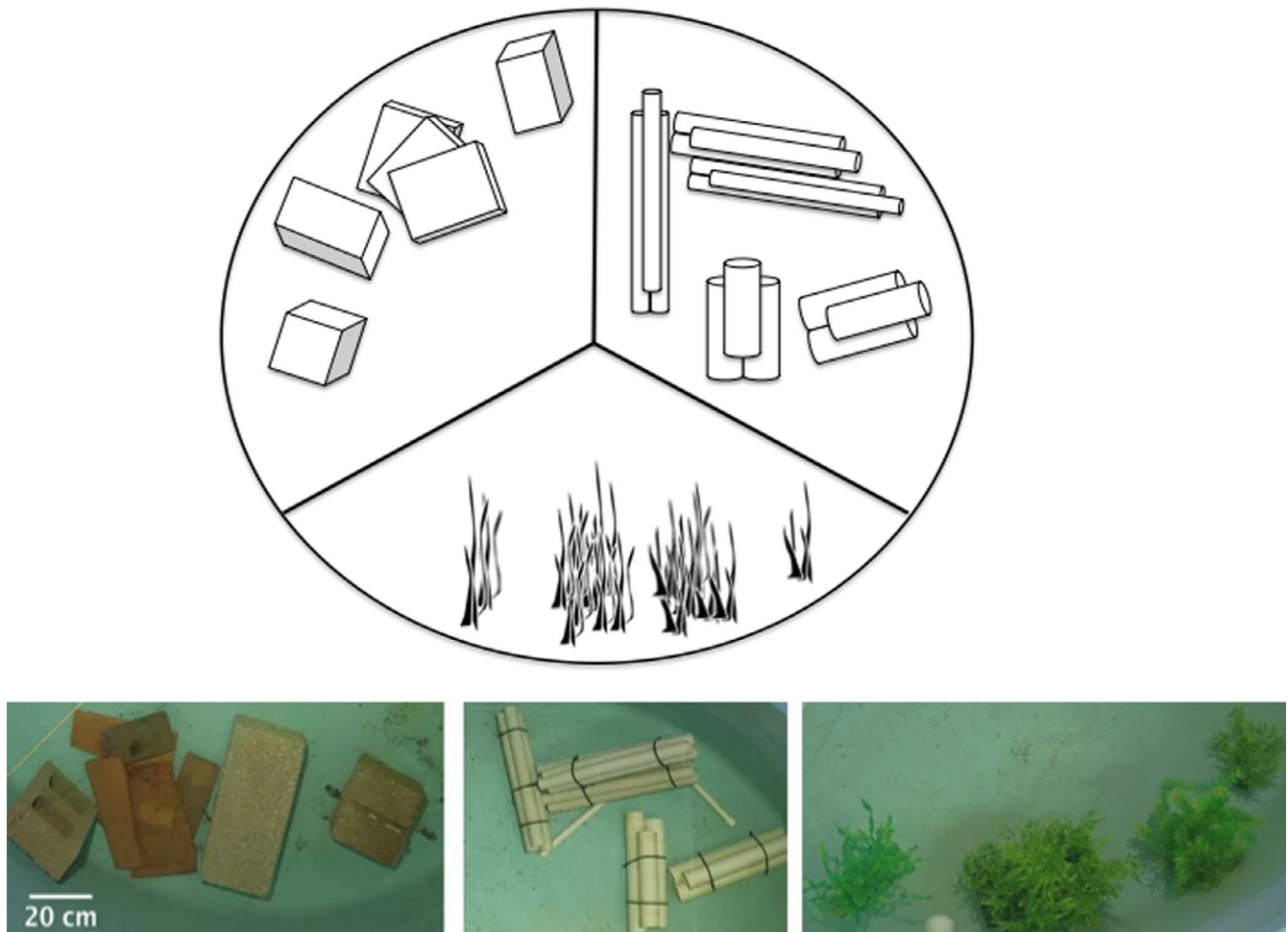
2.1 | Experiment

Trials were conducted in a round fibreglass tank (2,500 L: 2.1 m diameter × 0.9 m height, water depth 0.7 m) over which we attached a large LED (Husky: Model K40066). Water was maintained at salinity 32 ppt and pH 8.2, with dissolved oxygen near saturation. Ammonia and nitrite were kept at 0 ppm and nitrate <10 ppm. Immersion heaters held water temperatures at 24°C (±0.5°C) (Pentair Aquatics Part #H18T).

We used twine to divide the tank floor into three patches of equal area, which permitted unconstrained movement of predators and prey. Each patch contained a distinct habitat type (Figure 1). Habitats differed in availability of refugia (low, medium or high), providing prey temporary or permanent shelter from predation pressure (McNair, 1987). This design allowed us to examine implications of habitat heterogeneity on predation and predator–prey interactions.

The low-refuge patch mimicked natural hard bottom, the medium-refuge patch artificial reef, and the high-refuge patch seagrass. In the low-refuge patch, prey could seek cover inside four crevices of two cinder blocks (two crevices of 17.8 cm × 12.7 cm × 12.7 cm; two crevices of 14 cm × 19.1 cm × 12.7 cm). Surface area of refugia was least in this patch (SA = 0.52 m²), and prey were vulnerable irrespective of where they hid. The medium-refuge patch was comprised of clusters of open- and closed-ended stacked PVC pipes. Prey could seek refuge inside open-ended PVC pipes (interior of nine pipes measuring 1.27 cm radius × 47 cm length; six 3.8 cm radius × 38.1 cm length), which provided an intermediate level of refugia (SA = 0.95 m²). The high-refuge patch was comprised of four artificial aquarium plants (*first*: 25.4 cm top radius × 5.1 cm bottom radius × 53 cm height; *second*: 25.4 cm radius × 61 cm height; *third*: 8.9 cm top radius × 3.8 cm bottom radius × 15.2 cm height; and *fourth*: 30.5 cm × 16.5 cm × 45.7 cm), which provided the most usable structure for prey (SA = 2.12 m²). Using this arena, we then quantified the population FR of lionfish, foraging among these three dissimilar patches. Lionfish have high habitat plasticity (Cure, McIlwain, & Hixon, 2014; Schultz, 1986; Smith, 2010); thus, we had no a priori reason to expect an influence of habitat type on patch use.

2.2 | FR trials

To evaluate how predator density affected their FR and interactions with conspecifics, three lionfish group sizes (1, 2 and 4 lionfish per arena) were provided with seven prey densities (4, 7, 10, 13, 16, 19

FIGURE 1 The experimental tank in which trials were conducted. The tank was divided into three patches, differing in availability of prey refugia. Patches were distinguished based on a low (cinder blocks), medium (PVC) or high (aquarium plants) degree of refuge. Predators and prey were free to move within and among patches. A scale is drawn for size

and 22 shrimp per arena). We based predator densities on typical lionfish group sizes (Cure et al., 2014; Jimenez et al., 2016). Lionfish were randomly assigned to treatments (RAND function, Excel) but size-matched (TL) in multiple predator treatments. There were no significant size (TL) differences among predator densities (Kruskal–Wallis: χ^2 = 0.11, df = 2, p > .10) or across prey densities within each predator density (Kruskal–Wallis: df = 6, p > .10).

We conducted four replicates at each prey density. At a predator density of four, three replicates were conducted at prey densities 4 through 13 given limited field availability. We conducted additional trials at a prey density in instances where consumption rates were highly variable. A portion of experimental replicates for the single predator treatment was derived from a separate study (DeRoy, Scott, Hussey, & MacIsaac, 2020). Limited field availability necessitated reuse of fishes. To avoid pseudoreplication, lionfish were not reused in concurrent trials or with the same conspecifics at the same densities (Hurlbert, 1984).

We aimed to determine individual lionfish predatory behaviour under multi-predator scenarios. To identify individuals during experimental trials, lionfish were tagged at their posterior soft dorsal fin

with coloured numbered polyethylene streamer tags (Floy® FTSL-73, 10 cm) during their acclimation period (anaesthetized using 110 mg MS-222/L seawater).

One to three trials were run per day. As lionfish become sessile once satiated (Fishelson, 1997), they were subject to a 72-hr starvation period collectively in their housing tanks prior to trials. This standardized hunger and encouraged foraging (Jeschke, 2007). The experiment was initiated through addition of shrimp to the tank's centre via a bucket. Prey acclimated for 30 min before predators were introduced. Lionfish were likewise added using this method and allowed to feed for three hours. Pilot trials containing shrimp and no lionfish were also run to examine natural survivorship under experimental conditions at each of the experimental prey densities (N = 7). We observed 100% survivorship.

Overhead cameras (LOREX® 4K Ultra HD LNR6100 Series) connected to a desktop computer proximate to the tank were used to view trials in lieu of direct observation. An experimenter replaced prey as they were consumed throughout the trial to provide more accurate FR parameter estimates, particularly at low prey densities (Juliano, 2001). To avoid confounds associated with prey

additions—including experimenter presence—prey were added after lionfish vacated the patch. Lionfish often migrated to a different patch following prey consumption.

To understand the influence of habitat heterogeneity on foraging behaviour, we quantified several measures of behaviour, each predicted to vary across patches: successful attacks, unsuccessful attacks, stalking bouts and chases. Successful attacks ended in prey consumption. No shrimp was partially consumed. Stalking included instances where a lionfish hovered within striking distance of prey, whereas chases involved the unsuccessful pursuit of a shrimp. We measured a predator's foraging efficiency through their success rate of prey capture (consumption divided by attack rate). As neither stalking bouts nor chases ended in an attack, they were not included in success rate.

We also scored cooperative hunting (presence–absence) and gregariousness in multiple predator trials to detect synergisms among conspecifics and their effects on per-capita consumption rates. We operationally defined cooperative hunting as two or more lionfish actively pursuing a single prey item into a confined area with flared pectoral fins. Gregarious behaviour was defined as two or more lionfish hovering, resting or swimming together. This excluded lionfish occupying different regions within the same patch.

Streamer tags permitted examination of individual consumption rates. We recorded behaviours separately for each lionfish and each patch. For trials with multiple lionfish, we monitored individual behaviour separately and summed their cumulative effects. This allowed us to determine the distribution of feeding rates and other metrics of foraging behaviour among predators. It also allowed us to detect emergent MPEs. To understand whether foraging behaviour differed as a function of refugia, we recorded behaviours separately for each patch. Overall estimates of predation impact for a given trial were obtained by summing these values across patches.

2.3 | Patch preference

At the trial's start, we determined relative shrimp abundance in each patch in the absence of predators. In addition to surface area of refuge provided by each habitat, prey patch use was used as a proxy of refuge availability, as prey prefer high-refuge habitats (Hugie & Dill, 1994). Prey distribution is a prominent driver of predator distribution (Lima, 2002) and was used to guide expectations of predator patch use and foraging behaviour. To determine lionfish patch preference and assess shrimp patch preference in the presence of predators, a portion of experimental trials was recorded and analysed *post hoc*.

2.4 | Data analysis

All statistical analyses were performed using R, v. 3.5.3 (R Core Team, 2018). Data exploration was carried out following Zuur, Ieno, and Elphick (2010). Results are presented cumulatively and per capita.

2.4.1 | FR curves

To test how consumption rate varied as a function of predator density across prey densities, we fit separate Beddington–DeAngelis (Beddington, 1975; DeAngelis, Goldstein, & O'Neill, 1975) and Crowley–Martin (Crowley & Martin, 1989) predator-dependent FR models to per-capita consumption rate data for each predator density (1, 2, 4) via maximum likelihood estimation ("bbmle," Bolker & R Development Core Team, 2016). For trials with multiple predators, total consumption rate was divided by predator density to derive per-capita estimates. For each model, we bootstrapped consumption data 1,000 times, stratified over number of prey. We initialized parameters for the optimization process using those obtained by fitting the models on all data. The data we present are the median of all model parameters and performance measures (−2LL and AIC). In addition to observed attack rates, attack rates and handling times were inferred from FR parameters, the latter estimating prey pursuit and digestion (Stier, Geange, & Bolker, 2013).

Both FR models distil down to a Type II FR in the absence of conspecifics (Holling, 1959):

$$f = \frac{aN}{1+abN} \tag{1}$$

where a refers to attack rate, N prey density, and b handling time.

Beddington (1975) and DeAngelis et al. (1975) extended upon (1) to include implications of multiple predators foraging in an arena:

$$f = \frac{aN}{1+bN+c\,(P-1)} \tag{2}$$

where P denotes predator abundance and c describes the interference magnitude between predators. Crowley–Martin FR (Crowley & Martin, 1989) incorporates the same parameters as the Beddington–DeAngelis FR model but allows for simultaneous prey handling and interference between predators:

$$f = \frac{aN}{(1+bN)\,(1+c\,(P-1))} \tag{3}$$

At each predator density, we compared competing FR models using Akaike's information criterion (AIC) and relative fit to raw data. We compared model parameters among predator density treatments using Kruskal–Wallis rank-sum tests and—where significant—Wilcoxon rank-sum tests ("stats," R Core Team, 2018).

2.4.2 | MPEs

Single predator FRs were used to quantify emergent MPEs of multiple predator treatments and explore their risk-reducing and risk-enhancing effects on prey. To assess whether FRs of multiple predator treatments could be predicted by summing per-capita impacts of individuals, we

TABLE 1 Table of coefficients for predator-dependent FR models, where a = attack rate; b = handling time; c = magnitude of interference between predators; σ = standard deviation for the normal distribution assumed; $-2LL$ = -2 log likelihood; and AIC = Akaike's information criterion

	Crowley–Martin						Beddington–DeAngelis					
Predator density	a	b	c	σ	$-2LL$	AIC	a	b	c	σ	$-2LL$	AIC
1	1.4	0.5	1	2.0	184.4	192.4	1.4	0.4	1.0	1.9	183.5	191.5
2	11.7	0.6	5.2	2.2	164.4	172.4	85	20.5	29.1	2	157.1	165.1
4	3.5	0.3	1	1.4	82.6	90.6	5.5	1.9	1.8	1.4	82.7	90.7

calculated expected consumption rates for each predator density scenario ("bbmle," Bolker & R Development Core Team, 2016). We bootstrapped the data 1,000 times using median model parameters. We then produced 95% confidence intervals (CIs) by selecting 2.5% and 97.5% percentiles of curves. Finally, we multiplied these CIs for single predators by two and four to obtain 95% CIs for pairs and groups of lionfish, respectively. This produced predictions of expected predator consumption rates and prey survival based on independent effects of multiple predators. Predictions for treatments with two and four lionfish were then compared with observed per-capita consumption rates. We used the Jaccard index (e.g. Intersection over Union) to compute overlap between expected and observed FRs. We inferred predators had linear effects on prey survival if 95% CIs between observed and expected per-capita consumption rates overlapped.

2.4.3 | Main effects

In all analyses described below, nonparametric tests were used given deviations from normality. To test how metrics of foraging and consumption varied as a function of the manipulated factors (degree of prey refuge [3 levels], predator density [3 levels], prey density [7 levels]), we ran the following statistical tests.

Using Kruskal–Wallis rank-sum tests, we assessed overall effects of the fixed factors on patch preference, foraging activity, consumption rate, attack rate, prey mortality rate, success rate of prey capture, stalking bouts and chases. We examined significant differences among levels of a factor using *post hoc* pairwise Wilcoxon rank-sum tests with Bonferroni correction. Wilcoxon rank-sum tests were used to compare cooperative hunting and gregariousness between multiple predator treatments. We assessed effects of the fixed factors on prey mortality rate using a beta regression ("betareg," Cribari-Neto & Zeileis, 2010) with log–log link function. We determined the significance of main effects using the *joint_tests* function ("emmeans," Lenth, 2019).

Negative binomial-distributed generalized linear mixed models (GLMM) ("fitdistrplus," Delignette-Muller & Dutang, 2015) ("glmmTMB," Brooks et al., 2017) were used to analyse differences in lionfish success rate of prey capture and consumption rate as a function of the fixed factors. Both GLMMs included lionfish ID as a random effect, which accounted for their repeated use. The best model blended a

low AIC with biological relevance (Bolker, 2008). Assumptions were verified by plotting residuals versus fitted values ("DHARMa," Florian, 2019). Analysis of deviance ("car," Fox & Weisberg, 2019) was used to determine significance levels of main effects, following which we conducted *post hoc* Tukey-adjusted pairwise comparisons ("emmeans," Lenth, 2019), where appropriate. Wald chi-square statistics are presented for GLMMs. For models with interactions, Wald chi-square Type III tests were used, setting sum-to-zero contrasts on factors (Brooks et al., 2017).

2.4.4 | Patch preference

To test whether predator patch preference was dictated by prey availability or mediated by conspecifics, we analysed lionfish patch use using BORIS, v.7.4 (Behavioral Observation Research Interactive Software, Friard & Gamba, 2016). Using recorded trials (N = 60), we classified lionfish behaviour as either resting or foraging and determined the proportion of time spent in each patch (foraging and total residency, over a randomly selected 30-min duration). We computed averages for multiple predator trials. Prey abundance in each patch at the onset of a trial was used to assess predator-induced changes in patch occupancy. Using the same complement of trials used to determine predator preference, we documented changes in relative prey abundance in each patch (N = 6 trials per prey density: sampling 10 time points per 30-min period over three hours).

We assessed congruence between predator and prey patch preference to resolve which party dictated space use (Sih, 1984, 2005). A positive spatial correlation would suggest that lionfish spent the most time in the patch with the most prey, per classic foraging theory. If lionfish patch preference was negatively related to proportion of prey in that patch, it would suggest that lionfish valued prey vulnerability over prey density.

3 | RESULTS

3.1 | FR models

FR models produced similar fits to consumption data save for our paired treatment, in which the Beddington–DeAngelis FR provided
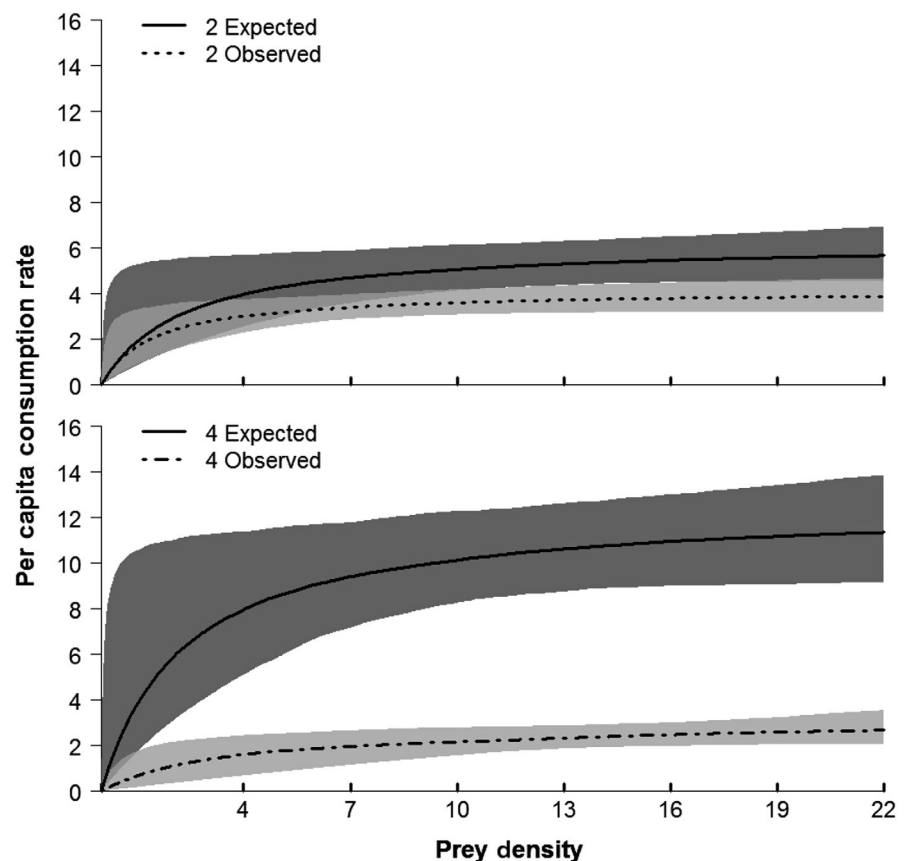
FIGURE 2 Beddington–DeAngelis predator-dependent FR depicting lionfish mean (± *SE*) per-capita consumption rates as a function of increasing prey density. Lines for each of one (solid), two (dotted) and four (dot-dash) lionfish are plotted. Per-capita consumption rates represent the total consumption rates divided by the number of predators in the system
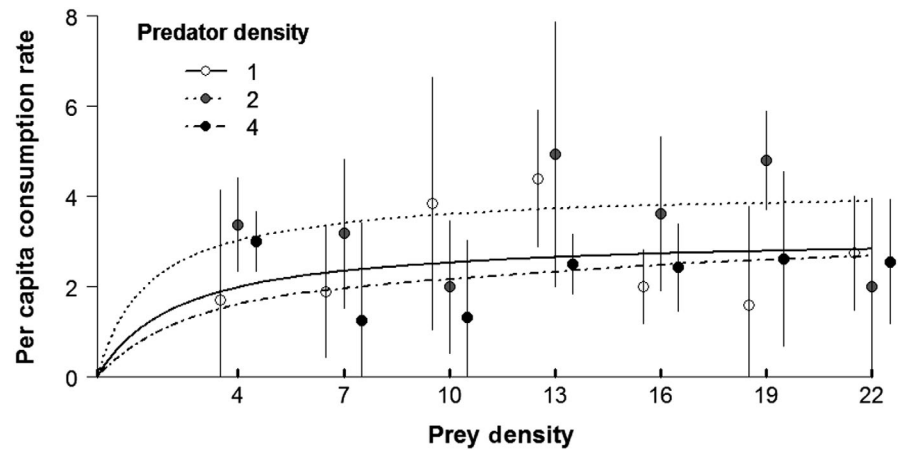

a better fit (Table 1). We therefore report the Beddington–DeAngelis FR alone. FR-derived attack rates (Kruskal–Wallis: $\chi^2 = 2,225.8$, $df = 2$, $p < .0001$) and handling times (Kruskal–Wallis: $\chi^2 = 2085.3$, $df = 2$, $p < .0001$) varied significantly among predator density treatments. Lionfish foraging in pairs had the greatest FR-derived feeding and attack rate (Figure 2, Table 1). When in groups, lionfish attack rate was intermediate to single lionfish (lower) and pairs (higher). We also observed greater interference between pairs of lionfish relative to groups (Wilcoxon rank-sum: $W = 884,680$, $p < .0001$).

3.2 | MPEs

Relative to their performance in individual trials, effects of lionfish in pairs combined additively, evidenced by overlapping observed and predicted FR CIs (Figure 3; Jaccard Index: 0.1). Conversely, we observed emergent antagonist MPEs and prey risk reduction when lionfish foraged in groups of four. In this treatment, per-capita consumption rates were lower—and inversely, prey survival rates were higher—than predicted by MPEs assuming independent foraging (Jaccard Index: 0.002).

FIGURE 3 Emergent multiple predator effects for treatments with two and four lionfish. Observed mean (± *SE*) per-capita consumption rates are plotted with Beddington–DeAngelis predator-dependent FRs for each of two (upper panel) and four (lower panel) lionfish. Expected consumption rates for each multiple predator treatment were calculated from the performance of individuals, plotted with mean responses (solid line). 95% CIs are presented for both expected (dark grey) and observed (light grey) consumption rates
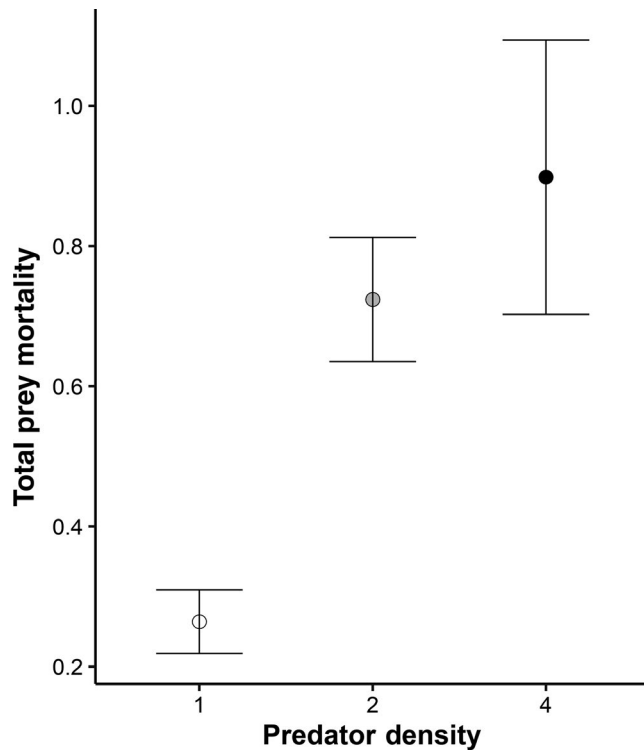
FIGURE 4 Mean (± *SE*) total shrimp mortality rate as a function of predator density

TABLE 2 Kruskal–Wallis rank-sum output summarizing metrics of foraging efficiency as a function of predator density. Significant values (*p* ≤ .05) are marked with an asterisk (*)

Response variable	χ^2	*df*	*p*
Total consumption rate	69.6	2	<.0001*
Per-capita consumption rate	8.3	2	.02*
Total attack rate	37.2	2	<.0001*
Per-capita attack rate	8.3	2	.02*
Total prey mortality rate	26.8	2	<.0001*
Total number of chases	21.4	2	<.0001*
Per-capita chases	5.0	2	>.05
Total stalking bouts	11.5	2	.003*
Per-capita stalking bouts	0.1	2	>.1

3.3 | Overall effects

Total and per-capita consumption, attack and prey mortality rates varied significantly among predator density treatments (Figures 2, 4, Table 2). Lionfish foraging in pairs had greater per-capita consumption rates relative to individuals foraging alone or those in groups of four (*p* < .05) and higher per-capita attack rates relative to those in groups (*p* = .01). Total rates of attack, consumption and prey mortality increased monotonically with predator density, which were significantly higher for multiple predator treatments relative to lone fish (*p* < .001) but were similar between these groups (*p* > .10; Figure 4).

Despite their moderate rates of consumption, we observed a greater frequency of cooperative hunting in groups (Kruskal–Wallis: χ^2 = 46.2, *df* = 2, *p* < .0001), which were also more gregarious relative to pairs (Wilcoxon rank-sum: *W* = 109.5, *p* = .08). While cooperative hunting was associated with a higher success rate of prey capture, this effect was not significant (Wilcoxon rank-sum: *W* = 560.5, *p* > .10). Predator density influenced the frequency of total but not per-capita chases and stalking bouts (Table 2), in which groups made moderately more chases than pairs (*p* = .07), which were significantly greater in multiple versus single predator treatments (4–1: *p* < .0001; 2–1: *p* = .01). Groups of four made more stalking bouts relative to single predators (*p* = .004), though rates were similar among other treatments (*p* > .1).

Metrics of foraging did not vary significantly among patches. Consumption rates (per capita: Kruskal–Wallis: χ^2 = 1.2, *df* = 2, *p* > .10; *total*: Kruskal–Wallis: χ^2 = 1.2, *df* = 2, *p* > .10) and success rates of prey capture (Kruskal–Wallis: χ^2 = 0.2, *df* = 2, *p* > .10; Figure 5) were robust to changes in refuge availability. Similarly, predator foraging efficiency was largely consistent across prey densities. Attack rates (*total*: Kruskal–Wallis: χ^2 = 9.7, *df* = 6, *p* > .10; per capita: χ^2 = 8.8, *df* = 6, *p* > .10), foraging time (Kruskal–Wallis: χ^2 = 4.1, *df* = 6, *p* > .10) and success rates of prey capture (Kruskal–Wallis: χ^2 = 2.3, *df* = 6, *p* > .10) did not vary significantly across prey densities. Rather, only the number of stalking bouts increased with increasing prey density (Kruskal–Wallis: χ^2 = 18.3, *df* = 6, *p* < .01).

3.4 | Combined effects

Per-capita consumption rates varied among predator densities as a function of prey availability (GLMM: predator density x prey density interaction, *p* = .04; Figure 2), but did not vary significantly among patches (*p* > .1) (Table 3). Single lionfish (GLMM: 0.8 ± 0.3, *p* = .007) and pairs (GLMM: 0.5 ± 0.2, *p* = .06) had greater success rates of prey capture relative to groups. However, success rates were not influenced by either prey density (*p* > .1) or refuge availability (*p* = .1; Table 3, Figure 5).

Total and per-capita prey mortality rates varied by prey density, predator density and their interaction (Figures 4, 6). Predation risk decreased with increasing prey density, wherein per-capita mortality rates were inversely density-dependent across predator abundances. Relative to single predators, we observed prey risk enhancement in multiple predator density treatments at low or high prey densities. Total and per-capita mortality rates were analogous between multiple predator treatments in all but the lowest two prey densities, in which lionfish pairs consumed a significantly greater proportion of shrimp (*total, density* = 7, *p* = .002; per-capita, *density* = 4, *p* = .04, *density* = 7:1.4 ± 0.3, *p* = .0002).

3.5 | Patch preference

There was a negative spatial correlation between lionfish and their prey. Prey exhibited significant patch preferences (Kruskal–Wallis:

FIGURE 5 Mean (± *SE*) success rate of prey capture of lionfish as a function of prey density. Rates are broken down for each level of prey refuge (low, medium and high) and separated by predator density (1, 2, 4)
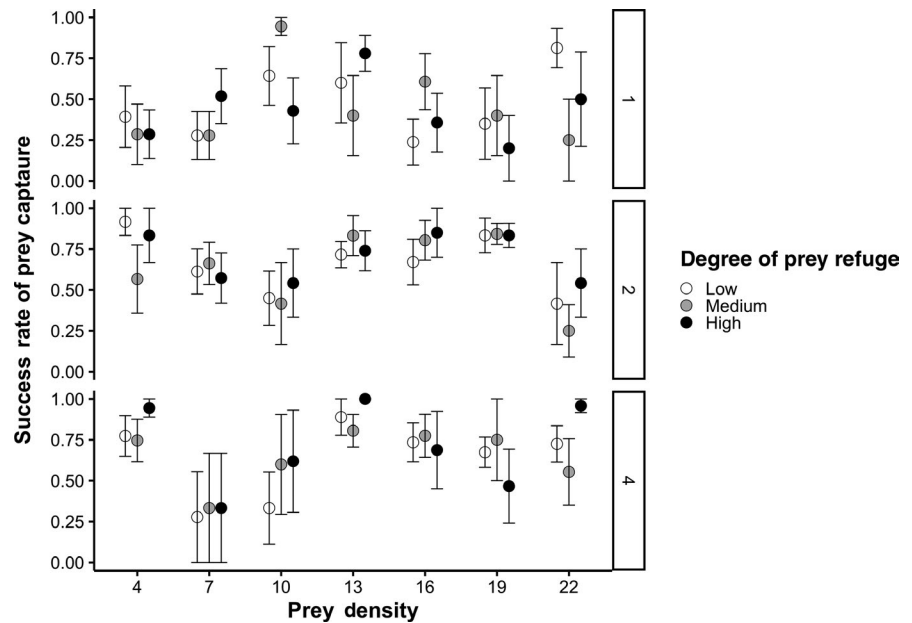
TABLE 3 GLMM main effects of the fixed factors (predator density, prey density and habitat refuge). Significant values (*p* ≤ .05) are marked with an asterisk (*)

| Response variable	Predictor variables	χ^2	df	p
Per-capita consumption rate	(Intercept)	10.9	1	.0009*
	Predator density	6.3	2	.04*
	Prey density	12.5	6	.05*
	Habitat refuge	3.8	2	.2
	Predator density:Prey density	21.6	12	.04*
Success rate of prey capture	Predator density	10.0	2	.007*
	Prey density	3.0	6	.8
	Habitat refuge	4.5	2	.1

χ^2 = 43.2, *df* = 2, *p* < .0001), such that abundance was higher in the high-refuge patch over low- and medium-refuge patches (*p* < .0001), irrespective of predator presence. Lionfish also displayed significant patch preferences (*total time* Kruskal–Wallis: χ^2 = 66.9, *df* = 2, *p* < .0001; *time foraging* Kruskal–Wallis: χ^2 = 22.0, *df* = 2, *p* < .0001) (Figure 7) and spent more time foraging in either low- (*p* < .0001) or medium-refuge (*p* = .0004) patches relative to the high-refuge patch. However, patch occupancy was strongly dependent on both predator and prey density (beta regression: prey density x predator density x patch interaction: *F* = 2.6, *df* = 24, *p* < .0001). While multiple predator treatments spent significantly more time in the low-refuge patch at the lowest prey density (groups: *low* versus *high refuge*: 1.4 ± 0.5, *p* = .02; pairs: *low* versus *high refuge*: 1.5 ± 0.6, *p* = .03), singletons allocated time among patches more evenly (*p* > .1). Lone lionfish also displayed non-significant patch preferences at the highest prey densities, as did groups of lionfish (*p* > .05). Only pairs spent significantly more time in patches of higher vulnerability at the highest prey densities (*low* versus *high refuge*: 1.6 ± 0.4, *p* = .001; *medium* versus *high refuge*: 2.6 ± 0.7, *p* = .001).

4 | DISCUSSION

In this study, we attempted to tease apart density and context dependencies underlying the ecological impact of a prominent invader. Herein, we determined the degree to which prey survival was influenced by predator density, and whether the magnitude of this effect was mediated by prey refuge, across increasing prey density.

4.1 | Density-dependent effects

Intraspecific interactions among predators often influence their per-capita effects (Griffen & Byers, 2009). We observed both facilitation and inference among predators, the relative strengths of which were density-dependent. In the former, co-occurring predators indirectly benefitted their conspecifics' capture efficiencies by increasing prey encounter rates and conspecific consumption rates (Johnson, 2006; Mols et al., 2004). In the latter, exploitative competition between conspecifics mitigated per-capita effects on prey. Exploitative competition is apparent through unequal consumption rates, by
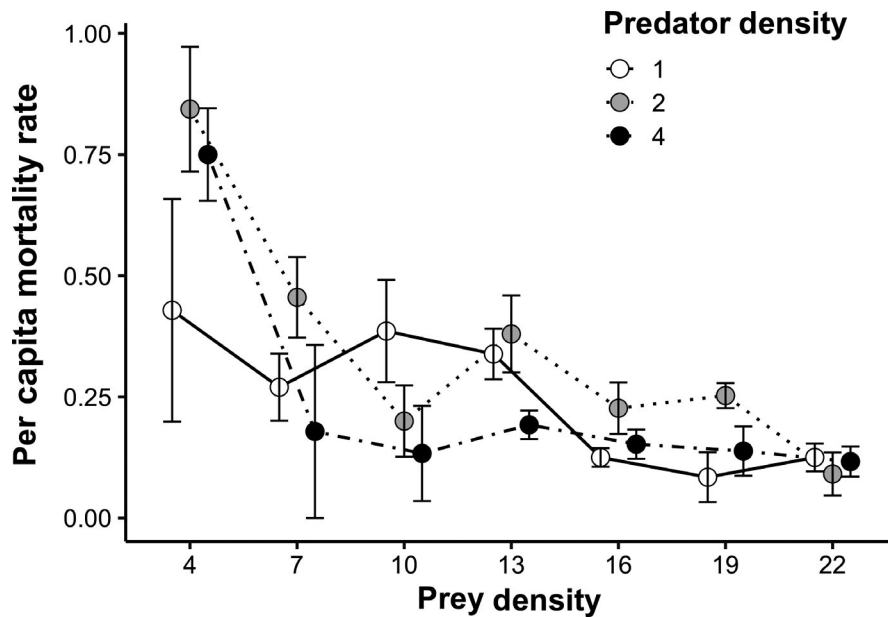
FIGURE 6 Mean (± *SE*) per-capita prey mortality rate as a function of prey density, separated by predator density. Data are fitted for each of one (solid), two (dotted) and four (dot-dash) lionfish
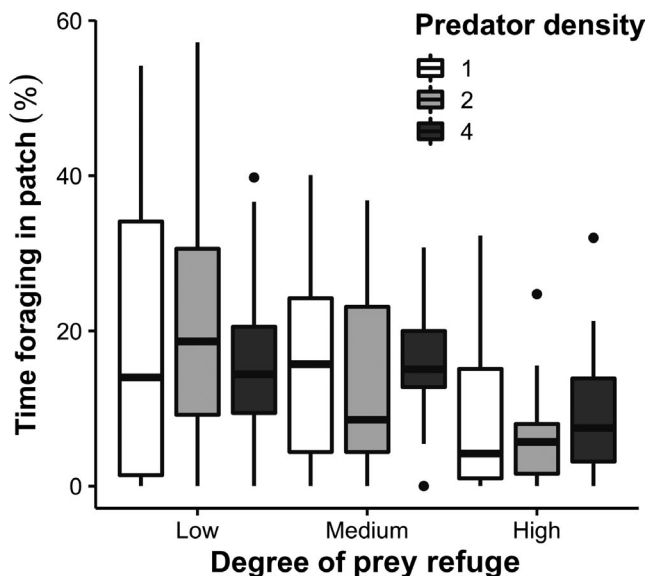
FIGURE 7 Box and whiskers plot of median (± interquartile range) foraging time by degree of prey refuge, separated by predator density. Whiskers extend from lower and upper hinges of the box and represent minimum and maximum values, respectively. Solid dots depict outliers

nature of its negative effect on resource acquisition by conspecifics. Accordingly, consumption and attack rates—as well as prey stalking and chases—were unequally distributed among predators. This suggests that some lionfish were more dominant foragers and precluded effective foraging of subordinates.

Facilitative and antagonistic effects appeared to offset one another at an intermediate predator density, in which interactions between pairs combined additively in the context of prey risk. Of the densities tested, pairs had the highest per-capita feeding and attack rates. However, their high FR-derived interference coefficient and handling time suggest longer search times as a function of

competition. Competing synergistic and antagonistic effects likely produced the neutral risk MPE. Increasing predator density precipitates more frequent interactions between conspecifics (Mansour & Lipcius, 1991), often lowering their per-capita effect. Accordingly, higher conspecific densities decreased consumption rates, whereby groups of lionfish had the lowest per-capita effect. Prey risk was also similar among multiple predator treatments, in which total rates of prey mortality were analogous between groups and pairs of lionfish. These data imply that negative effects of competition among conspecifics in groups outweighed the relative positive effects of their presence. Analysis of MPEs for groups of lionfish—whereby observed per-capita consumption rates were significantly lower than predicted rates—corroborates this conclusion.

Mutual predator interference can account for food web stability (Arditi & Ginzburg, 2012) and in our study prompted risk-reducing effects for prey. Intraspecific competition may reduce a predator's foraging efficiency (Stier & White, 2014) and growth rate (Post, Johannes, & McQueen, 1997). Exploitative competition observed here may underpin density-dependent growth rates in lionfish (Benkwitt, 2013) and their stagnating densities in the Bahamas (Benkwitt et al., 2017). While intraspecific competition in invasive species can precipitate "boom and bust" population growths (Simberloff & Gibbons, 2004), the degree to which conspecifics stabilize this species' overall ecological effects at broad spatial scales—across their invaded range—is unclear.

4.2 | Incorporating FR into studies of MPE

Whether an invasive predator interacts antagonistically, neutrally or synergistically with conspecifics can foretell prey persistence or loss. However, few studies have investigated MPEs through predator-dependent FRs in invasive species (Wasserman et al., 2016). More generally, few studies to date have examined these

relationships in conspecific predators; those available have produced conflicting results (Barrios-O'Neill et al., 2014; Wasserman et al., 2016).

Emergent MPEs are often assessed at a single prey density (Porter-Whitaker et al., 2012). In our study, prey risk varied across both predator and prey density treatments, underscoring the utility of considering predator impact in a FR context. MPE studies also often determine an overall consumption rate of predators by enumerating surviving prey at the end of an experiment, which obscures antagonistic or synergistic interactions. Analysis of individual-level consumption and attack rates—as well as bouts of stalking and chases—revealed effects of competition even at low predator densities. Had we not considered individual foraging rates, these effects would have otherwise been masked. To our knowledge, this is the first study to examine conspecific MPEs in the context of FR, using consumption data of individual foragers. Only one other study has examined individual-level consumption in MPEs, which involved heterospecific pairs and stomach content analyses (Mofu et al., 2019).

4.3 | Abundance–impact relationship

Understanding invasive species' density-dependent interactions is important, wherein intraspecific competition is often strong (Connell, 1983). An invasive species' abundance and per-capita effect are both integral in assessing their overall impact (Ricciardi et al., 2013), as is unravelling the relative influence of each factor (Sofaer et al., 2018). Considerable research has attempted to predict invasive species' impacts (Blackburn et al., 2014). However, how overall and per-capita impacts change as a function of predator density is often unclear and may scale nonlinearly (Bradley et al., 2019). Indeed, singletons and pairs of lionfish had greater per-capita effects relative to groups.

Higher per-capita consumption rates are often reported for invasive relative to native species (Crookes, DeRoy, Dick, & MacIsaac, 2019). Whether these individual-level per-capita impacts translate into higher population-level effects hinges on intraspecific interactions, which can either bolster or—as in our study—impede their overall ecological impacts. Nonlinear scaling of impact is important to understand how invasive species change community dynamics. Specifically, consideration of abundance can strengthen our predictive capacity to forecast impacts across habitats (Thomsen, Olden, Wernberg, Griffin, & Silliman, 2011).

Prey risk varied more owing to effects between predators relative to prey density or refuge availability. This strong predator dependence infers that lionfish abundance may drive their ecological impact and affect heterogeneity in observed field impacts. The population density of other invasive species, such as the zebra mussel (*Dreissena polymorpha*), similarly mediates their ecological impact (Latzka et al., 2016). Future research should refine abundance–impact curves for lionfish and other invasive species, the shape of which has important management implications (Yokomizo, Possingham, Thomas, Buckley, 2009).

4.4 | Influence of habitat heterogeneity

Invasive species' impacts often exhibit considerable spatiotemporal variation (Ricciardi et al., 2013), wherein interactions with their environment are likely to influence per-capita effects (Thiele, Kollmann, Markussen, & Otte, 2010). Notwithstanding such context dependencies, invasive species often exert strong negative effects with increasing abundance, regardless of habitat (Bradley et al., 2019). Prey sought shelter in the high-refuge patch irrespective of predator presence, implying patch selection occurred in the absence of information on predation risk (Abrams, 1994). Irrespective of prey behaviour, lionfish consumed prey indiscriminately across patches. Furthermore, analysis of their FR indicated that lionfish had high foraging efficiency at low prey densities. High proportional consumption rates suggest that lionfish may have destabilizing effects on prey populations under low-resource conditions, similar to that reported for other invasive species (Dick et al., 2013). This ability to take advantage of heterogeneity in resource distribution—even under low prey densities—may foreshadow the breadth of their effects within a broader community.

Predators must maximize energy gain by balancing costs of foraging with benefits of prey consumption (Sih, 2005; Stephens & Krebs, 1986). Lionfish spent more time in the low-refuge patch in which prey were at greatest risk (Hugie & Dill, 1994). However, patch use was contingent on predator density, through which we observed facilitative and antagonistic MPEs.

Myriad factors contribute to predator patch selection, including foraging success (Sih, 2005). In spite of their high interference, pairs of lionfish appeared to forage most efficiently. They preferentially occupied patches of greater prey vulnerability at both ends of the prey density spectrum, which likely bolstered consumption rates. Fish learn to recognize the foraging behaviour of individuals around them to inform patch profitability (Johnson, 2006). By leveraging advantages of group foraging, pairs of lionfish maximized energy intake while minimizing search costs. When alone, lionfish displayed indiscriminate patch preferences under both low and high prey densities. Without conspecifics, singletons were forced to gauge patch profitability through trial and error and appeared to employ random search tactics. Conversely, mutual interference among conspecifics foraging in groups may have been responsible for their non-selective patch preferences at high prey densities. Potentially, competition spurred foraging to patches with fewer conspecifics and higher likelihoods of prey capture.

Predator–prey spatial distributions are likely to differ in heterogeneous relative to homogenous environments, as are predator feeding rates (Ives et al., 1999). While habitat-mediated predator–prey interactions are poorly understood in reef fishes (Catano et al., 2016), our study underscores their importance. It is possible that predators and prey used some other ephemeral landscape feature to guide their behaviour; however, our results indicate that habitat refugia played a strong role in regulating their use. We acknowledge that use of multiple habitat types affected our ability to systematically quantify prey refuge, as we did not

standardize predator-free space (Barrios-O'Neill, Dick, Emmerson, Ricciardi, & MacIsaac, 2015). Nonetheless, our results convincingly show that across the investigated range of predator and prey densities, refuge availability appears to be of little consequence for this invasive predator's foraging efficiency. Furthermore, by manipulating habitat heterogeneity these results may permit more robust predictions of invader impact over space, as they estimate the population FR (Ives et al., 1999). Complementary field studies are needed to verify whether the relationships shown here translate at greater spatial scales.

5 | CONCLUSION

Our study highlights the utility of employing multiple interrelated approaches to assess predator interaction effects and invasive species' impacts. Doing so facilitates a more holistic picture of invader impact relative to use of any metric in isolation. Density and context-mediated impacts of invasive species underscore the need to mechanistically test concomitant effects of predator density, prey density and heterogeneity on resultant impact, as was done in this study. Analysis of MPEs in the context of FRs provides meaningful insight into predator–prey dynamics and an efficient way to assess invasive species' density-dependent per-capita impacts. Future studies should continue to quantify MPEs in studies of invasive species' predator-dependent FRs, about which we know little. Habitat use provides additional insight into behaviourally mediated predator–prey interactions and lends practical significance to FR studies.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data are accessible via Dryad.

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