Prey naiveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs

Andrea Anton[1],*, **Katherine Cure[2], Craig A. Layman[3], Riikka Puntila[4],**
Michael S. Simpson[5], John F. Bruno[5]

[1]Curriculum for the Environment and Ecology, University of North Carolina, Chapel Hill, NC 27599, USA
[2]School of Plant Biology and Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia
[3]Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695, USA
[4]Department of Environmental Sciences, University of Helsinki, Helsinki 000014, Finland
[5]Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

ABSTRACT: Native prey can be particularly vulnerable to consumption by exotic predators. Prey naiveté, the failure to recognize a novel predator due to lack of recent co-evolutionary history, likely facilitates the disproportionate impact that some exotic predators exert on prey populations. Lionfish *Pterois volitans*, exotic predators from the Pacific, have invaded coral reefs and other coastal habitats along the western Atlantic. Prey naiveté towards novel lionfish was tested in field experiments and with observations using closest approach distance as the anti-predator response. We quantified the distance of prey fishes to exotic lionfish in both the Atlantic and Pacific (invasive and native ranges of lionfish) as well as to native predators in the Atlantic. In the Atlantic, experiments indicated that *Haemulon plumierii*, prey of lionfish, generally display a closer approach distance to exotic than to native predators, and field observations of free-ranging fish revealed that at least 5 other species of small fishes (*Halichoeres bivitattus*, *Halichoeres garnoti*, *Scarus taeniopterus*, *Stegastes leucostictus* and *Thalassoma bifasciatum*) also might exhibit limited predator-avoidance behaviour towards invasive lionfish. We also found that 3 families of small fish (Labridae, Pomacentridae and Scaridae) maintained greater distances from lionfish in the Pacific compared with the Atlantic in both experimental and field observations. These results suggest prey naiveté to exotic lionfish by at least 8 species of fish (*Abudefduf saxatilis*, *H. plumierii*, *H. bivitattus*, *H. garnoti*, *S. taeniopterus*, *Sparisoma aurofrenatum*, *S. leucostictus* and *T. bifasciatum*) in the Atlantic, which could be contributing to the rapid expansion of this invasive species by enhancing its fitness and reproductive output through high predation efficiency.

KEY WORDS: Co-evolution · Exotic species · Food webs · Non-native species · Predator avoidance · Predator–prey interaction

INTRODUCTION

The evolutionary 'arms race' between predators and their prey implies a dynamic equilibrium (Geffeney et al. 2002). Through natural selection, prey species have evolved chemical, structural and behavioural characteristics to reduce predation risk. When facing a novel predator with which the prey has no shared evolutionary history, predator avoidance behaviours by native prey may not be elicited or are ineffective (Cox & Lima 2006). This phenomenon is termed prey naiveté (Diamond & Case 1986, Cox & Lima 2006, Banks & Dickman 2007, Sih et al. 2010, Carthey & Banks 2014), and may occur at multiple stages within the predator–prey interaction. For instance, tadpoles of the Iberian green frog *Rana perezi* fail to display anti-predator responses to invasive red swamp crayfish *Procam-*

*Corresponding author: andreantongamazo@yahoo.es

barus clarkii in southwestern Spain (Gomez-Mestre & Diaz-Paniagua 2011), where invasive crayfish can reduce the survival of the native green frog species by more than 95% (Cruz & Rebelo 2005). Prey naiveté also occurs when prey recognize the novel predator as a threat, but respond with ineffective anti-predator behaviours. For instance, the aquatic European water voles *Arvicola terrestris* hide in burrows when in the presence of the exotic American mink *Mustela vison* (Macdonald & Harrington 2003). Whilst this response allows effective escape from native European mink, it does not help against the smaller invasive American mink females, which can fit into these burrows (Macdonald & Harrington 2003).

The degree of prey naiveté may often be related to the degree of evolutionary isolation the prey population has experienced (Cox & Lima 2006). Hence, naiveté is expected to be more common on islands, in rivers and in lakes, and less pronounced within larger terrestrial and marine ecosystems. Circumstantial evidence in support of this hypothesis comes from the introductions of invasive Nile perch into Lake Victoria and of the brown tree snake onto the island of Guam, both of which had devastating effects on endemic fauna, resulting in extinctions of hundreds of species (Fritts & Rodda 1998, Wiles et al. 2003). In continental terrestrial ecosystems, long-term biogeographic connectivity between predators and prey could lead to recognition of the threat posed by widespread predatory taxa or archetypes (Cox & Lima 2006). Invasions by predators in marine systems are rarely documented and prey naiveté has been hypothesized to be low because of the high connectivity in marine communities (Cox & Lima 2006).

The lionfish (*Pterois volitans*) invasion of the Atlantic is a notable example of the successful establishment of a predatory marine fish outside of its native range. Lionfish, predators from the Pacific, have proliferated over a vast area in the western Atlantic in just a few decades (Schofield 2010). Lionfish densities in the Pacific can be up to 15 times lower than in the Atlantic (Kulbicki et al. 2012), where they have been shown to exert dramatic impacts on native fish biomass in just a few years (Green et al. 2012). The substantial ecological impact of lionfish could result from a combination of factors, such as the release from their natural enemies (Hackerott et al. 2013, Anton et al. 2014) or their novel hunting strategy (e.g. lionfish can produce jets of water to confuse their prey; Albins & Lyons 2012). Also, lionfish invasion success could stem from prey naiveté in the Atlantic. The behavioural response of small fishes towards invasive lion-

fish in the western Atlantic has been tested for 4 species of fishes (*Coryphopterus laucofraenum*, *C. thompsoni*, *Stegastes leucostictus* and *S. planifrons*) of different ontogenetic stages, revealing contrasting results (Marsh-Hunkin et al. 2013, Black et al. 2014, Kindinger 2015). Kindinger (2015) found that a native fish species from the Atlantic (*S. planifrons*) responded similarly to invasive lionfish as to a control treatment, while Black et al. (2014) found that 2 species of Atlantic gobies (*C. laucofraenum* and *C. thompsoni*) did not display consistent anti-predator responses to lionfish when compared to a native predator (*Epinephelus striatus*).

The purpose of our study was to experimentally test prey naiveté to lionfish for multiple species of prey fishes using both experiments and field observations. First, we compared predator avoidance responses by prey fish in the presence of invasive lionfish and in the presence of native predators in 2 experiments and with field observations in the Atlantic (invasive range of lionfish). Second, we compared predator avoidance behaviour by several species of prey fish to lionfish in the Pacific to avoidance behaviour in the Atlantic using a third experiment and additional field observations.

MATERIALS AND METHODS

Experiments

Experimental setup

Three experiments were performed to test anti-predator responses of prey fish to lionfish. Distance to a predator has been considered a reasonable quantitative metric of predator avoidance in fish (Johnsson et al. 1996, Arai et al. 2007, Black et al. 2014) and it is a conspicuous fish behaviour (see Fig. S1 in the Supplement at www-int-res.com/articles/suppl/m544 p257_supp.pdf). In our experiments, the distance that the prey fish maintained towards the predator (from now on termed 'focal fish') was used as a proxy to quantify predator avoidance behaviour, termed 'closest approach distance', and was defined as the minimum separation distance between the prey fish and the mouth of the focal fish.

In the experiments, a cage (80 × 18 × 18 cm) divided by 1 mm mesh to separate the focal fish from the prey was utilized (Fig. 1). This cage size was chosen to maintain the focal fish in close proximity to the prey, yet allow enough space for the prey fishes to swim freely inside the cage (e.g. prey could choose
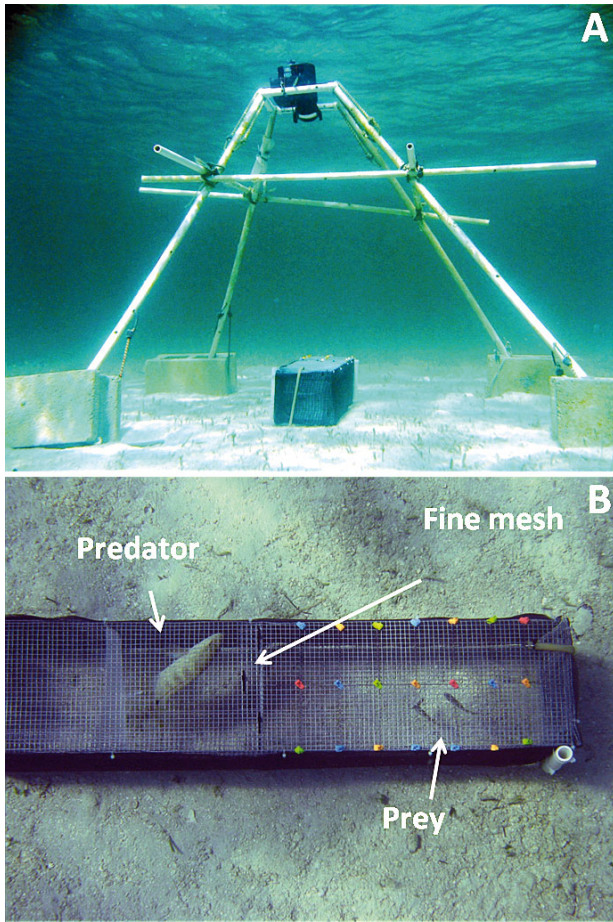
Fig. 1. Setup of the experiments, showing (A) the cage and the underwater camera mounted on a tripod, and (B) a close-up of the cage

small invertebrates. Focal fishes of the species *Epinephelus guttatus*, *E. striatus*, *Holocentrus rufus*, *Lutjanus apodus* and *Ocyurus chrysurus* were collected using fish traps (61 × 61 × 46 cm), while lionfish were caught with small hand nets and *Halichoeres garnoti* using gill nets. All predators were held in large cages in shallow habitats near the experimental sites and, if kept for more than 24 h, fed daily ad libidum with queen conch *Lobatus gigas* in the Atlantic and commercial frozen shrimp in the Pacific. All predators were starved for 24 h prior to the experimental trails to standardize hunger levels. Experiments were performed in 2 to 4 m deep sandy areas in the back reef, which contained sparse turtle seagrass, *Thalassia testudinum* in the Atlantic and *Thalassia hemprichii* in the Pacific, and small patch reefs. Experiments were only conducted on calm days with good visibility (>7 m). All fishes were released after trials, except for lionfish, which were euthanized.

In each experiment, videos of the cage were taken using an underwater Sony Digital Handycam DCR-PC101 camera (Fig. 1) for 2 min per focal fish. Prey were given 1 min to acclimate to the cage, then focal fish were added and the video recording began. Researchers left the area to minimize any disruption of natural fish behaviour. Replicates were run on separate days (i.e. 1 replicate per day) between 11:00 and 15:00 h, with n = 7 per experiment (except for the family Labridae in Experiment 3, in which n = 4 in the Pacific), which is within the range of replication used in previous experimental behavioural studies assessing predator recognition (Jedrzejewski et al. 1993, Nunes et al. 2013, Pujol-Buxo et al. 2013, Bourdeau et al. 2013). Videos were analysed in the laboratory, extracting an image from each video at 10 s intervals for a total of 12 images per 2 min trial. The prey compartment of the cage was marked with pins as a frame of reference to calculate distances between the mouth of the focal fish and each of the prey fish from the pictures using ImageJ, yielding 3 measurements per image and 36 images per trial. The shortest of these 36 measurements was selected as the closest approach distance.

the distance to the focal fish), as well as to let the focal fish to display some natural behaviours (e.g. the extension of the pectoral fins by lionfish). A set of 3 conspecific juvenile prey fishes was used to allow some natural shoaling behaviour, as in other comparable studies (e.g. Blake et al. 2015). In the cages, prey could use visual and chemical cues to identify the focal fish, but the focal fish could not consume the prey. The cage did not include shelter for the prey as this might influence the distance between the prey and the focal fish. Prey and focal fishes were collected from nearby reefs. *Haemulon plumierii* (prey) were collected using unbaited fish traps (35 × 35 × 35 cm), while the other prey species (*Abudefduf saxatilis*, *Chromis viridis*, *Scarus* sp., *Sparisoma aurofrenatum*, *Thalassoma bifasciatum* and *T. quinquevittatum*) were caught with small hand nets. All prey fish were kept in large cages (100 × 100 × 100 cm) in the experimental location for less than 24 h, where the prey fishes could feed on seagrasses, epiphytes and

Experiment 1

Experiment 1 was run in the Atlantic from October to November 2009 in The Bight, Abaco, The Bahamas (26° 20′ 43″ N, 77° 01′ 21″ W). In this experiment, juvenile *H. plumierii* was chosen as the prey because the *Haemulon* genus does not co-occur with lionfish in the Pacific (Rocha et al. 2008) and lionfish consume

H. plumierii in the Atlantic (Anton et al. 2014). *H. plumierii* were collected from a population that had been syntopic with lionfish for approximately 4 yr since lionfish were first observed in Abaco in 2005 (Schofield 2010).

Experiment 1 had a focal fish treatment (factor) with 3 levels (Table 1): lionfish (exotic predator; mean ± SD total length [TL] = 18.9 ± 1.7 cm); *E. striatus* (native predator; mean TL = 19.9 ± 1.1 cm); and *H. garnoti* (invertivore control fish; mean TL = 18.2 ± 0.9 cm). New focal fishes were used in each replicate and a new set of 3 prey was used in each trial (mean TL = 4.9 ± 0.8 cm for *H. garnoti*; mean TL = 4.7 ± 0.7 cm for lionfish; and mean TL = 4.8 ± 0.8 cm for *E. striatus*). The temporal sequence of focal fish treatments was randomized each day. Neither the TL of the focal fish nor the prey varied significantly among focal fish levels (see Table S1 in the Supplement).

Experiment 2

To test whether the difference between lionfish and native *E. striatus* in Experiment 1 was species specific (e.g. prey respond to *E. striatus* more strongly than to other native predators), Experiment 2 was conducted with 4 native predator species in the same location and under conditions similar to those of Experiment 1 (Table 1). Experiment 2 also had *H. plumierii* as prey species but included a focal fish treatment with 6 levels (Table 1): lionfish (exotic predator; mean ± SD TL = 18.9 ± 1.7 cm); *E. guttatus* (native predator; mean TL = 19.6 ± 1.6 cm), *L. apodus* (native predator; mean TL = 20 ± 1.1 cm), *E. striatus* (native predator; mean TL = 20.1 ± 1.7 cm) and *O. chrysurus* (native predator; mean TL = 20.1 ± 1.5 cm), each of which consumed *H. plumierii* in captivity; and *H. rufus* (non-piscivorous control fish; mean TL = 19.4 ± 2.9 cm). New focal fishes were used in each replicate, but the same set of 3 prey fish were sequentially exposed to a randomized sequence of each focal fish level on a given day. Neither predator nor prey size varied significantly among focal fish levels (see Table S1 in the Supplement).

Experiment 3

Experiment 3 was performed in the Atlantic (Abaco, The Bahamas; 26° 33′ 14″ N, 77° 02′ 02″ W) and the Pacific (Guam, Mariana Islands; 13° 28′ 45″ N, 144° 44′ 37″ E) from June to August 2010 to test responses of prey fish from 3 families (Pomacentridae, Scaridae and Labridae; Table 1) to lionfish in the Atlantic and Pacific (e.g. prey avoidance behaviours to lionfish in the Atlantic may differ from those in the Pacific). In both locations we deployed a cage similar to the one described for Experiments 1 and 2, with a lionfish compartment of 35 cm and a prey fish compartment of 45 cm. Experiment 3 had 2 factors (Table 1): (1) location with 2 levels (mean ± SD lionfish TL was 25.6 ± 2.6 and 24.7 ± 3.5 cm in the Pacific and Atlantic, respectively) and (2) prey fish family with 3 levels (Table 1; Pomacentridae family with *A. saxatilis* and *C. viridis*, with mean TL of 4.6 ± 0.5 and 5 ± 0.4 cm in the Atlantic and Pacific respectively; Scaridae family with *S. aurofrenatum* and Scarus sp. with mean TLs of 5.4 ± 0.9 and 4.5 ± 0.6 cm in

Table 1. Random factors, fixed factors and levels within fixed factors for Experiments 1, 2 and 3

Experiment	Fixed factor	Levels within fixed factor	Random factor
1	Focal fish treatment	(1) *Halichoeres garnoti* (yellowhead wrasses; invertivore control fish), (2) *Pterois volitans* (lionfish; exotic predator), and (3) *Epinephelus striatus* (Nassau grouper; native predator)	–
2	Focal fish treatment	(1) *Holocentrus rufus* (squirrelfish; non-piscivorous control fish), (2) *Pterois volitans* (lionfish; exotic predator), (3) *Lutjanus apodus* (schoolmaster snapper; native predator), (4) *Ocyurus chrysurus* (yellowtail snapper; native predator), (5) *Epinephelus guttatus* (red hind grouper; native predator), and (6) *Epinephelus striatus* (Nassau grouper; native predator)	Prey-group ID
	Treatment order	(1) 1 (if predator species was added to cage in first half of trial); (2) 2 (if predator species was added to cage in second half of trial)	
3	Location	(1) Atlantic Ocean (invaded range of lionfish) and (2) Pacific Ocean (native range of lionfish)	Lionfish ID
	Prey family	(1) Scaridae (*Sparisoma aurofrenatum* in the Atlantic and Scarus sp. in the Pacific), (2) Pomacentridae (*Abudefduf saxatilis* in the Atlantic and *Chromis viridis* in the Pacific), and (3) Labridae (*Thalassoma bifasciatum* in the Atlantic and *Thalassoma quinquevittatum* in the Pacific)	

the Atlantic and Pacific, respectively; and Labridae family with *T. bifasciatum* and *T. quinquevittatum*, with mean TL of 6.9 ± 0.7 and 7.8 ± 0.9 cm in the Atlantic and Pacific, respectively). Across regions and for comparison purposes, we selected prey species that were from the same families, shared habitat with lionfish and belonged to families that are known prey of lionfish (Lönnstedt & McCormick 2013, Anton et al. 2014). Although we compared different species of prey, a requisite to test prey naiveté across biogeographic regions, they generally had a similar ecology and potentially analogous anti-predator strategies. Different newly collected lionfish and prey fishes were used in each replicate (one per day). Neither lionfish nor prey species size varied significantly across location (Atlantic versus Pacific; see Table S1 in the Supplement).

Field observations of free-ranging fish

Interactions among free-ranging, unconstrained predators (including invasive lionfish) and small prey fish were observed in the Atlantic to test potential prey naiveté under natural conditions (Fig. 2). We quantified how close smaller prey fishes approached to each of 5 species of larger fish (also termed 'focal fish'): lionfish as exotic predator; *E. guttatus*, *L. apodus* and *E. striatus* as native predators; and *H. garnoti* as a non-piscivorous control fish (Fig. 2). Focal fishes were chosen as encountered over 2 extensive shallow coral reefs (1–10 m depth) in Abaco (the Bight 26° 20′ 43″ N, 77° 01′ 21″ W and Sandy Point 25° 59′ 51″ N, 77° 24′ 12″ W) between 09:00 and 16:00 h from October to November 2009. The observer swam only in 1 direction to avoid re-encountering the same focal fish individuals, which were selected within the range size of 15–45 cm TL to control for size effects, and their size was assigned to 1 of 6 categories (15–20, 20–25, 25–30, 30–35, 35–40 and 40–45 cm) using a graduated slate. The level of activity of individual focal fish could affect the behaviour of prey fish, and no measurements were taken on individuals that were resting inside crevices or swimming away from the observer.

After examination of the focal fish and smaller fish in its vicinity to ensure that they appeared unaffected by the observer's presence, the surveyor haphazardly selected 1 small fish <5 cm TL, within 60 cm of and approaching the focal fish. Its movements were observed, and the distance at which it turned away from or stopped approaching the focal fish was recorded as a metric of closest approach distance.

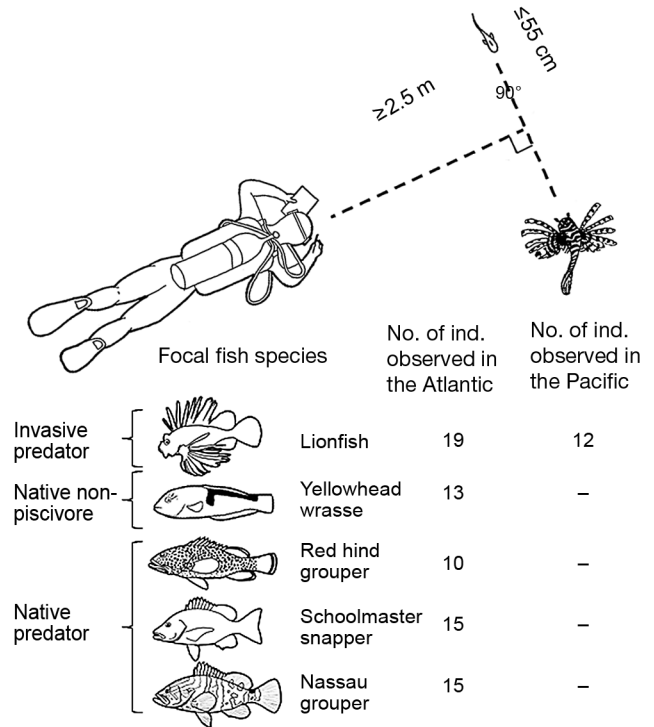| Focal fish species		No. of ind. observed in the Atlantic	No. of ind. observed in the Pacific
Invasive predator	Lionfish	19	12
Native non-piscivore	Yellowhead wrasse	13	–
Native predator	Red hind grouper	10	–
	Schoolmaster snapper	15	–
	Nassau grouper	15	–

Fig. 2. Position of the observer relative to each focal fish during field observations of behavioural responses of free-ranging fishes. At each location (Atlantic and Pacific), number of individuals observed of each focal fish species (yellowhead wrasse *Halichoeres garnoti*, lionfish *Pterois volitans*, Nassau grouper *Epinephelus striatus*, schoolmaster snapper *Lutjanus apodus*, and red hind snapper *Epinephelus guttatus*) were noted. (–) not applicable

The assessment of this prey behaviour allowed us to contrast findings across experiments and field observations. The surveyor remained as still as possible to minimize influence on fish behaviour and was always at least 2.5 m away, a distance considered reasonable to assess field fish behaviour (Cure et al. 2012). Because of the greater mobility of *L. apodus* and *H. garnoti*, the surveyor swam slowly along a parallel path separated by >2.5 m from the focal fish while taking measurements. For 3 min, the distance between each prey fish and the mouth of the focal fish was visually estimated using a graduated slate and assigned to one of 8 categories (0–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50 and 50–60 cm). Observed prey were <5 cm TL to standardize the size class of potential prey among all focal fish species and sizes. Observations were only made within 60 cm of the focal fish because fish at greater distances could fall outside the observer's fixed field of vision. Observations of individual prey fish were recorded around each species of focal fish, totalling 147, 95, 96, 83 and 92 observations for 13 *H. garnoti*,

19 *Pterois volitans*, 15 *E. striatus*, 10 *E. guttatus* and 15 *L. apodus*, respectively (Fig. 2), on days of light winds and good visibility. All observed prey species were identified to the species level, except for the blennies and gobies, which were difficult to identify at those distances.

Additional similar observations of free-ranging lionfish and prey fish were performed in the Pacific and compared with observations in the Atlantic to further assess potential prey naiveté to this invader under natural conditions (Fig. 2). In the Pacific, 12 lionfish were observed in 4 reefs at 1 to 10 m depths on Guam (Pago Bay 13° 25′ 36″ N, 144° 47′ 56″ E, Tumon Bay 13° 30′ 43″ N, 144° 48′ 07″ E, Togcha Bay 13° 21′ 42″ N, 144° 46′ 48″ E and Bile Bay 13° 16′ 1″ N, 144° 40′ 3″ E) from 09:00 to 16:00 h during June and July 2010. These records were compared with our observations of the 19 lionfishes in the Atlantic, totalling 71 and 35 observations around lionfish in the Atlantic and Pacific, respectively.

Statistical analyses

Experiments

In Experiment 1, a fixed-effects model was used with the focal fish treatment (species) as a fixed fac-tor and closest approach distance as a continuous response variable fitted by a normal distribution (Table 1). From results of the model's regression and using lionfish as the reference group, any significant differences in *H. plumierii* (prey) proximity

Table 2. Summary of the best regression models for the experiments. Experiments 1 and 2 quantified the closest approach distance of *Haemulon plumierii* (white grunts) to focal fish (lionfish, native predators and fish controls). Experiment 3 measured the closest approach distance of prey fish (belonging to 3 families) to lionfish in the Atlantic and Pacific. Post hoc analysis results are presented in Figs. 2 and 3

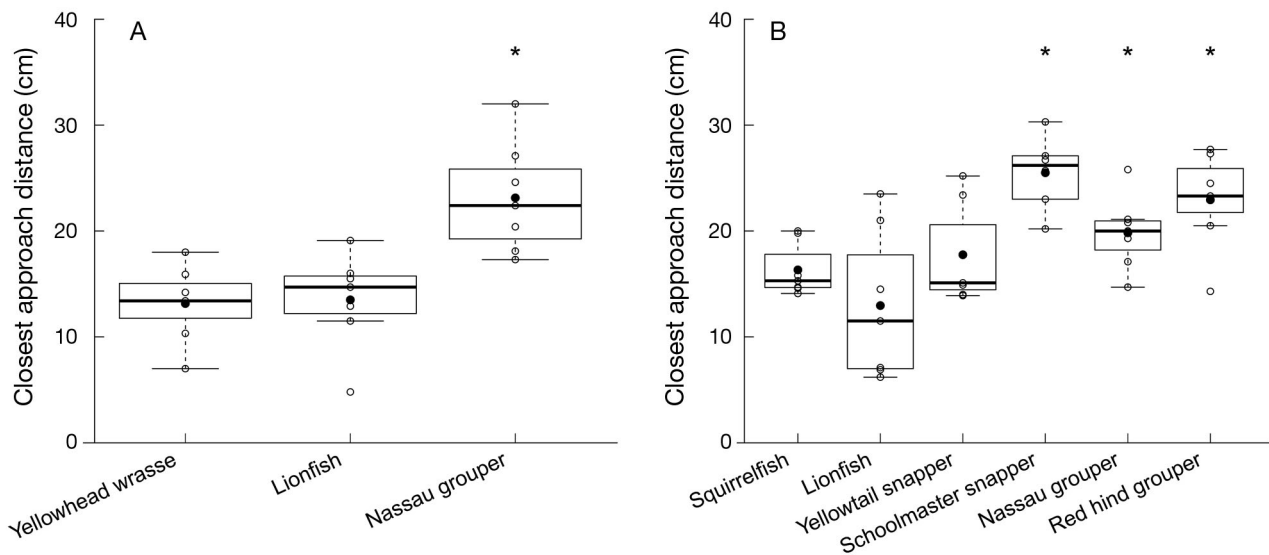|	Closest approach distance		
	df	*F*	p
Experiment 1			
Focal fish treatment	2	11.07	<0.001
Experiment 2			
Focal fish treatment	5	14.94	<0.001
Treatment order	1	6.46	0.018
Focal fish treatment: treatment order	5	1.96	0.123
Experiment 3			
Location	12	10.08	0.008
Prey family	18	1.7	0.211
Location: prey family	18	3.15	0.067

Fig. 3. Box plot of the results from (A) Experiment 1 and (B) Experiment 2, depicting the closest approach distance between juvenile white grunts *Haemulon plumierii* and each species of focal fish (yellowhead wrasse *Halichoeres garnoti*, lionfish *Pterois volitans*, Nassau grouper *Epinephelus striatus*, squirrelfish *Holocentrus rufus*, yellowtail snapper *Ocyurus chrysurus*, schoolmaster snapper *Lutjanus apodus* and red hind snapper *Epinephelus guttatus*). *Significant differences in closest approach distance of *H. plumierii* to exotic lionfish and native focal fish species. Black filled circles denote mean values, open circles represent the value of each replicate treatment, lines are median values, the box represents the middle 50% of scores with the upper and lower quantiles representing 75 and 25% of the scores, respectively, and the upper and lower whiskers represent scores outside the middle 50%

to exotic lionfish and the other 2 species of focal fish were identified (Table 2, Fig. 3). In Experiment 2, a randomized block design was used to assess the differences in closest approach distance between the treatments, where focal fish treatment and treatment order were included as fixed factors and prey-group ID as random factor, because the same set of 3 prey fishes was exposed sequentially to all focal fish levels (Table 1). Although the order of focal fish species on each replicate was randomized, the set of prey could have been sensitized over time to the presence of 'a fish' on the other side of the cage. Hence, treatment order assessed the degree of acclimation or sensitization that could occur for the same prey-group ID over the course of 1 trial. Experiment 2 was not designed to account for treatment order, which was classified *a posteriori* as 1 or 2 (1 if the predator species was added into the cage in the first half of the trial or 2 in the second half), to ensure replication within the 2 categories. A stepwise model simplification approach was used to find the best model (Crawley 2012), with a ΔAIC cut-off of ≤2 to include predictors in the model (Burnham & Anderson 2004). Post hoc analysis identified any significant differences in the response variable between lionfish and the other focal fish species (Table 2, Fig. 3). In Experiment 3, a randomized block design was used, where location and prey family were included as fixed factors and lionfish ID as random factor, because each individual lionfish

was sequentially exposed to the 3 families of prey (Table 1). The data for Experiment 3 were unbalanced and restricted maximum likelihood (REML) estimation was necessary (Payne 2014); data were thus analysed as described in Zuur et al. (2009).

Field observations of free-ranging fish

To analyse how closely a small free-ranging fish approached different species of focal native fishes and invasive lionfish in the Atlantic, a mixed-effects model was used. The model included 3 fixed factors (focal fish treatment, prey fish species and focal fish TL) plus the paired interactions of the 3 factors, and a random factor (focal fish ID) because multiple observations were conducted on each individual focal fish. Only those prey species that were observed interacting with all 5 species of focal fish at least 3 times were included in the analysis (*Halichoeres bivittatus*, *H. garnoti*, *Stegastes leucostictus*, *Scarus taeniopterus* and *T. bifasciatum*; see Table S2 in the Supplement). Our field observations were also unbalanced (e.g. the number of observations of the 5 prey species differed among focal fish species) and were analysed as described in Experiment 3. From results of the best model, and using lionfish as our reference group, any significant differences in prey proximity between lionfish and each focal fish species were identified (Fig. 4A).
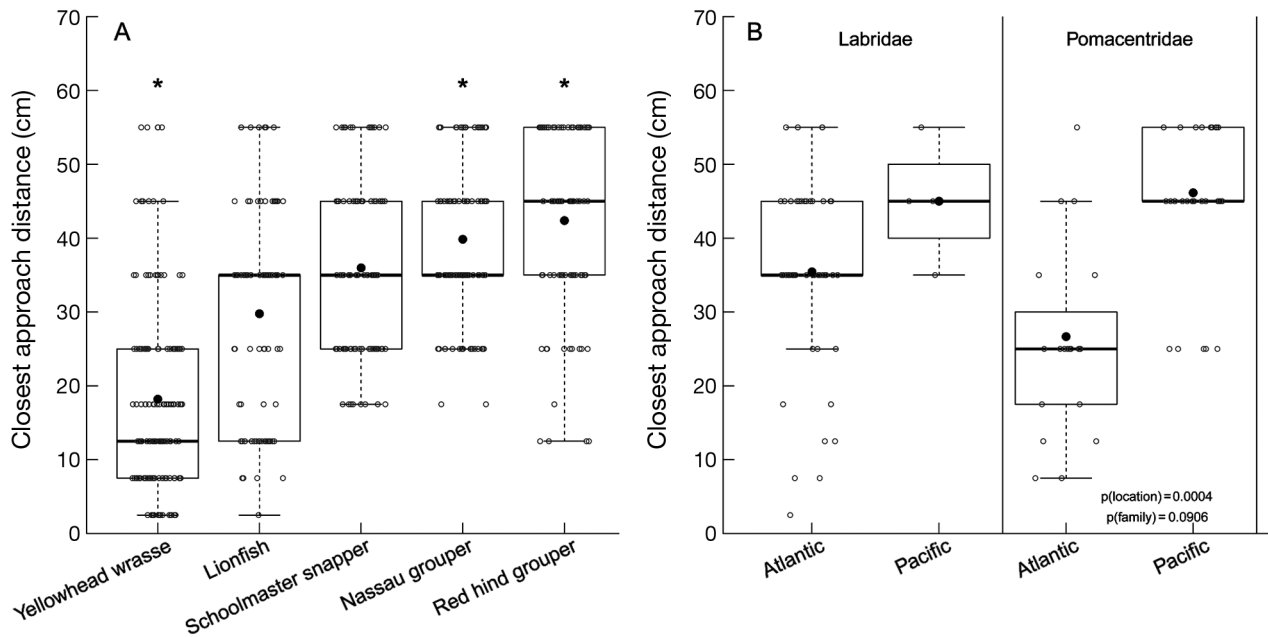

Fig. 4. Box plot of closest approach distance from field observations of free-ranging prey and focal fishes in (A) the Atlantic and (B) the Atlantic and the Pacific. Replication for each treatment and the scientific names of the focal fishes are shown in Fig. 2. *Significant differences in closest approach distance of prey fish to focal fish species (A). See Fig. 3 legend for explanation of the box plots

Observations of free-roaming lionfish in the Atlantic and Pacific were analysed using a randomized block design. Only individual observations from potential prey species that were observed interacting with lionfish at least 3 times were included in the statistical analyses (*A. saxatilis*, *H. bivittatus*, *H. garnoti*, *S. leucostictus* and *T. bifasciatum* in the Atlantic and *C. viridis*, *Chromis xanthura* and *Labroides dimidiatus* in the Pacific; see Table S2 in the Supplement). The unbalanced mixed-effects model for the field observations across geographic regions included 3 fixed factors plus their paired interactions, and lionfish ID as a random factor because multiple observations were conducted on each individual lionfish. From results of the best model, any significant differences in small fish proximity to lionfish were identified (Fig. 4B). Statistical analyses were performed in R 3.1.0 using the nlme package (Pinheiro et al. 2015) for mixed-effects models, and statistical significance was determined at p-values < 0.05.

RESULTS

Experiments

Experiment 1

In Experiment 1, the closest approach distance maintained by *Haemulon plumierii* (prey) from exotic lionfish was 42% shorter than the distance maintained from native predatory *Epinephelus striatus*, but similar to the distance separating them from *Halichoeres garnoti*, the control fish (Table 2, Fig. 3). Experiment 1 documented one instance in which *H. plumierii* swam at 4.8 cm from the mouth of lionfish (Fig. 3).

Experiment 2

In Experiment 2, *H. plumierii* maintained a closest approach distance that was on average 35 to 49% shorter from exotic lionfish than the distance maintained from the native piscivores—*E. striatus*, *E. guttatus* and *Lutjanus apodus* (Table 2, Fig. 3). The closest approach distance of *H. plumierii* from exotic lionfish was 27% shorter than for *Ocyurus chrysurus*, also a native piscivore, although this difference was not significant (Table 2, Fig. 3). Lionfish and the non-piscivorous control squirrelfish did not differ in closest approach distance (Table 2, Fig. 3). An effect of treatment order on closest approach distance was detected, increasing as the treatments ran in the sec-

ond half of each replicate. This effect of treatment order was independent of the species of focal fish, as suggested by a lack of interaction between focal fish treatment and treatment order (Table 2). Three instances in which *H. plumierii* swam less than 10 cm (6.2, 6.9 and 7.1 cm) from the mouth of lionfish were documented (Fig. 3).

Experiment 3

The mean closest approach distance for small fishes with respect to lionfish was 35% shorter in the Atlantic than in the Pacific (Table 2, Fig. 5). No significant effect of prey family or interaction between prey family and location was detected (Table 2). This experiment identified 3 instances of prey fishes swimming less than 10 cm from a lionfish's mouth in the Atlantic (a *Thalassoma bifasciatum* at 9.1 cm and *Scarus* sp. at 4 and 7.4 cm), but only 1 record of a parrotfish swimming 9.5 cm from a lionfish's mouth in the Pacific (Fig. 5).

Field observations of free-ranging fish

Field observations of 5 species of fish from 3 families (Pomacentridae, Labridae and Scaridae) in the Atlantic revealed larger closest approach distances to 2 native predators—*E. striatus* by 25% and *E. gut-*
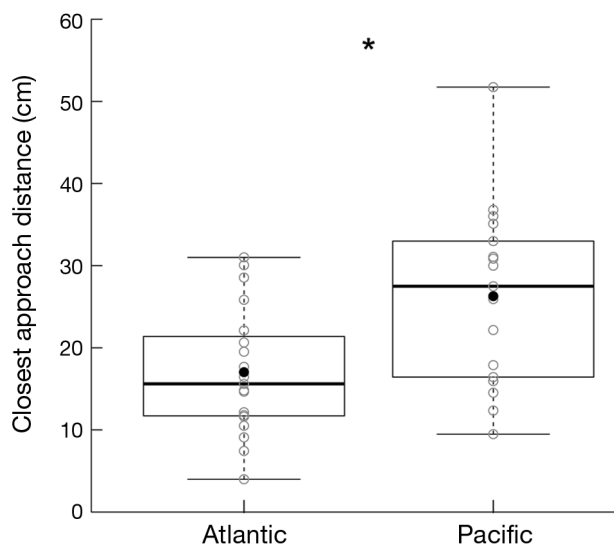

Fig. 5. Box plot of results from Experiment 3, depicting the closest approach distance between lionfish and prey fish (from 3 families) native to the Atlantic and Pacific. *Significant difference in closest approach to lionfish between native prey fish from the Atlantic and the Pacific. See Fig. 3 legend for explanation of the box plots

Table 3. Summary of the mixed-effects models selected for behavioural analysis of free-ranging fishes. For the Atlantic observations, the table depicts results for closest approach distances between small fish (5 species) and focal fish species (5 species). For the Atlantic and Pacific observations, the table reflects results for closest approach distance between lionfish and native fishes from the Atlantic and Pacific for 2 families of prey fishes. Post hoc analysis results are presented in Fig. 4

| | | Closest approach distance | |
	df	F	p
Atlantic observations			
Focal fish treatment	4	21.737	<0.001
Atlantic and Pacific observations			
Prey family	1	2.932	0.091
Location	1	17.929	<0.001

tatus by 30% — than to exotic lionfish (Table 3, Fig. 4). An analogous 17% larger average approach distance to a third native predator, *L. apodus*, was not statistically detectable. Prey fish were 39% closer to non-predatory *H. garnoti* than to lionfish (Table 3, Fig. 4). Focal fish TL, prey fish species and their interaction did not affect the distance that prey fish maintained from the focal fish (Table 3).

In the field observations performed in the Atlantic and the Pacific, location affected the distance prey fish maintained from lionfish (Table 3, Fig. 4). Prey fish maintained a 27% closer approach distance to lionfish in the Atlantic than in the Pacific (Table 3, Fig. 4). Prey family and its interaction with location did not affect the distance that prey fish maintained from lionfish (Table 3). In the Atlantic (invaded range of lionfish), we identified 5 instances at which free-roaming prey fishes swam within less than 10 cm of a lionfish's mouth (1 *H. garnoti* at 2.5 and 7.5 cm, 1 *Stegastes leucostictus* twice at 7.5 cm, and 1 *T. bifasciatum* at 7.5 cm; Fig. 4), while the closest distance detected in the Pacific was 25 cm for *Chromis xanthura* (Fig. 4).

DISCUSSION

When predators are introduced outside of their native range, prey might fail to recognize these novel species as threats (Gomez-Mestre & Diaz-Paniagua 2011, Blake et al. 2015). Observations and 3 field experiments performed in both the Atlantic and Pacific (the invaded and native ranges of lionfish, respectively) suggest prey naiveté by 8 species of fishes (*Abudefduf saxatilis*, *Haemulon plumierii*, *Halichoeres bivitattus*, *Halichoeres garnoti*, *Scarus taeniopterus*, *Sparisoma aurofrenatum*, *Stegastes leucostictus* and *Thalassoma bifasciatum*) towards the exotic predator in the Atlantic. Specifically, our experiments in the Atlantic indicate that juvenile *H. plumierii* fail to exhibit avoidance behaviours towards exotic lionfish to the same degree they respond to native predators. Prey fishes in the Atlantic maintained a closer approach distance from lionfish than in the Pacific, indicating a limited predator avoidance response to lionfish by 3 species of native Atlantic fishes. Our field observations of free-ranging fishes in the western Atlantic partially support our experimental findings, indicating that 5 fish species maintained shorter distances from lionfish than from 2 species of native predators. Additional observations of free-ranging lionfish in both its invaded and native biogeographic ranges revealed that prey fishes made closer approaches to lionfish in the Atlantic (invaded range) than in the Pacific (native range).

Maintaining a safe distance from predators is a common avoidance response found across the animal kingdom (Holmes et al. 2005, Parris et al. 2006). Although we presume, like others before us (Parris et al. 2006, Arai et al. 2007, Takahara & Yamaoka 2009), that a shorter separation distance implies a higher risk of predation, we have no basis to convert our behavioural metric into a quantitative measure of risk of predation. Indeed, risk of predation as a function of separation distance could differ depending on predator hunting mode, which has been shown to affect prey behaviour (Schmitz 2008). A meta-analysis on predator hunting modes (Preisser et al. 2007) found that cues from stationary predators evoke stronger anti-predator behaviours than cues from actively hunting predators because the presence of sedentary predator cues indicate proximity to the predator and, hence, higher predation risk. Based on Preisser et al. (2007) our predator fish species would fall into 2 hunting mode categories: (1) active predators (predators that continuously patrol for prey such as *Lutjanus apodus* and *Ocyurus chrysurus*, and (2) sit-and-pursue predators (predators that remain in a fixed location but move to attack prey that move within the predator's pursuit distance, such as *Epinephelus striatus*, *E. guttatus* and, to a certain extent, lionfish). Hunting mode fails to explain the differences among predator avoidance behaviors in Experiments 1 and 2, while in the field observations, we did not find stronger avoidance of sedentary lionfish than of active *L. apodus*, as would have been predicted by Preisser et al. (2007).

It is unknown whether prey fish in the Atlantic are at risk of predation by exotic lionfish at the distances

reported in this study. For instance, guppies around the island of Trinidad approach known predators quite closely but avoid the attack-cone region near the mouth (Magurran & Seghers 1990). Hence, prey might recognize a novel predator as a threat, but the distance maintained might be fine-tuned to the specific predator. The closest approach distance of prey to exotic lionfish reported in the Atlantic might arise not from a lack of recognition of the threat but from a shorter striking distance of lionfish compared with native predators. A recent study by Albins & Lyons (2012) reports that lionfish produce jets of water directed towards the prey while hunting. The study showed that the maximum distance that a visible jet reached from the mouth of the lionfish was 9.6 cm (Albins & Lyons 2012). Our experiments and observations documented prey fish in the Atlantic swimming less than 5 cm from the mouth of lionfish, which is well within the putative feeding range of lionfish reported by Albins & Lyons (2012). In the Pacific, free-roaming prey of 3 species (*Chromis viridis*, *Chromis xanthura* and *Labroides dimidiatus*) maintained at least a 25 cm distance from the predator's mouth, and our experiment in the Pacific identified only 1 instance of a prey fish (a parrotfish) swimming 9.5 cm from a lionfish's mouth, which supports the hypothesis that the putative feeding range of lionfish could be ~10 cm from their mouths. Still, the evidence provided by our experiments and observations is limited because we do not know the effective striking distance of lionfish. Future research exploring the effective feeding ranges of native and invasive fish predators in the Atlantic, or research comparing prey responses of native predators in the Pacific (including lionfish), could serve to further explore our hypothesis.

Previous studies investigating the behavioural response of native fishes towards exotic lionfish report contrasting results. Two studies, Marsh-Hunkin et al. (2013) and Kindinger (2015), reported that 3 native species in the Atlantic (*Stegastes planifrons*, *Coryphopterus laucofraenum* and *Coryphopterus thompsoni*) displayed a behavioural response to lionfish similar to that in non-threatening control treatments. Our findings in Experiments 1 and 2 agree with those 2 studies, suggesting that an additional native prey species, *H. plumierii*, might display limited recognition of lionfish as a threat in the Atlantic. However, Marsh-Hunkin et al. (2013) also reported that for more than half of the anti-predator responses assessed, prey gobies (of the species *C. laucofraenum* and *C. thompsoni*) responded similarly to exotic lionfish and to a native predator, *E. striatus*; this dif-fers from our experimental and observational findings for 6 species of prey towards *E. striatus* in the Atlantic. Similarly to our field findings, Black et al. (2014) reported that a native species of Atlantic prey (*S. leucostictus*) approached closer to invasive lionfish than to a native predatory fish (*Synodus intermedius*), but only when *S. leucostictus* males were in the presence of females.

Our results diverge from recent lionfish research performed in the species' native range. Lönnstedt & McCormick (2013) reported that lionfish were virtually undetected by *C. viridis* (Pomacentridae family) in the Pacific, where this juvenile prey fish failed to react to either scent or visual presentation of the native lionfish as compared with other native predators from the Pacific. In our field observations, we did find that 2 fish species from the Pomacentridae family maintained a larger distance to exotic lionfish in the Pacific than in the Atlantic, indicating evidence of high risk of predation by lionfish in the latter region. Unfortunately, we did not assess closest approach distance of native fishes towards lionfish and other native predators from the Pacific, because we assumed lack of prey naiveté to lionfish in its native range, precluding a direct contrast of our findings with those reported by Lönnstedt & McCormick (2013).

We did not investigate the specific mechanism(s) behind the putative prey naiveté to invasive lionfish in the Atlantic, but 2 plausible hypotheses may explain it. First, lionfish and Atlantic fish species lack recent co-evolutionary history because of geographical isolation. The Pliocene formation of the Isthmus of Panama between the Atlantic and the Pacific has segregated marine species for over 3 million years (Collins et al. 1996). Second, prey may still respond to novel predators if visual and/or chemical cues of the novel predator are similar enough to those of native predators to invoke anti-predator avoidance by prey (Blumstein et al. 2009). The Scorpaenidae family, to which lionfish belong, is represented in the Caribbean by 5 species and, although they are rare, the odour of these closely related native predators could be used by prey to identify novel lionfish as predators (Ferrari et al. 2007). However, the recognition of novel predators through olfactory cues might be limited to congeneric species and not necessarily extended to other species within the family (Mitchell et al. 2013). In addition to odour cues, the behavioural and morphological differences between invasive lionfish and native Scorpaenidae could be sufficient to render the visual cues of invasive lionfish unrecognizable. For instance, they have a striped

colouration pattern, possess large feathery pectoral fins and are able to swim and remain suspended while hovering, unlike Atlantic scorpionfish.

There were several potential limitations of the present study. In Experiment 2, the effect of treatment order, which led to greater closest approach distances of prey to the predator when tested later in the sequence of trials, suggests sensitization of the prey fish towards the fish on the other side of the cage. This experimental artefact probably led to overestimates of closest approach distances from all species of focal fishes, although the distance from invasive lionfish remained significantly shorter than for 3 species of native predators. We found 2 inconsistences between experimental and field observations. In Experiment 1, *H. plumierii* (prey) made similar approaches to exotic lionfish and to the non-piscivorous *H. garnoti*, but in the field, 5 species of prey made closer approaches to *H. garnoti* than to exotic lionfish. In Experiment 2, *H. plumierii* made closer approaches to exotic lionfish than to a native predator, *L. apodus*, but not in the field observations. These 2 inconsistences might be related to the level of activity of native *L. apodus* and *H. garnoti*, which were the more mobile species of the focal fishes. The closest approach distance was therefore harder to estimate for them in the field observations, which could have resulted in underestimation of these distances.

Lionfish are effective invaders, having spread throughout the western Atlantic in a few decades (Schofield 2010) and colonizing a broad variety of habitats (Whitfield et al. 2007, Barbour et al. 2010, Green et al. 2012, Anton-Gamazo 2013), typically at relatively high densities (Kulbicki et al. 2012, Cure et al. 2014). The enemy release hypothesis, the geographic escape from coevolved predators, competitors, parasites or disease in the invaded region, is a common top-down explanation for the successful invasion of certain exotic species (Keane & Crawley 2002, Mitchell & Power 2003). Although predators and parasites do not seem to control the lionfish invasion in the western Atlantic (Hackerott et al. 2013, Anton et al. 2014, Sikkel et al. 2014; but see Mumby et al. 2011), the natural enemies of lionfish might not exert a strong top-down control on lionfish populations in its native range either (Cure et al. 2014, Sikkel et al. 2014). In addition to a potential top-down release, we suggest that the success of the lionfish invasion in the Atlantic could also derive from a bottom-up process: prey naiveté facilitating food availability for the exotic invader in the new geographic range. Higher rates of food acquisition by exotic lionfish than by native predators have already been re-ported in the Atlantic (Layman & Allgeier 2012, Albins 2013). This ease in food procurement in the Atlantic might result in high fitness and reproductive output for lionfish, facilitating successful establishment and rapid spread in the invaded range.

Exotic predators have long been presumed to have greater impacts on freshwater ecosystems compared with terrestrial or marine ecosystems because prey naiveté is expected to be more pronounced in geographically isolated communities (Cox & Lima 2006). However, a meta-analysis by Salo et al. (2007) suggested that prey naiveté could also occur in highly connected ecosystems. Similarly, we found potential limited recognition of an alien predator by native prey in a marine ecosystem. Our study was performed in a tropical environment, where native species often experience faster evolutionary rates than in temperate ecosystems (Rohde 1992), perhaps contributing to the evolutionary isolation required to experience prey naiveté.

Long-term impacts of exotic consumers on prey populations can be mitigated by evolutionary adaptation of prey (Strauss et al. 2006). This rapid evolution of prey responses to novel predators can sometimes take place in just a few generations (Berger et al. 2001). Predator avoidance of prey towards lionfish might evolve quickly under intense selection. Yet, in the meantime, genetic variation of prey may be substantially reduced, thereby diminishing the potential for prey fishes to adapt to future environmental change (Strauss et al. 2006). Variability in the behavioural response of prey towards lionfish in our data suggests an opportunity for selection of avoidance behaviour. Repeating the naiveté trials that we conducted after a passage of time could serve to test whether rapid adaptation is taking place in lionfish prey. Even if prey do rapidly evolve to recognize this invasive predator, the dramatic reductions of populations of lionfish prey may have long-lasting effects. Given the wide geographical scale of the lionfish invasion, strong selection within multiple species of prey could have widespread consequences for marine ecosystems in the western Atlantic.

LITERATURE CITED

Albins MA (2013) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. Biol Invasions 15:29–43

Albins MA, Lyons PJ (2012) Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. Mar Ecol Prog Ser 448:1–5

Anton A, Simpson MS, Vu I (2014) Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. PLoS ONE 9:e106229

Anton-Gamazo A (2013) Ecology and evolution of the lionfish invasion of Caribbean coral reefs: resistance, adaptation and impacts. PhD Dissertation, University of North Carolina, Chapel Hill, NC

Arai T, Tominaga O, Seikai T, Masuda R (2007) Observational learning improves predator avoidance in hatchery-reared Japanese flounder *Paralichthys olivaceus* juveniles. J Sea Res 58:59–64

Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. Trends Ecol Evol 22:229–230

Barbour AB, Montgomery ML, Adamson AA, Diaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. Mar Ecol Prog Ser 401:291–294

Berger J, Swenson JE, Persson IL (2001) Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. Science 291:1036–1039

Black AN, Weimann SR, Imhoff VE, Richter ML, Itzkowitz M (2014) A differential prey response to invasive lionfish, *Pterois volitans*: prey naiveté and risk-sensitive courtship. J Exp Mar Biol Ecol 460:1–7

Blake CA, da Barbiano LA, Guenther JE, Gabor CR (2015) Recognition and response to native and novel predators in the largespring mosquitofish, *Gambusia geiseri*. Ethology 121:227–235

Blumstein DT, Ferando E, Stankowich T (2009) A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators. Anim Behav 78:873–878

Bourdeau PE, Pangle KL, Reed EM, Peacor SD (2013) Finely tuned response of native prey to an invasive predator in a freshwater system. Ecology 94:1449–1455

Burnham KP, Anderson DR (eds) (2004) Model selection and multimodel inference. Springer, New York, NY

Carthey AJR, Banks PB (2014) Naïveté in novel ecological interactions: lessons from theory and experimental evidence. Biol Rev Camb Philos Soc 89:932–949

Collins LS, Budd AF, Coates AG (1996) Earliest evolution associated with closure of the Tropical American Seaway. Proc Natl Acad Sci USA 93:6069–6072

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674–680

Crawley MJ (2012) The R Book, 2nd edn. Wiley-Blackwell, Chichester

Cruz MJ, Rebelo R (2005) Vulnerability of Southwest Iberian amphibians to an introduced crayfish, *Procambarus clarkii*. Amphib-reptil 26:293–303

Cure K, Benkwitt CE, Kindinger TL, Pickering EA, Pusack TJ, McIlwain JL, Hixon MA (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. Mar Ecol Prog Ser 467: 181–192

Cure K, McIlwain JL, Hixon MA (2014) Habitat plasticity in native Pacific red lionfish *Pterois volitans* facilitates successful invasion of the Atlantic. Mar Ecol Prog Ser 506: 243–253

Diamond J, Case TJ (eds) (1986) Community ecology. Harper Collins, New York, NY

Ferrari MCO, Gonzalo A, Messier F, Chivers DP (2007) Generalization of learned predator recognition: an experimental test and framework for future studies. Proc R Soc B 274:1853–1859

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annu Rev Ecol Syst 29:113–140

Geffeney S, Brodie ED, Ruben PC, Brodie ED (2002) Mechanisms of adaptation in a predator-prey arms race: TTX-resistant sodium channels. Science 297:1336–1339

Gomez-Mestre I, Diaz-Paniagua C (2011) Invasive predatory crayfish do not trigger inducible defences in tadpoles. Proc R Soc B Biol Sci 278:3364–3370

Green SJ, Akins JL, Maljkovic A, Cote IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7:e32596

Hackerott S, Valdivia A, Green SJ, Cote IM and others (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. PLoS ONE 8: e68259

Holmes N, Giese M, Kriwoken LK (2005) Testing the minimum approach distance guidelines for incubating royal penguins *Eudyptes schlegeli*. Biol Conserv 126:339–350

Jedrzejewski W, Rychlik L, Jedrzejewska B (1993) Responses of bank voles to odors of 7 species of predators: experimental data and their relevance to natural predator–vole relationships. Oikos 68:251–257

Johnsson JI, Petersson E, Jonsson E, Bjornsson BT, Jarvi T (1996) Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Can J Fish Aquat Sci 53: 1546–1554

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17: 164–170

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Environ Biol Fishes 98:487–498

Kulbicki M, Beets J, Chabanet P, Cure K and others (2012) Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. Mar Ecol Prog Ser 446:189–205

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Mar Ecol Prog Ser 448:131–141

Lönnstedt OM, McCormick MI (2013) Ultimate predators: Lionfish have evolved to circumvent prey risk assessment abilities. PLoS ONE 8:e75781

Macdonald DW, Harrington LA (2003) The American mink: the triumph and tragedy of adaptation out of context. NZ J Zool 30:421–441

Magurran AE, Seghers BH (1990) Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata*. Anim Behav 40:443–452

Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Antipredator responses to invasive lionfish, *Pterois volitans*: interspecific differences in cue utilization by two coral reef gobies. Mar Biol 160:1029–1040

Mitchell CE, Power AG (2003) Release of invasive plants

from fungal and viral pathogens. Nature 421:625–627

Mitchell MD, McCormick MI, Chivers DP, Ferrari MCO (2013) Generalization of learned predator recognition in coral reef ecosystems: How cautious are damselfish? Funct Ecol 27:299–304

Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. PLoS ONE 6: e21510

Nunes AL, Richter-Boix A, Laurila A, Rebelo R (2013) Do anuran larvae respond behaviourally to chemical cues from an invasive crayfish predator? A community-wide study. Oecologia 171:115–127

Parris MJ, Reese E, Storfer A (2006) Antipredator behavior of chytridiomycosis-infected northern leopard frog (*Rana pipiens*) tadpoles. Can J Zool 84:58–65

Payne RW (2014) Developments from analysis of variance through to generalized linear models and beyond. Ann Appl Biol 164:11–17

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2015) nlme: Linear and nonlinear mixed effects models. R package version 3.1–124. https://cran.r-project.org/package=nlme

Pujol-Buxo E, San Sebastian O, Garriga N, Llorente GA (2013) How does the invasive/native nature of species influence tadpoles' plastic responses to predators? Oikos 122:19–29

Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology 88:2744–2751

Rocha LA, Lindeman KC, Rocha CR, Lessios HA (2008) Historical biogeography and speciation in the reef fish genus *Haemulon* (Teleostei : Haemulidae). Mol Phylogenet Evol 48:918–928

Rohde K (1992) Latitudinal gradients in species diversity — the search for the primary cause. Oikos 65:514–527

Salo P, Korpimaki E, Banks PB, Nordstrom M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc R Soc B 274: 1237–1243

Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954

Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5: S117–S122

Sih A, Bolnick DI, Luttbeg B, Orrock JL and others (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621

Sikkel PC, Tuttle LJ, Cure K, Coile AM, Hixon MA (2014) Low susceptibility of invasive red lionfish (*Pterois volitans*) to a generalist ectoparasite in both its introduced and native ranges. PLoS ONE 9:e95854

Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? Ecol Lett 9: 357–374

Takahara T, Yamaoka R (2009) Temporal and spatial effects of predator chemical and visual cues on the behavioral responses of *Rana japonica* tadpoles. Curr Herpetol 28: 19–25

Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western North Atlantic. Biol Invasions 9:53–64

Wiles GJ, Bart J, Beck RE, Aguon CF (2003) Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. Conserv Biol 17: 1350–1360

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects modeling for nested data. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed effects models and extensions in ecology with R. Springer Science+Business Media, New York, NY, p 111–142