Homing decisions reveal lack of risk perception by Caribbean damselfish of invasive lionfish

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Abstract Prey naïveté, or the failure of prey to recognize non-native predators due to a lack of co-evolutionary history, is thought to underpin the large impact of invasive Indo-Pacific lionfish (*Pterois* sp.) on coral reef fish populations in the western Atlantic. Most previous studies of lionfish recognition have taken place in experimental tanks that did not mimic natural conditions or used bottle or cage field designs that constrained natural behaviour. To alleviate these issues, we compared the homing patterns of experimentally translocated Caribbean bicolor damselfish (*Stegastes partitus*) in the presence and absence of standardized models of a lionfish, of an ecologically similar native piscivore (black grouper; *Mycteroperca bonaci*), and of a native non-piscivore (French grunt, *Haemulon flavolineatum*) in the field. The native grouper model elicited a strong predator avoidance response: translocated damselfish became unlikely to home when released beyond ∼ 2 m from their territory and took longer to do so. In contrast, damselfish facing a lionfish model exhibited similar homing behaviours to those of damselfish in the presence of a non-piscivorous grunt and in the absence of any model. Fish length and translocation distance also influenced homing: damselfish stopped homing when released more than 5.6 m away from their territory and larger individuals crossed wider sand gaps. Overall, our findings are consistent with the idea that bicolor damselfish are naïve to the threat of predation presented by lionfish, but also with the notion that damselfish might be assessing, but deeming to be low, the threat of a stalking predator hunting over open sand. Both mechanisms point to inaccurate risk perception in relation to invasive lionfish. More broadly, we highlight a novel experimental translocation approach to evaluate behavioural responses of native prey species to novel predators under realistic field conditions.

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Introduction

Most animals move within and among habitat patches during their lifetime. Movement among patches is often important for ecosystem-level processes, such as herbivory, biomass production and nutrient transfer (Meyer et al. 1983; Lewis and Wainwright 1985; Mumby et al. 2004), but it is underpinned by

individual decisions. How an individual perceives the costs and benefits associated with inter-patch movements is influenced by both extrinsic factors, such as inter-patch distance, matrix quality, and resource availability, and characteristics that are intrinsic to the individual, such as mobility, perceptual range, and body size (Turgeon et al. 2010). Many of these factors ultimately shape the perception of risk of predation—a key consideration in movement decisions (Lima and Dill 1990).

While individuals might readily recognize native predators as posing a significant risk, they might not perceive the same of predators with which they have not co-evolved. The evolutionary phenomenon of prey naïveté transpires when prey species exhibit no or ineffective anti-predator behaviour towards novel predators. Maladaptive responses to novel predators might include agonistic reactions, failure to reduce fitness-related activities that entail reductions in vigilance (i.e., foraging, mating), and not seeking or moving away from refuges (Helfman 1989; Knapp and Matthews 2001). Invasive predators might therefore inflict disproportionately high mortality on naïve prey that are unfamiliar with the archetype and hunting strategies of their pursuer as a result (Diamond and Case 1986; Cox and Lima 2006; Sih et al. 2010).

In naturally fragmented coral reef habitats, the reluctance of small-bodied reef fishes to move over open expanses of sand is widely considered to be a predator avoidance response (Sweatman and Robertson 1994; Turgeon et al. 2010). Homogeneous matrices of sand surrounding coral patches offer low structural complexity and limited or no refuge from predators (Brock and Norris 1989; Syms and Jones 2000), which deters fish movement because of the perceived heightened predation risk. If willingness to cross sand is indeed tied to perceived risk of predation, then distance to safety, body size and predator recognition should be key determinants of the decisions of reef fish to move over sand. Translocations and gap-crossing experiments have shed light on the effects of distance to safety on reef fish movement. Studies of recolonization of depopulated patch reefs surrounded by sand show that inter-patch gaps as small as 10 m can provide at least a partial barrier to fish movement (Brock and Norris 1989; Syms and Jones 2000). Turgeon et al. (2010) further reported the homing probability of translocated longfin damselfish (*Stegastes diencaeus*) declined sharply and steeply as

sand gap distances between coral patches increased beyond 3.90 m. In addition, given that smaller fishes are prey to a wider range of predators than larger fishes (Mittelbach and Persson 1998; Scharf et al. 2000), perceived risk of predation should be higher for smaller prey, making them less likely to venture over open sand. To our knowledge, however, no study has evaluated how the explicit recognition of predation risk affects coral reef fish movement. One should expect anti-predator decisions affecting movement to be contingent on accurate assessment of the risk posed by larger fishes.

In this study, we used a natural predator avoidance behaviour—the reluctance of reef fish to move across open sand gaps (e.g., Turgeon et al. 2010)—as a novel assay to examine prey naïveté to an invasive fish predator, the Indo-Pacific lionfish (*Pterois* sp.). Since 1985, lionfish have spread at an unparalleled rate through the northwestern Atlantic, Caribbean Sea and Gulf of Mexico (Whitfield et al. 2007; Schofield 2010; Betancur-R et al. 2011). These generalist carnivores have caused major reductions in native fish recruitment and abundance on some reefs (Albins and Hixon 2008; Green et al. 2012). Prey naïveté is thought to have facilitated high predation rates of lionfish in the invaded range (Côté and Smith 2018). However, so far, most studies of lionfish recognition by native coral reef fish have taken place in experimental tanks that did not mimic natural conditions (e.g., Marsh-Hunkin et al. 2013) or in the field, where the behaviour of living predators constrained in translucent bottles or cages has been difficult to standardize (Anton et al. 2016; Black et al. 2014). In addition, captive lionfish have, at times, been too small to pose a credible threat to focal prey (e.g., Kindinger 2015). To alleviate these issues, we conducted experimental translocations in the wild to compare the homing probability of damselfish in the presence and absence of large, standardized models of native and non-native, piscivorous and non-piscivorous fishes.

Specifically, we asked how the likelihood that translocated damselfish would cross a sand gap to return to their territory, and the threshold distance they were willing to cross, changed in the presence and absence of an invasive lionfish, of an ecologically similar native piscivore (i.e., a grouper) and of a native non-piscivore (i.e., a grunt). We predicted that damselfish would be less likely to home as perceived risk of predation increased, that is with smaller body size

(Mittelbach and Persson 1998; Scharf et al. 2000), increasing translocation distance over sand (Helfman and Winkelman 2010; Turgeon et al. 2010), as well as in the presence of a native predator. The presence of a native predator should also elicit avoidance behaviours in translocated damselfish (Cox and Lima 2006), such as longer times spent seeking or using shelter, swimming farther to avoid proximity to the predator and swimming faster. These adaptive responses should be absent if damselfish do not perceive the risk posed by invasive lionfish.

Materials and methods

Ethics statement

The study conforms to the guidelines of the Canadian Council on Animal Care and was approved by the Simon Fraser University Animal Care Committee (permit 1234B-17).

Study sites and species

We conducted our field study on 132 coral reef patches along the west coast of Curaçao, one of the leeward islands of the Netherlands Antilles, between June and August 2017. The first sighting of lionfish in Curaçao was reported on 27 October 2009 (de Léon et al. 2013), and lionfish are now widely distributed on reefs around the island (personal observations). Our reef patches were distributed across eight sites (number of patches per site: 1–29; Fig. S1). The patches were small (mean area $\pm$ SD: 1.15 ± 0.60 m^2), in shallow water (mean depth $\pm$ SD: 3.22 ± 1.26 m^2) and were separated from each other by open expanses of sand and sparse seagrass. Each patch was occupied by at least one adult bicolor damselfish (*Stegastes partitus*), although most patches supported small aggregations of three or more individuals.

Bicolor damselfish are strictly diurnal planktivores. They form small colonies of up to 20 individuals, which are organised in size-based social hierarchies (Myrberg 1972), and both sexes aggressively defend small territories above which they feed (Hogan et al. 2012). The males are polygynous and provide parental care of the eggs, which they defend vigorously against potential predators such as wrasses (Knapp and Warner 1991). Territory acquisition and defence are therefore critical for foraging and reproduction of bicolor damselfish, which should generate motivation in translocated fish to return home. Bicolor damselfish have been shown to exhibit anti-predator responses (e.g., reduced feeding and chasing activity) in the presence of model predators, particularly when predators are large and nearby (Helfman and Winkelman 2010).

Translocations and experimental treatments

Using SCUBA, we translocated a total of 154 individuals, each only once, over sand gap widths varying from 1 to 7 m. One diver captured a bicolor damselfish in a scoop net and measured its total length to the nearest 0.1 cm. Only sexually mature adults (i.e., individuals $\geq$ 3.0 cm TL; Almada-Villela et al. 2003) were used in this study, and if capture was unsuccessful after 5 min, we moved to a new patch to avoid inducing high levels of stress on the focal individual. After size measurement, the diver immediately released the focal fish on a small pile of six pieces of coral rubble (i.e., the 'release site') set up at a predetermined, straight-line distance over sand from the outer edge of the focal fish's home patch. The release site was always closer to the individual's home patch than any alternative areas of refuge. Upon the release of a translocated fish, a second diver recorded the time spent by the fish in the release site prior to homing, and the time spent swimming from the release site to the home patch. Simultaneously, the first diver traced the homing path of the focal damselfish on a Plexiglass slate, noting the position of recognizable landmarks (e.g., coral pieces, shoots of seagrass, etc.). Fish that remained in the release site for the whole observation period (30 min), or that began to defend a new patch, were considered not to have homed (Turgeon et al. 2010). If homing was successful, the divers measured the length of the focal fish's homing path, as depicted on the hand-drawn map. At the end of each translocation, we counted the total number of bicolor damselfish on the focal patch. We also recorded depth and, using measuring tape, determined the length and width of the home patch. A small number of patches (n = 22) were used for two translocations because of the limited number of suitable territories. In these instances, we waited at least 20 days before revisiting patches a second time

and caught a fish of a different size from the first caught at that site.

Each translocated fish was assigned haphazardly to be a control (N = 45 damselfish) or exposed to one of three model treatments (N = 36–37 damselfish per treatment). In the control configuration, we placed a 30-cm Plexiglass rod vertically in the sand, 0.5 m from the release site, along the most direct route between the release site and home patch. In the model treatments, one of three formalin-preserved, resin-coated models was attached to the vertical rod, 20 cm above the sand: (1) a French grunt (*Haemulon flavolineatum*; non-piscivore treatment), (2) a black grouper (*Mycteroperca bonaci*; native piscivore treatment) or (3) a lionfish (*Pterois* sp., invasive piscivore treatment). All models were the same size (35 cm TL; i.e., more than three times the size of the largest damselfish used in this study, and hence piscivores were potential predators of all translocated damselfish), with their pectoral fins oriented in a strike pose to mimic foraging behaviour, since damselfish have been shown to be sensitive to both predator size and posture (Helfman 1989). The models therefore offered accurate and consistent visual cues, but we acknowledge that they did not provide other cues, e.g. olfactory cues, that could be important. A pilot experiment revealed that the homing probability of bicolor damselfish (n = 12 individuals) was significantly reduced when the distance between the release site and the grouper model (i.e., the native foraging piscivore predicted to elicit the strongest predator-avoidance response) became shorter (Fig. S2). Each model was therefore placed at a constant absolute distance from the release site (i.e., 0.5 m) for experimental translocations.

Analyses

To determine whether the presence of different fish models along the homing route affected the likelihood that damselfish returned to their territory, we used generalized linear mixed-effects (GLMM) models (lmer library in R with the restricted maximum likelihood methods) to examine the effects of model treatment (4 levels: control (no model), non-piscivore, native piscivore, invasive piscivore) on the homing probability of damselfish. We considered homing probability as a logistic response (0 = did not home; 1 = homed), and constructed 16 candidate models

(with binomial error structure and a log-link function), representing all possible combinations of three habitat-related explanatory variables (i.e., treatment type, translocation distance, and density of conspecifics on the home patch) and one intrinsic variable (i.e., focal fish size). We used site as a random factor in all models to account for replication of patches within sites. Visual examination of the residuals plot confirmed that the assumption of homogeneity of residual variance was met, and there was no significant correlation between explanatory variables. The candidate models corresponded to the following a priori hypotheses: (1) the effects of model treatment type on homing should be related to damselfish's ability to recognize predators and accurately assess the level of threat associated with each model (Helfman 1989; Sih et al. 2010), (2) homing probability might decrease as the distance fish need to travel across sand increases (e.g., Turgeon et al. 2010), (3) homing probability might increase as the density of conspecifics on the home patch increases, since conspecifics might offer predator protection via a dilution effect if a predator is unable to consume all prey in a group (Stamps 1988; Sieving et al. 2004; Schmidt et al. 2008) and (4) larger individuals might be more likely to home because risk of predation is often lower for larger fish (Rice et al. 2011; Hamilton et al. 2014). Using a model selection approach corrected for small sample size (i.e., Akaike Information Criterion, AIC_c; Burnham and Anderson 2002), we identified the best-supported GLMM model as that with the lowest AICc value (Burnham and Anderson 2002), although models that differed in AICc values by less than two units were considered equally well supported by the data (Burnham and Anderson 2002). We computed the AICc model-averaged coefficients for each parameter in the top model(s), and depicted them using the control (no model) treatment as a baseline. We plotted the binomial logistic regression (with a logit link function) from model-average coefficients for each treatment.

For the fish that successfully homed (n = 50 individuals), we compared total homing time, time spent at the release site (i.e., shelter time), detour distance swum, and swimming speed in the absence and presence of fish models. We calculated the 'detour' distance for every fish that homed in the control treatment (n = 24 fish) by subtracting the distance between the release site and home patch from the length of the actual homing route of the focal fish.

The detour distance therefore represents the additional distance swum beyond a straight path home. We calculated swimming speed as the total distance swum between the release site and home patch divided by the time spent swimming by each fish. We used separate linear models to test how each of the four responses co-varied with translocation distance in the absence of any fish model. We then used the line-of-best-fit of each linear model to predict the values of each of the four responses for each translocation distance tested with the different fish models. We subtracted the predicted from the observed values to obtain deviations in fish responses in the presence of each of the fish models and compared these values among fish model treatments using one-way analyses of variance (ANOVAs).

Results

The 154 translocated damselfish ranged in total length (TL) from 3.5 cm to 7.9 cm (mean ± SD: 5.51 ± 1.27 cm). There were no significant differences in mean damselfish size or in mean density of conspecifics at each territory across fish model treatments (one-way ANOVAs; TL: $F_{3,150} = 1.35$, $p = 0.26$; conspecific density: $F_{3,150} = 0.37$, $p = 0.78$). Following release, damselfish typically hid on or within the release site for variable amounts of time. Across all treatments, 62% of translocated damselfish (ranging from 53% in the no-model treatment to $\sim$ 80% in the native piscivore treatment) did not return to their home territory within 30 min. The proportion of fish homing was highest in the first 4 min after release, and declined nearly exponentially thereafter (Fig. S3). To reduce the potential effect of variation in threat assessment time by damselfish, we limited our analyses to fish that homed within the first eight minutes of observation. This time window captured 80% of homing damselfish (Fig. S3).

Two models of homing probability were strongly supported (i.e., ΔAICc < 2; Table 1) and explained 62% of the variation in homing probability. They both included the presence/absence of a fish model along the homing route, as well as translocation distance and fish size. The second top model also included conspecific density (Table 1). The simpler top model

obtained twice as much support as the second-ranked model (Table 1).

In the absence of a fish model, damselfish homing probability declined significantly (Fig. 1) but non-linearly (Fig. 2) with translocation distance, and damselfish stopped homing when released more than 5.6 m away from their territory (Fig. 2). Of all three fish models presented, only the native piscivore significantly decreased the probability that a damselfish would home compared to when no model was present (Figs. 2, S4). The presence of the native piscivore model reduced the threshold translocation distance, at which homing probability is 50%, from 3.3 m (in the absence of a fish model), on average, to 2.1 m (Fig. 2). In contrast, these threshold translocation distances in the presence of a non-piscivore model (3.8 m, on average) and of an invasive piscivore model (2.9 m, on average) were similar to that observed in the absence of any model (Fig. S4). The maximum homing distances were similar in the presence of the non-piscivorous grunt (4.8 m) and the invasive lionfish models (4.2 m; Fig. S4), but dropped to 3.4 m in the native piscivore treatment (Fig. 2).

Homing probability increased non-linearly with damselfish size (Fig. 3), such that the largest translocated damselfish (7.9 cm) was, on average, 70% more likely to return home than the smallest one (3.6 cm), in the absence of a fish model. Damselfish became more likely to home than not to home (i.e., homing probability = 50%) at 6 cm TL, on average (Fig. 3). Fish smaller than 4.1 cm, however, were never observed homing. The density of conspecifics at the home territory was not a determinant of damselfish homing (Fig. 1).

As expected, total homing time and the time spent in shelter upon release increased linearly with translocation distance in the absence of a fish model (homing time: adjusted $r^2 = 0.29$, $F_{1,17} = 8.53$, $p = 0.009$; time in shelter: adjusted $r^2 = 0.25$, $F_{1,17} = 7.14$, $p = 0.016$; Fig. S5a, b). Damselfish also took larger detours as translocation distance increased (adjusted $r^2 = 0.55$, $F_{1,17} = 7.54$, $p = 0.014$; Fig. S5c), but swimming speed did not co-vary with translocation distance (adjusted $r^2 = 0.07$, $F_{1,17} = 2.46$, $p = 0.13$) when fish models were absent. The presence of a fish model on the homing route significantly affected damselfish total homing time (one-way ANOVA; $F_{2,38} = 3.58$, $p = 0.038$) and time in shelter (one-way ANOVA;

Table 1 Results of AIC model selection analysis of logistic models describing homing probability of translocated bicolor damselfish in terms of fish model treatment (i.e., no fish, native non-piscivore (grunt), native piscivore (grouper), non-native piscivore (lionfish)), translocation distance (m), fish size (total length, cm) and density of conspecifics on the home patch (individuals per m^2). Site was included as a random factor in all models

Statistical model	k	-Log likelihood	AIC_c	Δ AIC	W_i	pseudo-R^2
Fish model + Translocation distance + Fish length	5	62.39	139.6	0.00	0.60	0.59
Fish model + Translocation distance + Fish length + Conspecific density	6	61.89	140.8	1.22	0.33	0.60
Translocation distance + Fish length	4	68.24	144.8	5.21	0.044	0.54
Translocation distance + Fish length+ Conspecific density	5	67.68	145.8	6.20	0.03	0.54
Fish model + Distance	3	72.98	158.8	18.98	0.00	0.47

K is the number of parameters in each model; ΔAIC_c is the difference in AIC_c value between the focal model and the model with the lowest AIC_c; Akaike weight w_i is interpreted as the probability that model i is the best model of the candidate set given the data at hand. Models shaded in grey differ in ΔAIC_c values by less than two and are considered equally well supported by the data
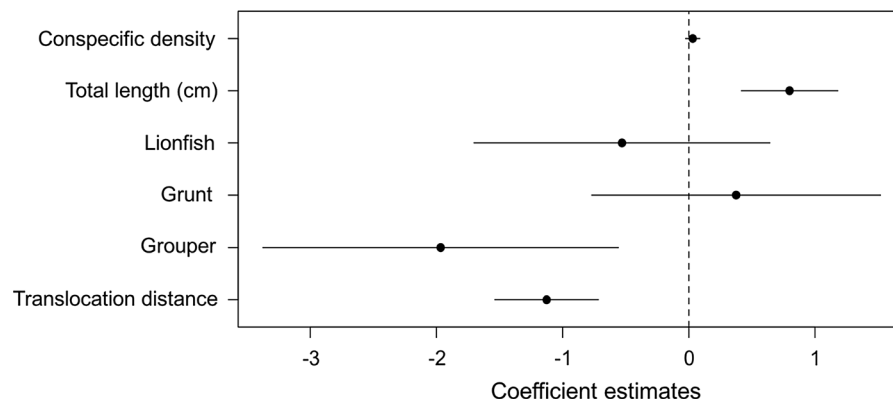

Fig. 1 Coefficients of the effects of various factors on the homing probability of translocated bicolor damselfish in Curaçao, Netherlands Antilles. Points were averaged across two top generalized mixed-effects models, and are shown bounded by 95% confidence intervals. Positive value (to the right of the dashed vertical line) indicate an increase in homing probability, while negative values indicate a decrease. The levels 'Lionfish', 'Grunt', and 'Grouper' refer to the type of preserved fish model placed along the homing route, and are compared against the baseline level of no fish model

$F_{2,38} = 2.80$, $p = 0.043$). On average, damselfish released in the presence of the native grouper model took 3.3 min longer to home (Fig. 4a) and remained in shelter 2.6 min longer (Fig. 4b) than damselfish in the absence of any fish model. Damselfish confronted with models of a non-piscivorous grunt and an invasive lionfish had similar homing times and times in shelter as damselfish in the absence of a fish model (Fig. 4a, b). In contrast, detour distances in the presence of fish models did not significantly deviate from what was expected in the absence of a fish model (one-way ANOVA; $F_{2,38} = 0.73$, $p = 0.49$). Since swimming speed did not co-vary with translocation distance in the absence of a fish model, we simply compared
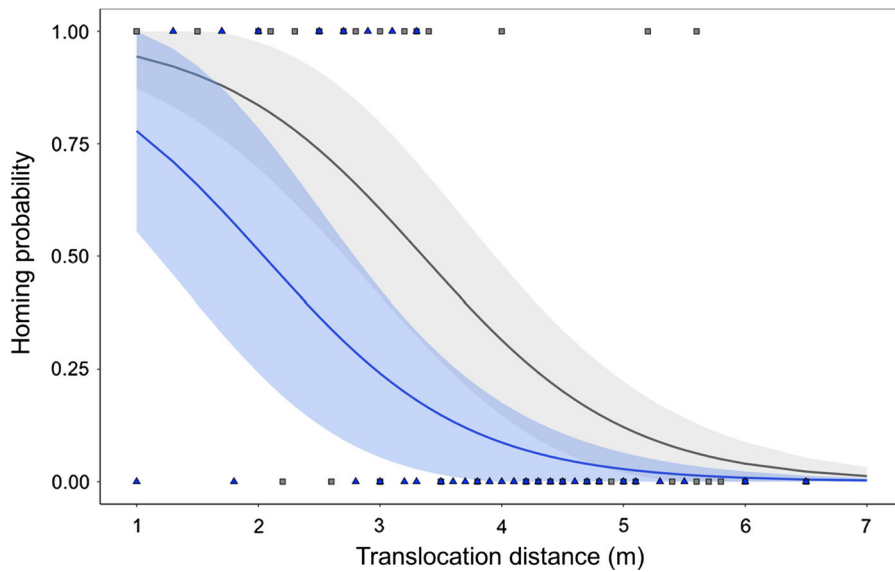
Fig. 2 Relationships between the homing probability of translocated bicolor damselfish and the distance (in m) between the release site and the home patch, in the absence (grey symbols and lines; distance range = 1–6.5 m) and presence (blue symbols and lines; distance range = 1–6.5 m) of a native piscivore (i.e., a black grouper) model along the homing route. The solid lines are the lines of best fit for the averaged, best-

supported generalized linear mixed-effects model identified by AICc (equation: homing probability = exp(− 1.31 * translocation distance) * exp(− 1.68 * Grouper) * exp(0.59 * Grunt) * exp(− 0.32 * Lionfish) * exp(0.83 * Fish length) * exp(0.01 * Conspecific density) * exp(6.23)). The shaded areas represent 95% confidence intervals

Fig. 3 Relationship between the homing probability of translocated bicolor damselfish and damselfish length (TL in cm) in the absence of a fish model on the homing route. The solid line is the line of best fit for the averaged best-supported generalized linear mixed-effects model identified by AICc (equation as shown in Fig. 2). The shaded areas represent 95% confidence intervals
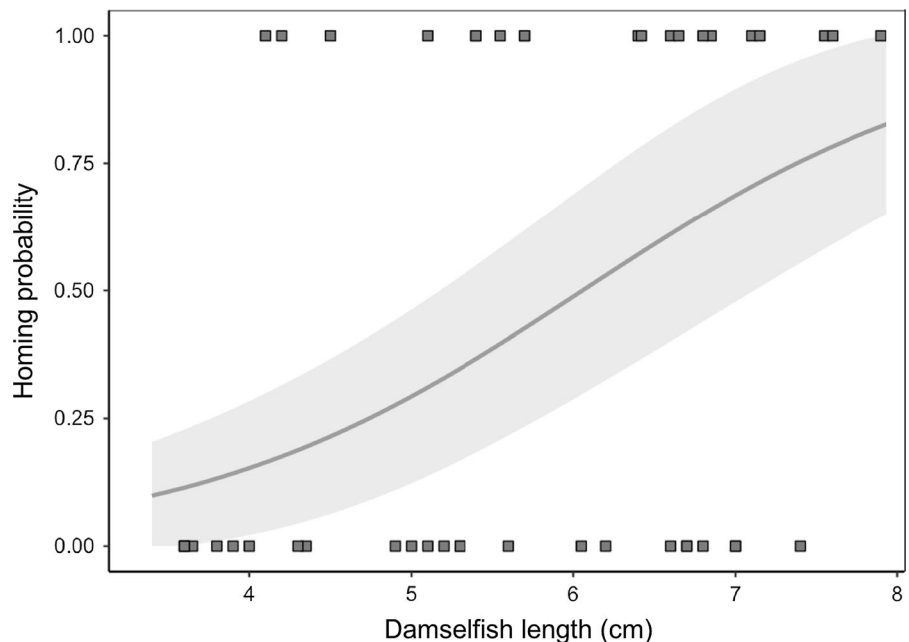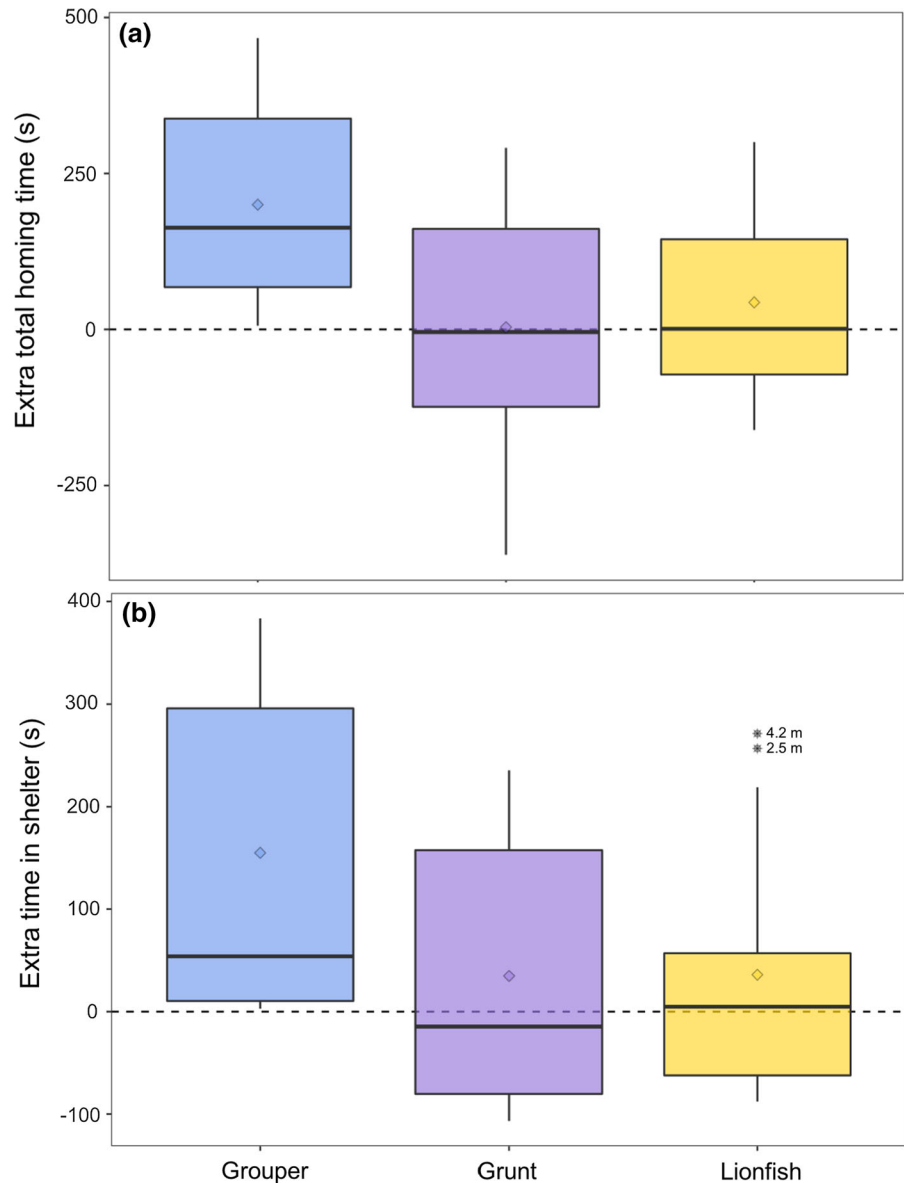

absolute speed of translocated damselfish among treatments and found no significant differences (one-way ANOVA; $F_{3,55}$ = 1.51, p = 0.22).

Discussion

In this study, we asked whether the homing patterns of experimentally translocated bicolor damselfish could

be used to infer recognition of invasive lionfish by native prey fish. In general, damselfish were more likely to home when they were larger and when they were released closer to their territory. As expected, a native grouper model elicited a strong predator avoidance response by bicolor damselfish: translocated fish were less likely to home, took longer to do so and stayed in the release shelter longer in the presence of the grouper model. In contrast, damselfish facing a lionfish model exhibited similar homing behaviours to those of damselfish in the presence of a non-piscivorous grunt and in the absence of any model. Our

results suggest that, at least on the basis of homing behaviour, bicolor damselfish do not correctly perceive the risk of predation presented by invasive lionfish. Translocations offer a novel experimental approach to evaluate predator recognition and behavioural responses of native prey species under realistic field conditions.

Fish aversion to crossing sand gaps appears to be strongly related to perceived risk of predation. Translocation distance over open sand and fish size were the determinants of fish homing probability in the absence of a fish model. Given the low shelter

availability presented by featureless sand habitat, and the likelihood of heightened encounter rates of predatory fishes (Shulman 1985; Sweatman and Robertson 1994; Turgeon et al. 2010), we expected that damselfish would be more reluctant to return to their home territory as translocation distance over sand increased. This prediction was confirmed. In the absence of a model, the negative sigmoidal shape of the overall relationship between fish homing and translocation distance mirrors that documented by Turgeon et al. (2010) for another species of highly territorial Caribbean damselfish, the longfin damselfish (*Stegastes diencaeus*). The homing probability of translocated longfin damselfish decreased steeply and non-linearly with increasing sand gap widths, and individuals were unlikely to cross sand gaps wider than 3.9 m (Turgeon et al. 2010). The same threshold distance (i.e., translocation distance at which homing probability is 50%) was ∼ 3.3 m in bicolor damselfish. This difference is consistent with the slightly smaller size of bicolor damselfish (Froese and Pauly 2016). Indeed, we demonstrated that smaller bicolor damselfish were less likely to home following experimental translocation than larger conspecifics. This pattern was expected, given the size-structured nature of predator–prey relationships in marine environments: smaller fish should be under greater risk of predation than larger fish away from areas of refuge (Boaden and Kingsford 2015).

In contrast to our prediction, conspecific density on the home territory was not a determinant of damselfish homing probability. Since the presence and/or abundance of conspecifics might indicate patch safety (Stamps 1988; Sieving et al. 2004; Schmidt et al. 2008), we had anticipated that damselfish removed from high-density patches would be strongly motivated to home to avoid the costs associated with loss of good or safe territories. However, bicolor damselfish colonies are organized in dominance hierarchies that are strongly size-dependent (Myrberg 1972; Sadovy 1985), with aggressive behaviour most frequently occurring between individuals similar in size (Sadovy 1985). The size distribution of individuals on a home territory, and particularly where a translocated fish falls in this distribution, might therefore play a more important role in motivating focal fish to home than conspecific density.

The explicit predation risk presented by a native piscivore model triggered several changes in homing behaviour of bicolor damselfish. In the presence of a grouper model, the likelihood of damselfish homing was depressed across all translocation distances. Damselfish spent more time in the release shelter, an anti-predator response frequently recorded when perceived risk of predation is high (Shulman 1985; Sweatman and Robertson 1994; Madin et al. 2016; Turgeon et al. 2010). As a result, average homing times of damselfish were longer than when no fish model was present. The fact that these behavioural alterations in prey were observed in the absence of 'normal' olfactory or movement cues by our stationary model reassures us that the visual cues presented by the grouper model were realistic. In contrast, the behaviours of translocated damselfish in the invasive lionfish and native non-piscivore treatments mirrored those recorded in the no-model control, suggesting that damselfish were not perceiving the threat of lionfish, at least with the cues offered by our fish models in the environment examined (i.e., over open sand).

A lack of response by damselfish to lionfish does not necessarily reflect naïveté. It is possible that homing Caribbean damselfish do not recognize lionfish as a predator in any context, in which case they are truly naïve. Alternatively, they did recognize lionfish but they perceived a limited threat from the particular behaviour displayed by our lionfish model (i.e., hunting with flared pectoral fins) in an open, sandy habitat. Lionfish sometimes do stalk prey over low-complexity sand and seagrass habitats (e.g., Benkwitt 2016; personal observation), but more often and effectively, lionfish corral prey using their pectoral fins on coral reefs with complex structures (García-Rivas et al. 2018; Green et al. 2011). The mismatch between the lionfish model's posture and the more usual hunting habitat of lionfish might have resulted in a perception by damselfish that the stalking invader presented a low risk. Unfortunately, we cannot distinguish between these two alternatives, nor can most previous field tests of lionfish recognition by native Caribbean reef fishes. In previous field experiments, native prey fish usually display the same lack of fear or aggression towards lionfish in cages or bottles as they do towards constrained native non-predators or empty containers (Black et al. 2014; Kindinger, 2015; Anton et al. 2016); these results can also be explained by recognition and perception of low risk. To differentiate between these two mechanisms,

future studies could consider the movement of native fish translocated over risky (e.g., coral reef) habitat instead of sand, where a lack of response would clearly point to naïveté. Alternatively, a lesser response by native prey to a lionfish model than to the model of a less risky, native predator (e.g., a lizardfish or scorpionfish) in sandy habitat, where the predator's advantage of concealment is removed by the uniform habitat, would similarly suggest prey naïveté.

One might wonder whether we should expect predator recognition to evolve at all in lionfish prey in the invaded range. In the native rangeo of lionfish, damselfish (*Chromis viridis* and *Pomacentrus chrysurus*) showed no behavioural evidence of predator recognition, and were readily preyed upon by lionfish in captivity (Lönnstedt and McCormick 2013; McCormick and Allan 2016). The cryptic body shape, scent and colouration of lionfish might allow it to circumvent prey risk assessment abilities, perhaps contributing to its successful invasion of Caribbean marine ecosystems (Lönnstedt and McCormick 2013). However, the exceedingly high densities of lionfish in parts of their invaded range (Morris and Akins 2009; Darling et al. 2011), combined with high predation rates (Green et al. 2011), should give rise to stronger selection pressures on prey than those in the native range of lionfish, advancing the possibility that Caribbean fish populations might eventually adapt to the threat of this marine predator.

In conclusion, the presence of an invasive lionfish over sand did not affect bicolor damselfish homing at a Caribbean location invaded nearly a decade ago (de Léon et al. 2013). Future studies are needed to identify the mechanism underpinning this lack of accurate risk perception by native fish and to explore the role of non-visual cues (e.g., olfactory) in facilitating predator recognition and risk assessment. Perhaps more importantly, we combined two traditional approaches in behavioural studies, namely translocations and the presentation of models, to provide a novel, well-controlled and highly replicable method to evaluate threat recognition by native species in invaded communities in a natural setting. Repeating these naïveté trials over space and time might offer a powerful means to detect invader-induced changes in the behaviour of native species.

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