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Habitat plasticity in native Pacific red lionfish *Pterois volitans* facilitates successful invasion of the Atlantic

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ABSTRACT: Red lionfish were transported outside their native Pacific range to supply aquaria, subsequently escaped or were released, and have established breeding populations in Atlantic reefs. This invasion has negatively affected coral reef fishes, reducing recruitment success through predation. To provide insight into the factors explaining invasion success, we examined the distribution and abundance of native lionfish in 2 regions of the Western Pacific (Marianas and Philippines). Densities of lionfish and other predatory coral reef fishes were evaluated via stratified surveys targeting habitat preferred by lionfish. There were considerable regional differences in species composition of lionfishes in general and density of *Pterois volitans* in particular. Red lionfish were uncommon on Guam (3.5 fish ha^{-1}) but 6 times more abundant in the Philippines (21.9 fish ha^{-1}). Densities in both regions were an order of magnitude less than reported in the invaded Atlantic. There was no relationship between density of lionfish and that of other reef predators, including groupers. Both native populations of *P. volitans* were more common on reef-associated habitats (sandy slopes, reef channels, and artificial reefs) than on coral reefs. On Guam, *P. volitans* was more abundant in areas of low water visibility (reef channels and river mouths) compared to reefs with high water clarity. Lionfish in their native range are habitat generalists that occupy various environments, including areas with low salinity and high sediment loads. This plasticity in habitat use helps explain invasive success, given that ecological generalization is recognized as a major factor accounting for the successful establishment of invasive species.

KEY WORDS: Lionfish distribution · Native density · Habitat use · Invasion success · Western Pacific

INTRODUCTION

Many species have intentionally and unintentionally been delivered into new ecosystems, where they have the possibility to establish viable populations (Pimentel et al. 2000). Successful invasions most often involve species with a generalist diet and high tolerance to diverse environmental conditions, especially when they have been introduced to degraded habitats with low native biodiversity (Vila-Gispert et al. 2005, Duggan et al. 2006). Invasions are also usually accompanied by the invasive species being facilitated by ecological release from predation, competition, or parasite infestation in its native range (Williamson 1997, Mack et al. 2000, Crooks & Rilov 2009). Once established, invasive species can cause negative economic and ecological impacts (Grosholz 2002, Clavero & Garcia-Berthou 2005), such as spe-

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cies replacements, loss of diversity, and alterations of community and ecosystem structure and function (Fritts & Rodda 1998, Semmens et al. 2004, Dierking et al. 2009).

Introduced to the Western Atlantic in the vicinity of Florida via the aquarium trade, Pacific red lionfish *Pterois volitans* and its congener *P. miles* reached reproductive population densities during the 1990s (Semmens et al. 2004, Meister et al. 2005, Freshwater et al. 2009) and are now distributed in tropical and subtropical coastal environments throughout the Western Atlantic, Gulf of Mexico, and Caribbean (Schofield 2010), despite local attempts at manual removal. The dramatic increase in lionfish density since their introduction (Green & Côté 2008, Morris et al. 2009, Albins & Hixon 2013) has raised considerable concern over the ecological and economic damage to coral reef fish communities in the region. Lionfish have caused substantial reductions in the abundance of newly settled coral reef fishes (Albins & Hixon 2008, Albins 2013) and may compete with native fishery species, such as small grouper (Albins 2013).

Red lionfish feed on a variety of small fishes and crustaceans (Harmelin-Vivien & Bouchon 1976, Myers 1999, Albins & Hixon 2008, Morris & Akins 2009) and are the only piscivorous species of lionfish (Myers 1999). They have few identified predators in both their native and invaded range, presumably because of the protection provided by multiple venomous spines (Allen & Eschmeyer 1973, Bernadsky & Goulet 1991, Maljkovic & Van Leeuwen 2008). Published records on parasite loads of lionfish are scarce but suggest low parasite loads in the invaded range (Ruiz-Carus et al. 2006, Bullard et al. 2011). Such characteristics of red lionfish make it an ideal species for establishing viable populations in new environments (Albins & Hixon 2013, Côté et al. 2013).

Understanding the underlying processes which shape the distribution and abundance of lionfish in their native range may provide further insight into the causes of their successful invasion of the Atlantic. By examining distribution patterns and lionfish density at 2 locations in the Western Pacific, together with a series of environmental correlates, we assessed some of the underlying environmental and habitat-associated factors which could be responsible for the observed low densities of lionfish in their native range (Kulbicki et al. 2012) compared to those reported for the invaded range (e.g. North Carolina: Whitfield et al. 2007, Bahamas: Green & Côté 2008).

MATERIALS AND METHODS

Survey methods

Lionfish density and distribution were estimated at 23 sites on Guam and 24 sites in the Philippines using stratified surveys that mainly targeted habitat preferred by lionfish (Fig. 1). Sites were chosen based on either preliminary surveys which indicated lionfish presence or local reports of the occurrence of lionfish in a particular area. Each transect covered an area approximately 5000 m^2 (500 × 10 m). Transect width was always 10 m, but specific transect length was variable and determined by a towed GPS attached to a float. Therefore, transect area was variable and individually estimated for each transect. Surveys at all sites were undertaken at 5 to 15 m depth, each along one particular habitat type (i.e. reef slope, reef channel, sandy slope), to evaluate potential differences among habitats. Long transects were chosen to increase the probability of encounter, as lionfish are uncommon (Kulbicki et al. 2012) and have patchy distributions, such that traditional visual census methods shorter in length (e.g. 50 m) tend to underestimate abundance (Brock 1982, Jones et al. 2006, Green et al. 2013). These methods were chosen to mirror those used by researchers in the invaded range (Whitfield et al. 2007, Green & Côte 2008) to ensure robust comparisons between native and invasive populations. Counts along transects were performed by 2 divers (5 m belt transect each) swimming side by side. As lionfish are cryptic in nature, the divers made systematic searches of reef holes and overhangs within the transect boundary to maximize accuracy in lionfish abundance estimates (Morris et al. 2009). This modification of the usual visual census method follows recent recommendations for accurate assessment of lionfish density (Green et al. 2013). Density estimates (number per transect area) were converted to number per hectare to allow comparison with published estimates of lionfish density for both the invaded and native ranges (Whitfield et al. 2007, Green & Côté 2008, Grubich et al. 2009, Kulbicki et al. 2012). Body size as total length (TL) to the nearest centimeter was estimated for every individual encountered. All surveys were conducted during the morning (between 06:00 and 11:00 h), which previous observations showed as the optimal time for 'encountering' lionfish because of their heightened foraging activity during this time (Cure et al. 2012). Surveys were conducted during April to June 2010 on Guam and June to July 2010 in the Philippines.

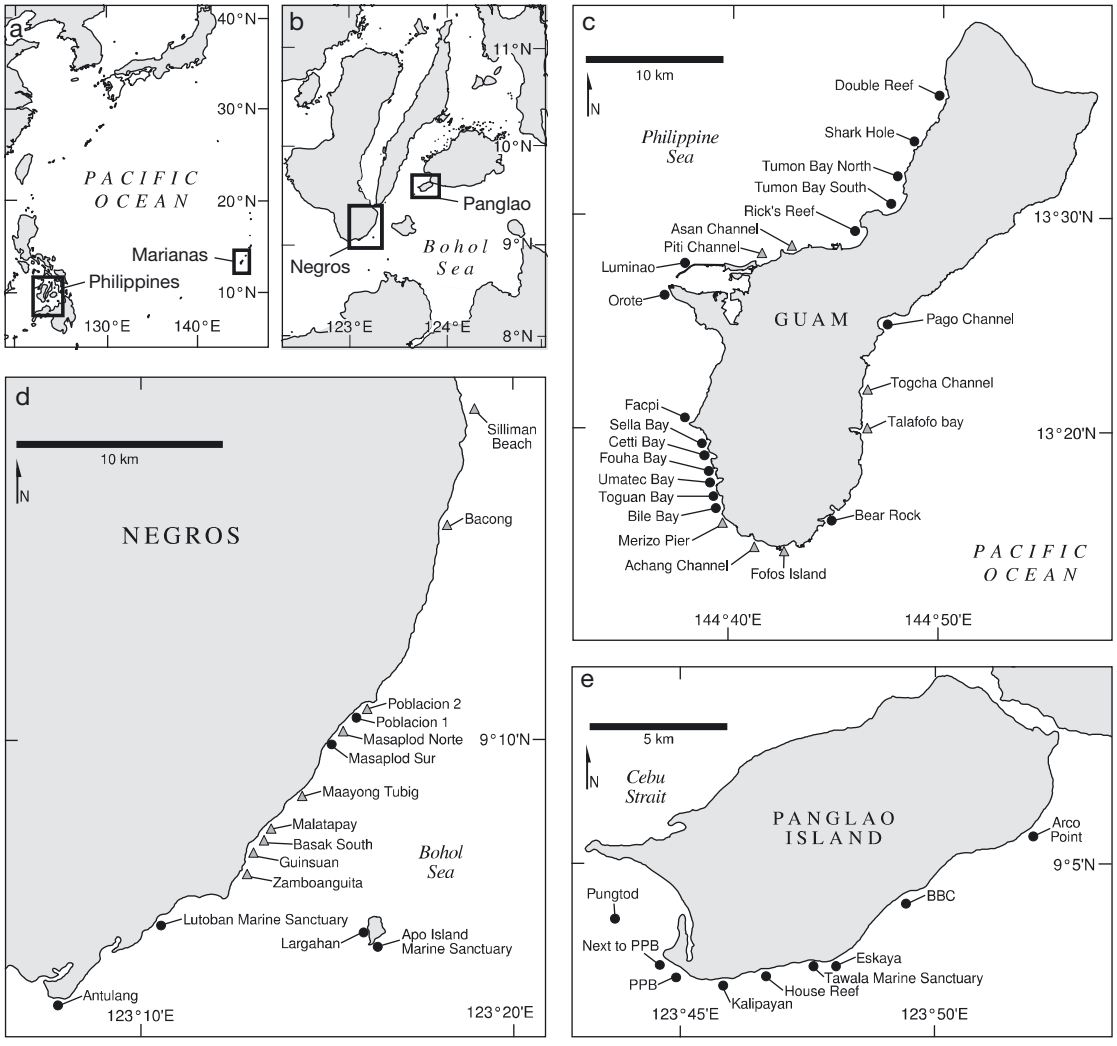

Fig. 1. General regions of lionfish survey sites (a) in the Philippines and Marianas and (b) in the central Philippines. Specific locations of lionfish survey sites at (c) the island of Guam (n = 23), and (d) Negros and (e) Panglao in the Philippines (n = 24). PPB and BBC: names given to local dive sites. Sites were classified as either reef slope (black circles) or non-reef slope (grey triangles). Transects per site varied from 1 to 4 on Guam and from 1 to 2 in the Philippines

To investigate potential correlations between lionfish and environmental characteristics, 10 environmental variables were measured during the course of the surveys (Table 1). These variables are known to influence fish density and distribution and were chosen for this reason. Similarly, to examine the relationship between the density of *Pterois volitans* and that of other lionfish species, abundances of all other lionfishes (*P. antennata, P. radiata, Dendrochirus biocellatus, D. zebra*, and *D. brachypterus*) were also recorded along each transect. Densities for all other species of lionfish were also converted to number per hectare for comparison with published estimates. When lionfish were found in a group, the size and species composition of the group were also recorded. Furthermore, abundances of other predators that could potentially consume or compete for food with lionfish were recorded on the same 5 m belt transects as lionfish (see Table S2 in the Supplement, available at www.int-res.com/articles/suppl/m506p243_supp.pdf, for complete species list). All species encountered were identified to the lowest taxonomic level possible, and species richness (total number of species) was determined for each transect. Microhabitat data were collected by recording the specific microhabitat where each lionfish was encountered at the time of the survey. Five microhabitat categories were noted: hard coral, rock/boulder, sand/silt, artificial, and other (including soft coral, barrel sponges, seagrass, or macroalgae). 'Other' categories were poo-

Table 1. Physical and biological variables measured at each transect conducted in the Philippines (n = 27) and on Guam (n = 36). Character of variables is denoted as B = biotic, S = spatial, and P = physical. Type of variable is denoted as either C = categorical or N = numeric. The 'Values' column lists the types (C) or range (N) of observed values for each variable. The 'Reference' column presents citations that justify each variable. TL: total length

Variable	Character	Type	Value	Reference
1. Density of lionfish (6 species; no. ha^{-1})	B	N	0–184	
2. Lionfish size (TL, cm)	B	N	0–39	
3. Density of other predatory reef fishes (no. ha^{-1})	B	N	0–2500	Hackerott et al. (2013), Mumby et al. (2011)
4. Species richness (other predatory reef fishes)	B	N	0–31	Hackerott et al. (2013), Mumby et al. (2011)
5. Microhabitat	S	C	Hard coral, rock/boulder, sand/silt, artificial, other	Smith & Shurin (2010), Biggs & Olden (2011)
6. Habitat	S	C	Reef slope, non-reef slope	Lee et al. (2011)
7. Rugosity	P	C	Low, medium, high	Green et al. (2013)
8. Distance from freshwater (m)	P	N	0–25000	Jud et al. (2011)
9. Current	P	C	Low, medium, high	Johnston & Purkis (2011)
10. Cloud cover (%)	P	N	0–100	Rickel & Genin (2005)
11. Wave action	P	C	None, moderate, strong	Santin & Willis (2007)
12. Visibility (m)	P	N	0–35	Jud et al. (2011), De Robertis et al. (2003)

led, as they represented a minority of the observations and were not comparable between Guam and the Philippines. Artificial habitats included wrecks (scattered pieces of cars and boats), tires, and abandoned fish traps.

Habitat along each transect was classified as either reef slope (slope dominated by continuous coral growth) or non-reef slope (channels on Guam and sandy slopes in the Philippines). Rugosity, current, cloud cover, and wave action were estimated based on preset categories (Table 1) and recorded as an overall value that best represented the area covered by each transect. To ensure that these variables were representative of overall site conditions during the year, surveys were conducted during the same season and during the most common environmental conditions for each site (e.g. if a site was usually subjected to high wave energy, then surveys were not conducted on a particularly calm day). Distance from freshwater was estimated on-site and calibrated using either Google Earth or ArcGIS (Philippines shapefiles are available for download from the Data Repository of the Geographic Information Support Team (https://gist.itos.uga.edu/). This variable was considered important based on preliminary searches around Guam which revealed an apparent association of lionfish with river mouths and estuaries. For assessment of underwater visibility, horizontal Secchi disc measurements were taken 3 times along each transect, with the mean of the 3 samples used as an overall index. All visibility measures were taken during the non-rainy season to facilitate comparisons among sites and regions.

Statistical analyses

Mann-Whitney *U*-tests were used to evaluate differences between regions for the total density of all lionfish species, mean size of each individual lionfish species, and all predator species recorded. Spearman rank correlation tested for relationships between *Pterois volitans* density and explanatory variables as an initial exploration of the independent influence of each of the measured variables with lionfish density. Non-parametric tests were chosen because data on *P. volitans* abundance were not normally distributed.

To further determine which environmental variables explained variation in *P. volitans* density, a multiple linear regression model was fitted to the data following the formula $y_i = \beta_0 + \beta_1 X_{i1} + \ldots. \beta_j X_{ij} + e_i$, where β is the correlation coefficient for each explanatory variable, and e is unexplained variance (Quinn & Keough 2002). Data for y were log(y + 1)-transformed *P. volitans* density (fish per hectare), and data for the explanatory variables X_{i1} to X_j included variables from Table 1 (variables 3 and 6–12) plus density of all other lionfish species. To ensure that the model complied with critical assumptions, residuals were checked for normality (Shapiro-Wilks test, $p > 0.05$) and heteroscedasticity (studentized Breusch and Pagan tests) (Quinn & Keough 2002). Collinear-

ity among independent variables was tested with Pearson correlation coefficients and scatterplots of the data. As significant collinearity was present between predator density and predator diversity, only predator density was selected for inclusion in the model.

Linear regression analyses were completed in R (R Development Core Team 2010) using the package 'Relaimpo' (Grömping 2006). This approach quantifies the individual contributions or 'relative importance' of each regressor in a multiple regression model. We selected the most important variables contributing to variance in *P. volitans* density without incurring overfitting problems common to multiple regressions (Quinn & Keough 2002). We also used bootstrapping techniques to obtain 90% confidence intervals for each of the relative importance metrics.

RESULTS

Species composition and density of lionfishes and other predators

Lionfish surveys covered 209 473 m^2 on Guam and 102 110 m^2 in the Philippines. Total species richness of lionfishes was identical between regions (4 species), but only *Pterois volitans* and *P. antennata* were common to both (Fig. 2). These 2 species were also the most abundant, with *P. antennata* having the highest density of all lionfishes on Guam and *P. volitans* being the most common in the Philippines. *P. radiata* and *Dendrochirus biocellatus* were unique to Guam, while *D. zebra* and *D. brachypterus* were found only in the Philippines. Lionfishes were observed at 19 of 23 sites on Guam and 23 of 24 sites in the Philippines.

Total density of lionfishes was almost 5 times higher in the Philippines than on Guam (mean ± SE: 44.99 ± 9.91 fish ha^{-1}, n = 27 vs. 9.86 ± 2.84 fish ha^{-1}, n = 36) (Fig. 2). For the 2 species common to both regions, *P. volitans* and *P. antennata*, densities in the Philippines were 6 and 3 times higher, respectively, than on Guam (mean ± SE: *P. volitans*: 21.94 ± 6.5 fish ha^{-1}, n = 27 vs. 3.53 ± 0.9 fish ha^{-1}, n = 36; *P. antennata*: 14.65 ± 3.68 fish ha^{-1}, n = 27 vs. 5.00 ± 2.49 fish ha^{-1}, n = 36). These differences in density between regions were significant for both species (*P. volitans:* Mann-Whitney *U*-test: 136, $p < 0.001$ and *P. antennata:* Mann-Whitney *U*-test: 237, $p < 0.001$). Other lionfishes had very low densities on Guam, but in the Philippines *D. zebra* was well represented, accounting for almost 16% of total lionfish density.

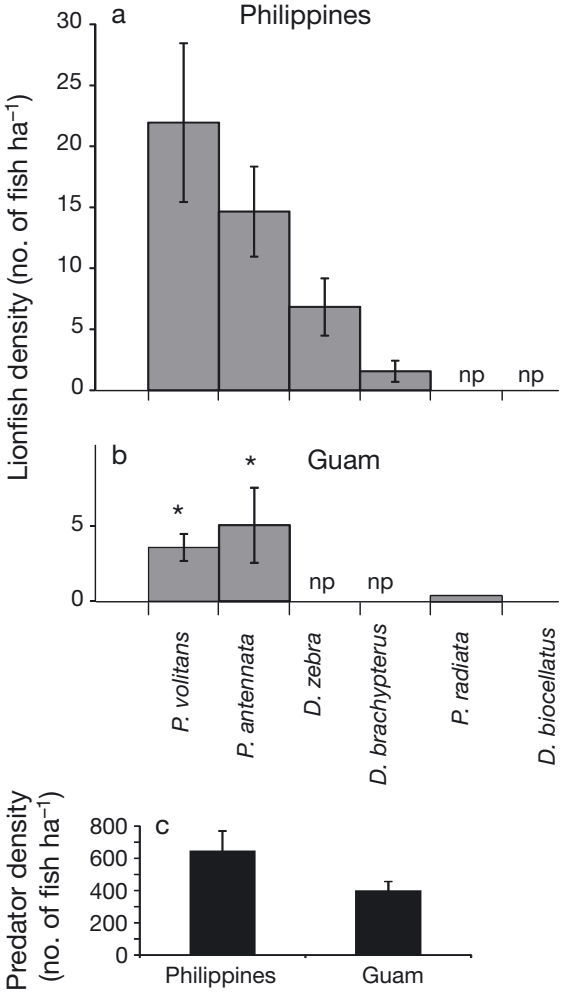

Fig. 2. Mean (±SE) densities of 6 lionfish species (*Pterois volitans, P. antennata, Dendrochirus zebra, D. brachypterus, P. radiata,* and *D. biocellatus*) along transects (a) in the Philippines (n = 27) and (b) on Guam (n = 36). (c) Densities of predatory fishes (black bars) along the same transects on Guam and in the Philippines. Asterisks denote significant differences ($p < 0.001$) in total density between these 2 regions for those species common to both. np: not present

A comparison of density and diversity of other predatory fishes between regions showed similar patterns to those of lionfishes. Mean species richness was very similar between Guam and the Philippines (Philippines = 16.05 species, Guam = 14.50 species; see Table S2 in the Supplement for complete species list), but mean density was higher in the Philippines (mean ± SE: 648.17 ± 121.28 fish ha^{-1}, n = 27 vs. 401.98 ± 54.33 fish ha^{-1}, n = 36) (Fig. 2). Differences in predator densities, however, were not as marked as for lionfishes and not statistically significant. When data for other predators were assessed at the family level, densities of lutjanids, labrids, and ser-

ranids were similar between regions. However, there were significantly more holocentrids on Guam (mean ± SE: 52.18 ± 10.68 fish ha^{-1}, n = 36 vs. 6.90 ± 3.83 fish ha^{-1} in the Philippines, n = 27, Mann-Whitney *U*-test: 114, p < 0.001) (Fig. 3).

Body size and group size

Mean body size (TL) of *Pterois* species common to both regions was significantly smaller in the Philippines than on Guam, although higher lionfish densities were found in the Philippines (mean ± SE: *Pterois volitans:* 24.14 ± 1.14 cm, n = 51 vs. 17.06 ± 0.47 cm, n = 182, Mann-Whitney *U*-test: 2345, p < 0.001 and *P. antennata:* 14.66 ± 0.45 cm, n = 76 vs. 10.51 ± 0.30 cm, n = 146, Mann-Whitney *U*-test: 2433, p < 0.001). Lionfish formed groups that were mostly monospecific but sometimes comprised of multiple species (Table 2). Groups were most common in the Philippines and comprised of individuals of the same species (e.g. *P. volitans* ~54% in monospecies groups vs. ~26% for Guam). Rarely (2% of the time) was *P. volitans* found in a multispecies group on Guam.

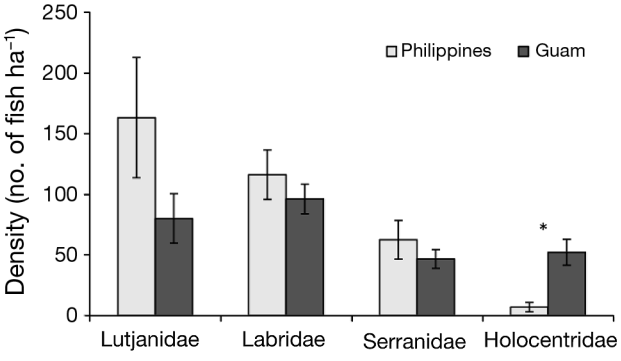

Fig. 3. Mean (±SE) densities of non-lionfish predatory reef fishes by family along transects on Guam (n = 36) and in the Philippines (n = 27). *Significant difference in total density between these 2 regions (p < 0.001)

Microhabitat use

The distribution of all lionfishes with respect to microhabitat showed considerable regional differences (Fig. 4). Lionfishes on Guam were mostly associated with rock/boulder or hard coral. In contrast, lionfishes in the Philippines were associated with a greater variety of habitats, with *Pterois volitans* showing greatest abundance at hard coral and artificial habitats (tire reefs and old fish traps).

Aside from regional differences in microhabitat associations, there were also species-specific differences. Among regions, *P. volitans* utilized sand/silt habitat the most compared to other species, although in the Philippines this habitat was mostly occupied by *Dendrochirus brachypterus*, which was absent from Guam. Other lionfishes seldom if ever occurred in sand/silt habitats. *P. antennata* was mostly associated with rock/boulder habitat on Guam and hard coral in the Philippines. Microhabitat associations of *P. volitans* also changed according to body size (TL), but this trend was evident only in the Philippines, where smaller lionfish were mostly associated with hard coral (mean ± SE: hard coral = 14.8 ± 0.47 cm, rock/boulder = 18.73 ± 1.28 cm, sand/silt = 20.18 ± 1.67 cm, artificial = 18.35 ± 0.98 cm, other = 16.00 + 2.92 cm, Kruskal-Wallis *H*-test = 14.244, df = 4, p = 0.007).

Table 2. Configuration of groups of lionfish found on Guam and in the Philippines. Multispecies groups refer to instances when each lionfish species was found with other lionfish species, while monospecies groups refer to a single lionfish species. Data are presented for total number of lionfish recorded for each location (n total), total number of groups observed (n group), percentage of each lionfish species that occurred in a group, and mean group size (no. of fish per group)

Species	n (total)	Multispecies			Monospecies		
		n (group)	% in group	Mean group size (no. of fish)	n (group)	% in group	Mean group size (no. of fish)
Philippines							
Pterois volitans	182	13	7.1	4.6 ± 0.8	99	54.4	4.9 ± 0.2
P. antennata	146	5	3.4	6.4 ± 1.1	47	32.2	4.0 ± 0.2
Dendrochirus zebra	58	9	15.5	4.9 ± 0.6	37	63.8	4.3 ± 0.2
D. brachypterus	11	2	18.2	2.5 ± 0.5	8	72.7	3.8 ± 0.2
Guam							
P. volitans	51	1	2	2	13	25.5	3.8 ± 0.2
P. antennata	76	1	1.3	2	36	46.2	3.8 ± 0.2

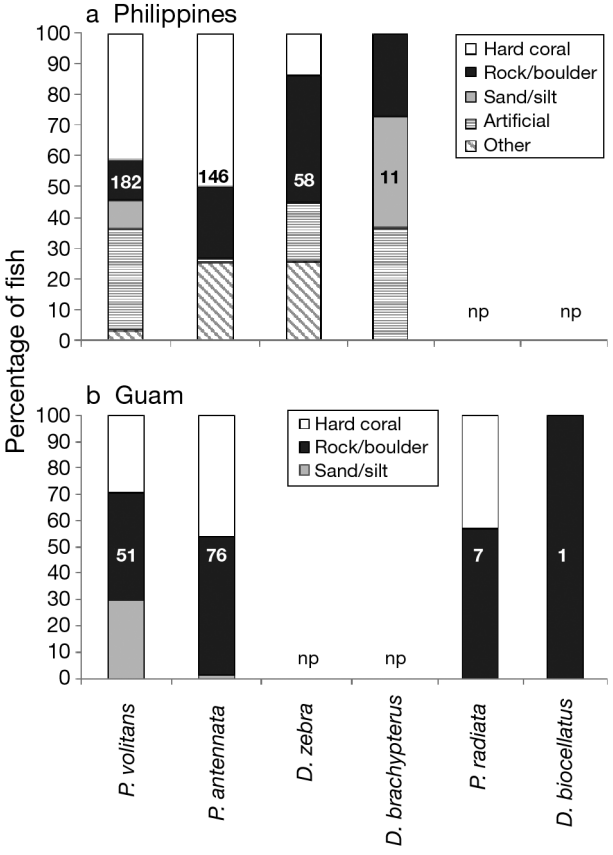

Fig. 4. Percentage of 6 lionfish species found in each microhabitat type along transects (a) in the Philippines (n = 27) and (b) on Guam (n = 36). Numbers in the bars indicate total number of fish recorded. Note that *Dendrochirus zebra* and *D. brachypterus* were found only in the Philippines, and *Pterois radiata* and *D. biocellatus* were found only on Guam. np: not present

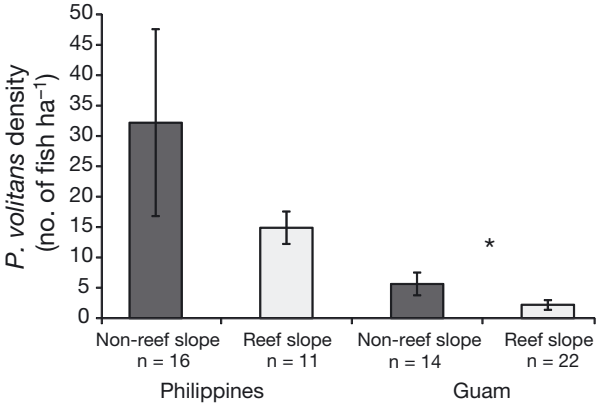

Fig. 5. Mean (±SE) density of *Pterois volitans* by habitat (reef slope and non-reef slope) in the Philippines and on Guam. *Significant difference in *P. volitans* abundance between habitats on Guam (p = 0.025). n: number of transects

Relationship between *Pterois volitans* density and environmental variables

Habitat was the only categorical variable for which there was a significant pattern in red lionfish density (see Table S1 in the Supplement). Non-reef slopes had double the number of *Pterois volitans* compared to reef slopes in both regions, but these differences were significant only for Guam (Mann-Whitney *U*-test: 81.5, p = 0.025) (Fig. 5). Rugosity, current, cloud cover, and wave action were not significantly related to lionfish density patterns.

When environmental factors were examined separately, only 2 significant relationships were found. First, densities of *P. volitans* increased as a function of other lionfishes present in both regions (Guam and the Philippines pooled into one dataset: *P. volitans*: r_s = 0.493, p < 0.001). Second, *P. volitans* densities were highest in low-visibility waters on Guam (r_s = –0.388, p = 0.019). Contrary to *P. volitans*, both density and diversity of all other predators decreased as a function of turbidity (r_s = 0.357, p = 0.035).

A multiple linear regression analysis on log(y + 1)-transformed densities of *P. volitans* revealed that lionfish densities were significantly related to (1) region of occurrence (p = 0.017), (2) habitat surveyed (p = 0.009), and (3) water clarity (visibility; p = 0.032) (see Table S1 in the Supplement). The complete model explained 53.22% of the variability in *P. volitans* density, with region and habitat accounting for half of this variation (see Table S1 in the Supplement). Presence of other lionfish and visibility were the third and fourth, respectively, in terms of rank importance.

DISCUSSION

Six species of lionfish in their native Pacific range were found in multi-species assemblages, each dominated numerically by a different species: *Pterois antennata* on Guam and *P. volitans* in the Philippines. When compared to the invaded Atlantic range of *P. volitans*, native Pacific regions show much lower population densities, consistent with data from non-targeted surveys elsewhere in their native range (Kulbicki et al. 2012). Mean densities are an order of magnitude higher in North Carolina than in the Western Pacific (mean of 150 ind. ha^{-1}, with some sites surpassing 450 ind. ha^{-1}, Morris & Whitfield 2009) and are even higher in the Bahamas (3 sites, mean of 390 ind. ha^{-1}, Green & Côté 2008). The

Atlantic density estimates are 7 to 15 times higher than those in the Philippines, which was the Pacific region with highest lionfish abundance. Such differences indicate the success of *P. volitans* populations in their invaded range.

What are the natural constraints on red lionfish abundances in their native range? There is some evidence of competition between sister species *P. miles* and groupers in the Red Sea. After experimental removal of adult *Cephalopholis* spp. at reef wall habitats, *P. miles* colonized vacated habitat and increased in density (Shpigel & Fishelson 1991). A recent study in Palau suggested that groupers act as both competitors and predators of lionfish based on an inverse relationship found between grouper abundance and lionfish density (Grubich et al. 2009). However, this correlation was based on a survey area of only 364 m^2, or 0.12% of the total area covered in this study. If groupers are indeed predators of lionfish, one would expect a similar pattern to be evident in other parts of their native range. However, even though lionfish abundance was 6 times higher in the Philippines than on Guam, grouper densities were similar between regions. We also found no evidence of predation on red lionfish during field observations in both this study and a separate study of *P. volitans* time budgeting (Cure et. al. 2012). Groupers have been suggested as both predators (Maljkovic & Van Leeuwen 2008, Mumby et al. 2011) and competitors (Albins 2013) of lionfish in the invaded range also, although substantial evidence for both competition with and predation of invasive lionfish by groupers or any other native predators is lacking, and the available data are controversial (Hackerott et al. 2013). Population limitation of *P. volitans* in their native range, and particularly how significant predation and competition are for shaping lionfish abundance, is an open field for investigation. One possibility, given the much greater reef fish diversity in the Pacific compared to the Atlantic, is that newly recruited lionfish in the Pacific are consumed by a small predator that does not occur in the Atlantic. This hypothesis is reasonable given that early post-settlement mortality, typically via predation, is a major gauntlet that many reef fishes run (Hixon 1991, Almany & Webster 2006).

What explains differences in red lionfish density within their native Western Pacific range? Distribution and abundance patterns were mostly correlated with region of occurrence. In general, ecosystems surveyed in the Philippines supported much higher lionfish densities than those on Guam, possibly related to (1) the drastically higher numbers of fish recruits observed on these reefs, likely indicating higher availability of resources for the piscivorous *P. volitans*; and/or (2) differences in habitat availability between the regions. High levels of fish recruitment are characteristic of the central Philippines region throughout the year and especially during July to October, when this study was conducted (Abesamis & Russ 2010). Invasive lionfish have also been found in higher abundances in habitats with higher prey abundance (Lee et al. 2012). Another important difference between the regions and possible reason for the high abundance of small juvenile fish prey was the presence of artificial habitats along surveys in the Philippines but not on Guam. About a third of the lionfish encountered in the Philippines were associated with artificial structures. Artificial reefs in the region of Negros Oriental, where a large part of the surveys in this study were conducted, have been established as part of a fisheries enhancement program since 1991 (~200 artificial reef clusters encompassing 12 200 m^2 of habitat) (Munro & Balgos 1995). The presence of artificial structures could potentially enhance recruitment of *P. volitans*, thereby accounting for the higher lionfish densities observed. In the invaded Atlantic region, experiments using artificial habitat have found that such structures facilitate recruitment and colonization by lionfish into both seagrass and hard-bottom habitats (Smith & Shurin 2010).

Within regions, seafloor habitat, presence of other lionfish, and underwater visibility were also correlated with *P. volitans* density. The greatest probability of encountering *P. volitans* was on non-reef slopes (rock/boulder channels and sandy slopes), in areas where other species of lionfish were also in high abundance, and where water visibility was low. Low visibility possibly presents multiple advantages for the piscivorous *P. volitans*, including enhanced crypsis (Rickel & Genin 2005) and perhaps high abundance of small planktivorous fish prey, which may be at an advantage in turbid environments where food availability is high (De Robertis et al. 2003). Also, because lionfish are predominantly crepuscular hunters (Fishelson 1975, Myers 1999, Randall 2005, Green et al. 2011, Cure et al. 2012), they may have adapted to finding prey in low light levels (see Helfman 1986, Rickel & Genin 2005). The association of *P. volitans* with turbid inshore areas also indicates a tolerance to freshwater influx and poor water quality, as is evident by invasive lionfish being found up a coastal river in Florida (Jud et al. 2011). The positive association of red lionfish *P. volitans* with other species of lionfish found in this study implies that there

are possible interactions between lionfish species in their native range, such as competition for resources (food and habitat, which could be acting to limit *P. volitans* population densities). Furthermore, this association implies that other lionfish species may also have the potential to become highly successful invasive species, should they be transported outside of their native range to supply aquaria.

Unlike other coral reef fishes, for which reef complexity and coral cover are typically important determinants of density patterns (Jones 1991), we found that lionfish are habitat generalists with no particular specificity for highly complex habitats, although they are nearly always found near structures of some kind, at least when not foraging. Studies on invasive lionfish also found no relationship between lionfish abundance and coral cover (Lee et al. 2012). However, unlike findings of this study, invasive lionfish are most abundant in more complex aggregate reef habitats than in patch reefs, reef flats, or seagrass beds (Biggs & Olden 2011). Native lionfish surveyed here preferred areas of low complexity (i.e. non-reef slopes) to high complexity (reef slopes) along the same depth gradient. A possible confounding factor is depth. Most studies on Atlantic reefs have compared deep complex habitats with shallow habitats of low complexity such as seagrass beds and patch reefs (Claydon et al. 2012, Lee et al. 2012). In these studies, lionfish have shown a preference for deeper and more complex sites.

For both native and invasive lionfish, high variability in microhabitat use including natural and artificial habitats has been reported. A previous study on *P. volitans* and sister species *P. miles* by Schultz (1986) found both species associated with a high variety of microhabitats in its native range. *P. volitans* was found on rock, coral, and sand substrates up to a depth of 50 m (Schultz 1986). Our study showed that lionfish can also associate with rock/boulder, sand, hard coral, and artificial habitat. In their invaded Atlantic and Caribbean range, red lionfish inhabit shallow reefs (Green & Côté 2008), seagrass beds (Claydon et al. 2012), mangroves (Barbour et al. 2010), wrecks, docks, and mesophotic reefs (Lesser & Slattery 2011). Such generalist habitat associations have been identified as a major factor contributing to the successful establishment of introduced species in new environments (Vila-Gispert et al. 2005). Of special importance is the association of *P. volitans* to artificial structures, which are increasing in abundance and are areas of high propensity to the establishment of non-native species (Mineur et al. 2012).

This study helps to clarify 2 characteristics of native *P. volitans* populations that may confer greater fitness in a new environment, making the species an effective invader. First, *P. volitans* is a habitat generalist, a life history trait that typically favors invasion success (Ribeiro et al. 2008). Plasticity in habitat use is often associated with flexibility in prey selection and foraging behavior, which are especially advantageous given the high spatio-temporal variation in food resources on coral reefs (Dill 1983, Beukers-Stewart & Jones 2004). Second, lionfish are present in turbid inshore areas, a sign of tolerance to variations in turbidity and salinity, which has also been a good predictor of invasion success in other marine communities (Ribeiro et al. 2008). The mechanisms limiting and regulating populations of red lionfish in their native vs. invaded ranges remain to be clarified.

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