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ORIGINAL PAPER

Parasite-mediated enemy release and low biotic resistance may facilitate invasion of Atlantic coral reefs by Pacific red lionfish (*Pterois volitans*)

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Abstract Successful invasions are largely explained by some combination of enemy release, where the invader escapes its natural enemies from its native range, and low biotic resistance, where native species in the introduced range fail to control the invader. We examined the extent to which parasites may mediate both release and resistance in the introduction of Pacific red lionfish (*Pterois volitans*) to Atlantic coral reefs. We found that fewer lionfish were parasitized at two regions in their introduced Atlantic range (The Bahamas and the Cayman Islands) than at two regions in their native Pacific range (the Northern Marianas Islands and the Philippines). This pattern was largely driven by relatively high infection rates of lionfish by didymozoan fluke worms and parasitic copepods (which may be host-specific to *Pterois* lionfishes) in the Marianas and the Philippines, respectively. When compared with sympatric, native fishes in the Atlantic, invasive lionfish were at least 18 times less likely to host a parasite in The Bahamas and at least 40 times less likely to host a parasite in the Cayman Islands. We found no indication that lionfish introduced Pacific parasites into the Atlantic. In conjunction with demographic signs of enemy release such as increased density, fish size, and growth of invasive lionfish, it is possible that escape from parasites may have contributed to the success of lionfish. This is especially true if future studies reveal that such a loss of parasites has led to more energy available for lionfish growth, reproduction, and/or immunity.

Keywords Introduced species · Helminths · Marine fish · Parasite escape · Biogeography

Introduction

Invasive species are rapidly transforming ocean ecosystems. Recent decades have witnessed a vast increase in the translocation of nonindigenous marine

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organisms, largely due to the globalization of shipping, aquaculture, and aquarium industries (Bax et al. 2003; Rilov and Crooks 2008). Not all exotic species become established and spread broadly across their new environments, but when they do, their effects can be substantial. To prevent and mitigate the ecological effects of marine invasive species, understanding the traits and mechanisms that facilitate their success is essential (Carlton 1996; Bax et al. 2001).

The enemy release hypothesis predicts how interactions with other species shape the success of an invader. This hypothesis has two primary predictions: (1) when compared to populations in their native range, invasive populations lack natural enemies (predators, competitors, and/or parasites and other pathogens), and (2) natural enemies affect native species' individual fitness and/or populations more than they affect those of introduced species, thus benefiting the non-native (Keane and Crawley 2002; Torchin et al. 2003). To test the first prediction, biogeographical studies have compared invasive and native populations of the same species (Torchin et al. 2002, 2003; Mitchell and Power 2003). To test the second prediction, studies have compared sympatric populations of invasive and native species. At least two studies have found that native species experience higher infection prevalence by parasites, thus affecting competition among invasive and native hosts (Hanley et al. 1995; MacNeil et al. 2003).

Another explanation for the successful establishment and spread of an exotic species is the biotic resistance hypothesis, which states that native communities with high diversity and/or abundant natural enemies reduce the success of invasions (Stachowicz et al. 1999; Levine et al. 2004). Biotic resistance is said to be low when members of a community fail to limit the success of an exotic species (Shea and Chesson 2002).

Recently identified as a top global conservation threat (Sutherland et al. 2010), Pacific red lionfish (*Pterois volitans*) are experiencing a population explosion in the tropical western Atlantic, Caribbean, and Gulf of Mexico (Schofield 2010). A field experiment in The Bahamas documented that a single lionfish can reduce the abundance of small fish on a coral patch reef by 79% in just 5 weeks (Albins and Hixon 2008), and recent evidence suggests that these results scale-up to stronger effects on larger reefs over longer time periods (Green et al. 2012; Albins 2015). Consistent with the possible demographic effects of enemy release, invasive lionfish are larger, more abundant, and grow faster (Darling et al. 2011; Kulbicki et al. 2012; Pusack et al. 2016) than native lionfish on Pacific reefs. Indicative of low biotic resistance, lionfish are rarely eaten by predators in either ocean (Bernadsky and Goulet 1991; Maljković et al. 2008), perhaps due to their venomous spines, and there is evidence that lionfish are dominant competitors over native mesopredators (Albins 2013).

There is an urgent need to understand what factors naturally limit lionfish populations in their native Pacific to inform management of invasive populations. Parasitism is one possible mechanism, as there are many examples of metazoan parasites affecting the individual fitness and/or population dynamics of their marine fish hosts (Adlard and Lester 1994; Finley and Forrester 2003; Forrester and Finley 2006; Grutter et al. 2011; Binning et al. 2012). There are three ways in which invaders and parasites may interact: an invader can (1) lose parasites during the invasion (enemy release, specifically parasite loss), (2) gain parasites in the new range, which may then dilute or amplify the threat of infection in native hosts (Thieltges et al. 2008; Paterson et al. 2011), and/or (3) serve as vectors/transport hosts that introduce new parasites that spillover to native hosts (Hatcher and Dunn 2011; Strauss et al. 2012). All of these potential changes in parasitism can directly and indirectly affect the interactions between native and invasive species, and therefore determine the success of an invasion.

Parasites of invasive marine invertebrates have been relatively well studied in recent years within the context of the enemy release hypothesis (Torchin et al. 2002; Blakeslee et al. 2013). For example, the Asian hornsnail (*Batillaria attramentaria*) and European green crab (*Carcinus maenus*) both seem to have experienced release from parasites, which has putatively resulted in superior competitive ability over sympatric native species in their introduced range (Byers 2000; Torchin et al. 2001, 2005). However, we know relatively little about parasites of invasive marine vertebrates, in particular fishes (Vignon and Sasal 2009), which are among the most commonly transported marine taxa (Molnar et al. 2008) and one of the most common hosts of metazoan parasites (Poulin and Morand 2000). Studies with biogeographical comparisons of the round goby (*Apollonia melanostoma*) (Pronin et al. 1997; Kvach and Skóra

2007), peacock grouper (*Cephalopholis argus*) (Vignon et al. 2009a), and two snappers (*Lutjanus fulvus* and *L. kasmira*) (Vignon et al. 2009b) have found lower parasite diversity in the introduced ranges of these fishes.

Regarding parasites of lionfish, there are several published records that note generalist parasites infecting lionfish in low numbers in the introduced range (Ruiz-Carus et al. 2006; Bullard et al. 2011; Loerch et al. 2015; Ramos-Ascherl et al. 2015; Sellers et al. 2015). Only one study compared invasive lionfish to native hosts, and found higher parasite richness and abundance in a native grouper (*Cephalopholis cruentata*) than in lionfish at one region in the invaded range (Sellers et al. 2015). Additionally, only a single study has compared lionfish parasites in both their native and invaded ranges. That study focused on one group of generalist external parasites, gnathiid isopods, and found that lionfish are weakly susceptible to gnathiids in both oceans (Sikkel et al. 2014). No prior study has combined between- and within-ocean comparisons of lionfish parasite communities. In fact, no previous study has combined these kinds of comparisons in both the native and introduced range of any marine invasive species.

To assess the degree to which parasites may have mediated both enemy release by and biotic resistance to lionfish on Atlantic coral reefs, we asked two questions: (1) How do infection rates and types of parasites differ among native Pacific and invasive Atlantic populations of lionfish? (2) How do infection rates differ between lionfish and ecologically similar fishes (carnivores inhabiting the same reefs) in both oceans? Consistent with patterns of both enemy release and low biotic resistance, we found that invasive lionfish had much lower rates of infection by parasites than native Pacific lionfish and ecologically similar native Atlantic fishes.

Materials and methods

Fish and macroparasite collection

Within the invaded Atlantic range of lionfish, our study regions were nearshore reefs off Lee Stocking Island in The Bahamas (hereafter, “Bahamas”; 23°46′00″N, 76°06′00″W) during the summer of 2009, and Little Cayman in the Cayman Islands (hereafter, “Caymans”; 19°41′56″N, 80°3′38″W) during the summers of 2010 and 2011. Lionfish have been established in The Bahamas since 2005, and in the Caymans since 2009 (Schofield 2009). We used SCUBA and handnets to collect all lionfish (Bahamas n = 47, Caymans n = 91) and native host fishes from four families: Haemulidae (grunts; Bahamas n = 29, Caymans n = 15), Holocentridae (squirrelfishes; Bahamas n = 15, Caymans n = 17), Lutjanidae (snappers; Bahamas n = 15), and Serranidae (groupers; Bahamas n = 16, Caymans n = 17) (see Online Resource 1 for sample sizes by host species and study region). These native fishes were chosen because they are similarly sized, abundant carnivores that inhabited the same reefs as lionfish at each respective field location, and which occupy similar regions of isotopic niche space as invasive lionfish (O’Farrell et al. 2014).

Within the native Pacific range of lionfish, our study regions were nearshore reefs off Guam in the Northern Mariana Islands (hereafter, “Marianas”; 13°15′51″N, 144°39′59″E) during the summer of 2010, and the island of Negros in the Philippines (hereafter, “Philippines”; 9°19′46″N, 123°18′43″E) during the summer of 2011. In the same manner as in the Atlantic, we collected Pacific lionfish (Marianas n = 14, Philippines n = 29) and syntopic host fishes from five families: Haemulidae (grunts; Philippines n = 11), Lethrinidae (emperors; Marianas n = 15, Philippines n = 14), Lutjanidae (snappers; Marianas n = 5, Philippines n = 19), Serranidae (groupers; Marianas n = 15, Philippines n = 8), and Scorpaenidae (scorpionfishes) in the genus *Pterois* (*P. antennata* in the Marianas n = 15, and *P. russelii* in the Philippines n = 3) (Online Resource 1).

We measured the total length of each fish to the nearest millimeter, then anaesthetized and pithed it. We removed the first two branchial gill arches from both sides of the fish and used a gut wash technique to locate any gill parasites. This technique consisted of placing the gill arches in a jar with 3:1 filtered freshwater to seawater, shaking vigorously for 30 s, and allowing material to settle for 5 min. After decanting the supernatant and pouring the sediment into a clean Petri dish, we scanned the dish under a dissecting microscope. To quantify skin parasites, we bathed each fish in freshwater for 10 min (Sikkel et al. 2004). We also scraped a 3-cm^2 area of skin with a scalpel blade to screen for encysting parasites, and used a small paintbrush and squirt bottle to brush off any parasites on the fish's fins. The freshwater and scalpel scrapings were filtered through 53-µm plankton mesh, and parasites were sorted under a dissecting microscope. We dissected each fish, and conducted the gut wash technique for the gastrointestinal tract and its contents. Upon dissection, we visually inspected the internal muscle tissue and lining of the body cavity for encysting parasites, after scraping approximately 5-cm^2 with a scalpel blade. Parasites recovered from the samples were identified to the level of Phylum and/or Class, and then preserved in either 70% ethanol or 10% buffered formalin solution for later identification to lower taxonomic levels.

We obtained permits to conduct this field study from the Bahamian Department of Marine Resources, the Cayman Islands Marine Conservation Board, and the Philippines Department of Agriculture, Bureau of Fisheries and Aquatic Resources. No protected species were studied. All methods were consistent and compliant with approved guidelines for the treatment of fishes in a research capacity by the Oregon State University Institutional Animal Care and Use Committee, which approved this study (ACUP number 3886).

Data structure and analyses

Macroparasites were identified to the lowest possible taxonomic level (to at least Family for the most abundant of parasites of Pacific lionfish; to at least Genus for all parasites of Atlantic lionfish, see Ramos-Ascherl et al. 2015). We then grouped parasites into one of seven categories based on taxonomy and location, i.e., where in/on the body of the host the parasite was found (internal = gastrointestinal tract or body cavity vs. external = gills or skin). The seven parasite categories were external copepod, external isopod, external monogenean, internal acanthocephalan, internal cestode, internal digenean, and internal nematode. One parasite type, external isopod, is a group of organisms that temporarily infests fish hosts in abundances that may vary by an order of magnitude over the course of a day (Sikkel et al. 2006). Because we did not account for the time of day when each fish was captured and sampled, we chose to constrain our analyses to the six other relatively permanent parasite types. While functional differences exist among parasites within the broad taxonomic categories we defined and use here, analyzing macroparasite infection rates at this scale still allows for meaningful ecological comparisons among/between hosts, infection locations on the body, study regions, and oceans. This is because most parasite species vary greatly in their distributions and relative local abundances, and because many marine macroparasites have yet to be described. Host species also vary in their distributions and relative abundances, which is why we chose to compare patterns of parasite infection by host family instead of host species per se.

We described infection rates of fish hosts by macroparasites in terms of (1) prevalence (proportion of fish examined that are infected with at least one parasite individual), and (2) mean abundance (mean number of parasite individuals per fish). We compared prevalence, or the probability of being infected, with logistic regressions (1 = infected with at least one parasite, 0 = uninfected) using a generalized linear model (GLM), and mean abundance with negative binomial regressions, also using GLM. We statistically compared the prevalence and abundance of each parasite type that infected lionfish among four study regions (predictor with four levels: Marianas, Philippines, Bahamas, Caymans). Within each region we also compared the prevalence and abundance of all parasites infecting lionfish vs. other host fishes (predictor with four–six levels, depending on the region: Haemulidae, Holocentridae, Lethrinidae, Lutjanidae, Serranidae, and scorpaenids *P. antennata*, *P. russelii*, and *P. volitans*). For all comparisons of parasite abundance we created Poisson (*Pois*), negative binomial (*NB*), and zero-inflated negative binomial (*ZINB*) regressions. We chose the best fit models based on likelihood ratio tests and relative Akaike's Information Criteria (AIC) scores, then visually assessed model residuals (see Online Resource 2 for model comparisons). To simultaneously test the null hypotheses of no difference in infection rates among study regions and among host families, we corrected *p* values and confidence intervals for multiple comparisons with *multcomp* (Hothorn et al. 2008), a package in the statistical software *R* v3.1.2 (R Core Team 2016). Our regressions were also constructed in *R*, with the packages *lme4* (Bates et al. 2015) and *pscl* (Zeileis et al. 2008; Jackman 2015).

Logistical constraints

Lionfish collection was logistically constrained at both Pacific regions by time (we collected as many as possible within a two-week period) and government permits (n = 30 lionfish limit in the Philippines). In the Marianas we captured every lionfish that we found (n = 14). Therefore, while the Marianas sample size is relatively small, we believe it is representative of the local lionfish population. In total, we were unable to capture as many lionfish in the Pacific (n = 43) as we were in the Atlantic (n = 138), where lionfish were relatively abundant and unprotected by local management authorities. In addition, parasite abundance is known to vary with a variety of environmental conditions which we were unable to control (Poulin and Morand 2000). Thus was the need for and value of comparing infection rates of lionfish with those of syntopic native fishes, which revealed variation in local parasite abundance both among and within our four study regions.

Results

Greater proportions of lionfish were infected at two regions in their native Pacific range (prevalence: Marianas = 0.714, Philippines = 0.966) than at two regions in their invaded Atlantic range (prevalence: Bahamas = 0.426, Caymans = 0.264) (Fig. 1a). Native lionfish in the Philippines had 4.9 times more abundant parasites than native lionfish in the Marianas (*ZINB*: 95% family-wise CI 1.8–13.5, $z = 4.015$, $p < 0.001$), 5.3 times more abundant parasites than invasive lionfish in The Bahamas (*ZINB*: 95% family-wise CI 2.1–13.2, $z = 4.624$, $p < 0.001$), and 3.5 times more abundant parasites than invasive lionfish in the Caymans (*ZINB*: 95% family-wise CI 1.5–8.0, $z = 3.816, p < 0.001$) (Fig. 1b, Online Resource 3 for GLM results).

External copepod parasites (Phylum Arthropoda, Class Maxillopoda) accounted for most of the relatively high infection rates of lionfish from the Philippines. The copepod *Taeniacanthus pteroisi* Shen 1957, a gill parasite recorded solely on hosts from the *Pterois* genus of lionfishes, was found on the gills of nearly all (27 of 29, prevalence = 0.931) lionfish in this region (mean abundance ± SEM = 6.8 ± 0.9, range 1–18; Table 1). *T. pteroisi* was also found on all three soldier lionfish (*P. russelii*) collected in the Philippines, with one host having 38 copepods (prevalence = 1.000, mean abundance ± SEM = 15.0 ± 11.5, range 2–38; Table 1). We also found internal acanthocephalan worms (Phylum Acanthocephala) infecting lionfish in the Philippines but not in lionfish from any of the other regions sampled. These were identified as juveniles of *Serrasentis* sp. Van Cleave, 1923 (prevalence = 0.276, mean abundance ± SEM = 1.5 ± 0.7, range 1–13; Table 1).

In the Marianas where lionfish are native, half of lionfish were infected with schistosomula (immature stage) of didymozoan fluke worms (Phylum Platyhelminthes, Class Trematoda; prevalence = 0.500, mean abundance ± SEM = 1.1 ± 0.4, range 1–4), which we also found in over half of the 15 spotfin lionfish (*P. antennata*) that we captured at this region (prevalance = 0.533, mean abundance ± SEM = 2.8 ± 0.9, range 1–10) (Table 1). However, didymozoans were found at low rates in lionfish from the Philippines (prevalance = 0.034, mean abundance ± SEM = 0.1 ± 0.1, range 1–3). By comparison, lionfish in the introduced range were also infected with didymozoans, but at lower rates than in the Marianas (*Neotorticaecum* sp. Kurochkin and Nikolaeva, 1978 in The Bahamas: prevalence = 0.192, mean abundance ± SEM = 0.5 ± 0.4, range 1–18, and in no lionfish from the Caymans). In the Caymans, 16 of 91 lionfish had the intestinal fluke *Lecithochirium floridense* (Manter, 1934) Crowcroft, 1946 (Phylum Platyhelminthes, Class Trematoda; prevalence = 0.176, mean abundance ± SEM = 0.4 ± 0.2, range 1–7), which we did not find in lionfish from The Bahamas. All other parasites found in lionfish in their introduced range were at prevalences less than 0.100, and have been previously described in Ramos-Ascherl et al. (2015).

In addition to comparing lionfish infection rates among regions, we also compared lionfish infection rates with those of ecologically similar (mid-sized, carnivorous) and syntopic fishes at each region. We found no significant differences in infection prevalence between lionfish and each of the comparison host families/species in both native Pacific regions (*LR*: all $p > 0.05$) (Fig. 2a, Online Resource 3). In contrast, at both introduced Atlantic regions sampled, we found that native syntopic fishes had much higher infection prevalence (odds of being infected) than invasive lionfish. In The Bahamas, after accounting for fish size, a native grunt (Family Haemulidae) was 26.2 times more likely than an invasive lionfish to be infected with at least one parasite of any type (*LR*: 95% family-wise CI 2.9–234.2, $z = 3.264$,

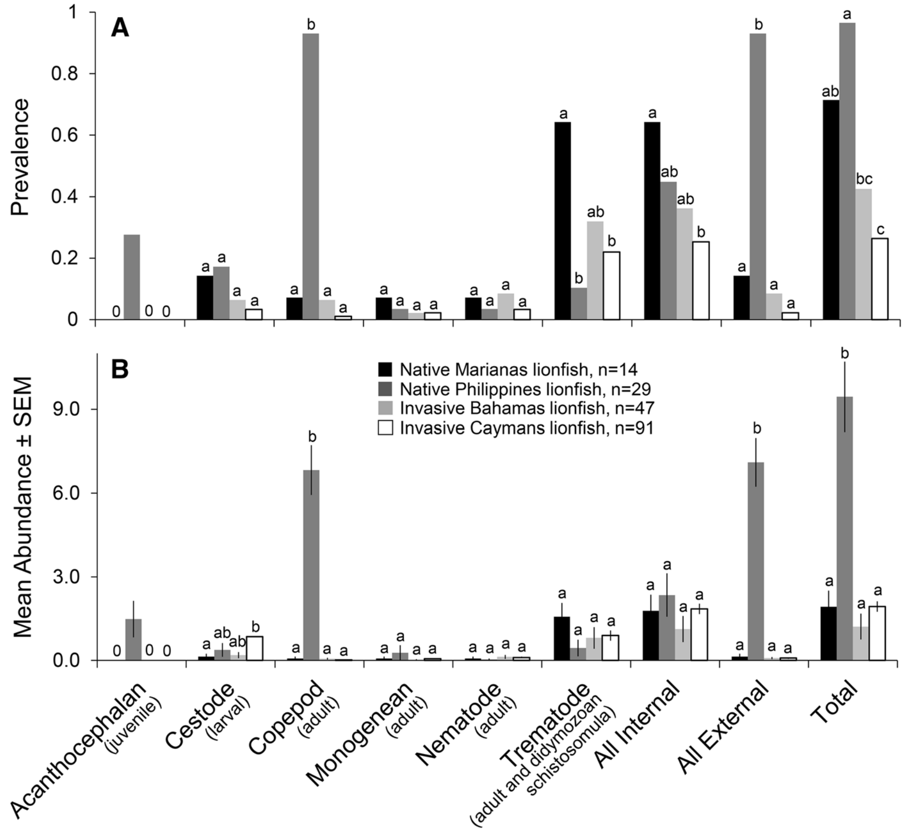

Fig. 1 Infection rates of lionfish (*P. volitans*) by parasite taxa (with associated developmental stage(s)) and region. "All Internal" represents the sum of acanthocephalans, cestodes, nematodes, and trematodes. "All External" represents the sum of copepods and monogeneans. "Total" is all parasite types combined. **a** Prevalence represents the proportion of fish that were infected with at least one parasite. **b** Mean (±SEM) abundance represents the number of parasites infecting a single fish. The results of statistical tests (logistic regressions for prevalence and negative binomial regressions for abundance) are represented by *letters above each bar*, whereby *different letters* indicate significant differences ($p \leq 0.05$, corrected for multiple comparisons) between regions, within parasite type. Only native Philippines lionfish were infected with acanthocephalans, therefore we did not statistically compare their infection rates

$p = 0.001$), a native squirrelfish (Family Holocentridae) was 18.3 times more likely to be infected (*LR*: 95% family-wise CI 1.2–267.0, $z = 2.694$, $p = 0.028$), and a native snapper (Family Lutjanidae) was 18.5 times more likely to be infected (*LR*: 95% family-wise CI 1.3–271.3, $z = 2.918$, $p = 0.027$) (Fig. 2a, Online Resource 3). Similarly, in the invaded region of the Caymans, a native grunt was 43.7 times more likely to be infected with at least one parasite of any type than was a lionfish (*LR*: 95% family-wise CI 3.5–550.6, $z = 3.777$, $p = 0.001$) and a native squirrelfish was 48.2 times more likely to be infected (*LR*: 95% family-wise CI 3.9–601.5, $z = 3.666$, $p = 0.001$) after accounting for fish size. Native groupers were, however, an exception to this trend; we found no significant difference in infection prevalence between invasive lionfish and native groupers (Family Serranidae) at either region in the introduced range (*LR*: both $p > 0.05$) (Fig. 2a, Online Resource 3). When considering external copepod parasites only, non-lionfish families had significantly more prevalent infections than had invasive lionfish in The Bahamas (*LR*: $z = 2.547$, $p = 0.014$) and the Caymans (*LR*: $z = 3.247$, $p = 0.001$) after accounting for fish size (Online Resource 3).

We found similar trends in the abundance of macroparasites infecting each host (instead of prevalence). There were no significant differences between lionfish and each comparison host family/species in the Philippines (*NB*: all $p > 0.05$) (Fig. 2b, Online

Table 1 Parasites infecting native Pacific *Pterois* spp. and their developmental stage, infection location on the body, study region (M = Marianas, P = Philippines), host species, number of host individuals (N), prevalence (P%), mean abundance (MA ± SEM), range of infection, and references for the parasite being previously recorded for the host species

Parasite taxon (stage)	Infection location	Study region	Host species	N	P %	MA ± SEM (range)	Recorded for host sp? [ref]
Acanthocephala							
Serrasentis sp. Van Cleave, 1923 (juvenile)	Intestines	P	*P. volitans*	29	27.6	1.5 ± 0.7 (1–13)	No
Cestoda							
Unidentified cestode(s) (larval)	Intestines	M	*P. antennata*	15	6.7	0.2 ± 0.2 (3)	
			P. volitans	14	14.3	0.2 ± 0.1 (1–2)	
		P	*P. volitans*	29	17.2	0.4 ± 0.2 (1–7)	
Crustacea							
cf. Bomolochidae Claus, 1875 (adult)	Gills	M	*P. antennata*	15	20.0	0.3 ± 0.2 (1–3)	No
Taeniacanthus pteroisi Shen, 1957 (adult)	Gills	P	*P. russelii*	3	100.0	15.0 ± 11.5 (2–38)	[1, 2]
			P. volitans	29	93.1	6.8 ± 0.9 (1–18)	[3]
Digenea							
Didymozoidae Monticelli, 1888 (schistosomulum)	Muscular tissue	M	*P. antennata*	15	53.3	2.8 ± 0.9 (1–10)	No
			P. volitans	14	50.0	1.1 ± 0.4 (1–4)	No
		P	*P. russelii*	3	33.3	0.3 ± 0.3 (1)	No
			P. volitans	29	3.4	0.1 ± 0.1 (1–3)	No
Unidentified trematode(s) (adult)	Intestines	M	*P. antennata*	15	53.3	0.7 ± 0.2 (1–2)	
			P. volitans	14	21.4	0.5 ± 0.3 (1-4)	
		P	*P. volitans*	29	6.9	0.3 ± 0.3 (2–8)	
Monogenea							
Haliotrema sp. Johnston & Tiegs, 1922 (adult)	Gills	P	*P. volitans*	29	3.4	0.3 ± 0.3 (8)	[4, 5]
Nematoda							
Unidentified nematode(s) (adult)	Intestines	M	*P. antennata*	15	6.7	0.1 ± 0.1 (2)	
			P. volitans	14	7.1	0.1 ± 0.1 (1)	
		P	*P. russelii*	3	33.3	0.3 ± 0.3 (1)	
			P. volitans	29	3.4	0.0 ± 0.0 (1)	

References: [1] Shen (1957); [2] Uma Devi and Shyamasunari 1980; [3] Dojiri and Cressey (1987); [4] Paperna (1972); [5] Colorni and Diamant (2005)

Resource 3). In the Marianas, however, lionfish had significantly fewer parasites than emperors (Family Lethrinidae; *NB*: $z = 5.816$, $p \leq 0.001$), snappers (*NB*: $z = 2.444$, $p = 0.049$), and groupers (*NB*: $z = 2.812$, $p = 0.018$) (Fig. 2b, Online Resource 3). Similarly, lionfish in their invaded range had relatively low abundances of parasites when compared to all other fishes except native groupers (*NB*: $p > 0.05$). In The Bahamas and after accounting for fish size, native grunts had 25.6 times more parasites than invasive lionfish (*NB*: 95% family-wise CI 11.1–58.9, $z = 9.611$, $p < 0.001$), native squirrelfishes had 6.0 times more parasites (*NB*: 95% family-wise CI 2.6–13.7, $z = 5.377$, $p < 0.001$), and native snappers had 22.8 times more parasites (*NB*: 95% family-wise CI 10.2–50.8, $z = 9.623$, $p < 0.001$) (Fig. 2b, Online

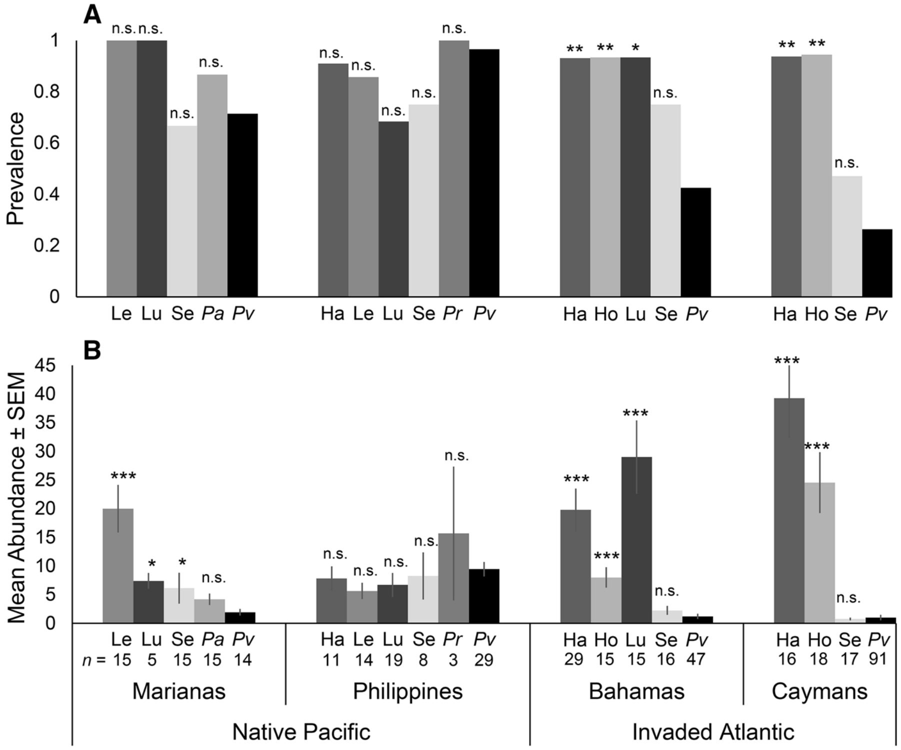

Fig. 2 Infection rates by all macroparasites of host fishes (*Ha* haemulid grunts, *Ho* holocentrid squirrelfishes, *Le* lethrinid emperors, *Lu* lutjanid snappers, *Se* serranid groupers, *Pa* scorpaenid *P. antennata*, *Pr* scorpaenid *P. russelii*, and *Pv* scorpaenid *P. volitans*), with sample sizes listed under their respective fish family/species. **a** Prevalence represents the proportion of fish that were infected with at least one parasite. **b** Mean (±SEM) abundance represents the number of parasites infecting a single fish. The results of logistic (for prevalence) and negative binomial (for abundance) regressions are indicated *above each bar*, all with respect to lionfish (*P. volitans*) in their respective region (*** is $p \leq 0.001$; ** is $p \leq 0.01$; * is $p \leq 0.05$; n.s. is $p > 0.05$; all corrected for multiple comparisons)

Resource 3). In the Caymans, native grunts had 15.2 times more parasites than invasive lionfish (*ZINB*: 95% family-wise CI 6.6–34.9, $z = 7.385$, $p < 0.001$), while native squirrelfishes had 9.6 times more parasites (*ZINB*: 95% family-wise CI 4.3–21.6, $z = 6.209$, $p < 0.001$) (Fig. 2b, Online Resource 3).

Discussion

To best predict and manage the outcomes of biological invasions, it is essential to understand the mechanisms that underpin successful invaders. Parasitism is one interaction that can modify the success of invasions (Hatcher and Dunn 2011). Therefore, we compared the infection rates of one highly invasive coral-reef fish, the red lionfish (*Pterois volitans*), in its native versus invaded ranges, and within each range, we compared their infection rates with those of other carnivorous fishes at the same reefs. Overall, we found that fewer lionfish were parasitized at two regions in their introduced range than at two regions in their native range, and that lionfish have fewer parasites than most ecologically similar native fishes in their invaded range.

The relatively higher infection prevalence of lionfish in their native Pacific was mainly driven by the presence of didymozoan tissue flukes in the Marianas and of the gill copepod *Taeniacanthus pteroisi* in the Philippines, which we did not find at any other study region or on any non-*Pterois* fish in either ocean. While we did not find *T. pteroisi* in the Marianas, it has been documented on soldier lionfish (*Pterois russelii*) in China and on lionfish (*P. volitans*) in the Red Sea (Dojiri and Cressey 1987). *Taeniacanthus* sp. also infected soldier lionfish in India, suggesting that these copepods have a broad geographic distribution (Uma Devi and Shyamasunari 1980). *T. pteroisi* has been reported only in the gill cavities of *Pterois* fishes, and members of the Family Taeniacanthidae exhibit a high degree of host specificity at both the genus and species level (Dojiri and Cressey 1987). Therefore, *T. pteroisi* is likely to be host specific to *Pterois* fishes, although more work should be done to determine both the relative abundance of *T. pteroisi* and its effects on host fitness across the native range of lionfish.

Gill copepods are relatively large-bodied parasites that can affect the fitness of their coral-reef fish hosts (Finley and Forrester 2003; Forrester and Finley 2006). The difference in mean copepod abundance between lionfish from the Philippines versus the Atlantic regions was approximately seven copepods. This difference may be ecologically important; one experimental study of another coral-reef fish, albeit a small-bodied goby, found that an infection of seven gill copepods was associated with reduced growth and gonad mass, and increased instantaneous mortality rates (Finley and Forrester 2003). Atlantic fishes were much more likely to host a copepod than were syntopic invasive lionfish, suggesting that the difference between Philippines and Atlantic lionfish in copepod infection may not be due to lower exposure to copepods, but rather to lower susceptibility of lionfish to these parasites in their introduced range. In fact, two experimental studies in the Atlantic have demonstrated low susceptibility of lionfish to generalist external parasites, even after accounting for exposure (Sikkel et al. 2014; Loerch et al. 2015).

Our within-region comparisons in the Atlantic revealed that native grunts, squirrelfishes, and snappers were more likely to be infected, and with more parasites than were invasive lionfish. However, we did not test whether or not Atlantic parasites induced differential effects on the fitness of their hosts. Therefore, we cannot know if the native hosts' parasite burdens necessarily disadvantaged them, or made them competitively inferior to relatively less infected lionfish. We noted similarly low numbers of parasites infecting lionfish and native groupers at all regions, both in the Pacific and the Atlantic. Of the comparison host families, serranid groupers are the most closely related to scorpaenid lionfish, phylogenetically and ecologically [i.e., they have the most overlap in diet (Randall 1967) and isotopic niche space (O'Farrell et al. 2014), and are likely outcompeted by lionfish (Albins 2013)]. One study found that Epinephelinae groupers have maintained relatively low internal trematode diversity over evolutionary time (Cribb et al. 2002). Given the evolutionary and ecological relatedness of groupers and lionfish, lionfish might also be less susceptible to trematodes, although this remains to be tested. Consistent with this hypothesis is our finding that native Pacific populations of lionfish were host to relatively low abundances of internal trematodes.

Our finding that invasive lionfish experience low infection rates is consistent with findings from other studies across the invaded range, which observed generalist macroparasites infecting lionfish in low numbers (Ruiz-Carus et al. 2006; Bullard et al. 2011; Loerch et al. 2015; Ramos-Ascherl et al. 2015; Sellers et al. 2015). What are the mechanisms by which Atlantic lionfish largely evade parasitism? Lionfish are generalist predators of reef invertebrates and fishes, which might make them differentially susceptible to trophically-transmitted parasites (e.g., most internal acanthocephalans, cestodes, nematodes, and trematodes). However, the life cycles of most coral-reef parasites are not well-known, meaning that diet-based inferences about differential host susceptibility may be overly speculative. Other possible mechanisms include the inability of Atlantic parasites to recognize and/or attach to Pacific lionfish, and/or lionfish being well defended mechanically, immunologically, or otherwise against Atlantic parasites. It is also possible that lionfish are so well fed and have such high fat stores (Morris and Whitfield 2009) in their invaded range that they can energetically afford to invest heavily in their immune system, thus warding off parasites. To assess the mechanism(s) by which lionfish evade parasites, future studies should investigate and compare the immune profiles of lionfish in their native Pacific and introduced Atlantic ranges.

The parasites we found on lionfish in The Bahamas and the Caymans were identified to genus or species, and included in a descriptive parasitological study (Ramos-Ascherl et al. 2015). Ramos-Ascherl et al. (2015) was the first descriptive account of parasite communities infecting lionfish at multiple regions within the introduced range, yet this study did not make ecological comparisons with lionfish in the Pacific, or with non-lionfish in either ocean. There is neither evidence from our study, nor from other descriptive studies of lionfish parasites to suggest that lionfish brought parasites with them from the Pacific (Ruiz-Carus et al. 2006; Bullard et al. 2011; Ramos-

Ascherl et al. 2015; Sellers et al. 2015). Furthermore, lionfish were likely introduced via the aquarium trade (Semmens et al. 2004), which most likely subjected captive fish to chemical products to remove external parasites. Even in the absence of rigid quarantine protocols, more resistant host genotypes may have been selected (Colautti et al. 2004).

Parasites are ubiquitous and abundant members of biological communities that often affect their host's behavior, growth, fecundity, and mortality (Adlard and Lester 1994; Finley and Forrester 2003; Forrester and Finley 2006; Grutter et al. 2011; Binning et al. 2012). Can release from parasites and their deleterious effects therefore explain the recent success of invasive lionfish? Overall, the relative presence of parasites in the native range (didymozoans in the Marianas and copepods in the Philippines) versus relative absence of parasites in the invaded range is consistent with patterns of enemy release from parasites, a pattern common among other introduced species (Torchin et al. 2003). In fact, invasive lionfish are larger, grow faster, and exist in denser populations than native lionfish (Green and Côté 2009; Kulbicki et al. 2012; Pusack et al. 2016), which are all demographic signs of enemy release. The relatively low infection rates of lionfish in the Atlantic indicate that parasites are not and have not been likely sources of biotic resistance to the lionfish invasion. In fact, given the widespread success of invasive lionfish and the relative lack of natural enemies (including predators, competitors, and parasites) in the Atlantic, there appears to be no or very little biotic resistance to lionfish at present. Another explanation for the relative success of invasive lionfish may be prey naïveté, whereby the exotic predator experiences an advantage over native species due to its unique appearance and hunting mode (Cox and Lima 2006). However, lionfish consume prey at similar rates in the invasive and native ranges (Cure et al. 2012), and evidence of naïveté among invasive lionfish's prey is mixed (Marsh-Hunkin et al. 2013; Lönnstedt and McCormick 2013; Kindinger 2014; Black et al. 2014).

To definitively test whether enemy release has contributed to the success of invasive lionfish, future studies should sample parasite communities of lionfish across a broader geographic range, especially in the native range where relatively little is known about their interactions with other species, including other possible "enemies" (i.e., predators and competitors). Broader geographic studies would be especially fruitful given the high degree of variability in parasite type and abundance found at different regions, a pattern we witnessed when comparing the Marianas and the Philippines, both in the Pacific. Furthermore, future studies should explicitly test the effect of common lionfish parasites on their fitness in the Pacific, and how the loss of these parasites in the Atlantic may lead to changes in how energy is allocated to invasive fish growth, movement, reproduction, and immunity. In fact, surprisingly few studies have quantified the effect of parasite loss on host fitness and invasion success (Colautti et al. 2004; Blakeslee et al. 2013), despite the importance of these mechanisms to the phenomenon of enemy release.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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