

Low susceptibility of invasive Indo-Pacific lionfish *Pterois volitans* to ectoparasitic *Neobenedenia* in the eastern Caribbean

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Abstract Since its introduction to the tropical western Atlantic in the 1980s, the Indo-Pacific lionfish, *Pterois volitans*, has become one of the most devastating species invasions in the marine environment. It remains unclear whether release from parasitism has played a role in its success. The capsalid monogenean *Neobenedenia pargueraensis* is a common Caribbean ectoparasite with a broad host range that, in high numbers, can kill hosts. However, previous research found that lionfish collected from the Bahamas, Puerto Rico and the US Virgin Islands were not parasitized by *N. pargueraensis*. Possible explanations for this are that 1) lionfish do not occupy habitat where infective stages are present; and 2) lionfish are not susceptible to this parasite. The goal of this project was to determine the susceptibility of lionfish to *N. pargueraensis*. Experiments were conducted in spring and summer of 2012 and 2013 on St. Thomas, US Virgin Islands. Lionfish ($n=24$) and control blue tang, *Acanthurus coeruleus* ($n=19$) were caught from nearby shallow reefs, treated to remove pre-existing ectoparasites, and exposed to high concentrations of *N. pargueraensis* for 14 days. Despite exposure to high concentrations of parasites, only one of 24 lionfish was parasitized, and

only one individual parasite was found on the infected fish. In contrast, all blue tang were infected with an average of ten parasites per fish. These results suggest that invasive lionfish are not highly susceptible to *N. pargueraensis*, which may contribute to their successful invasion of the Caribbean.

Keywords Invasive species · Monogenea · Capsalid · Parasite · Scorpaenidae

Introduction

Because of their effects on host population dynamics, parasites may influence the dynamics and structure of ecological communities (Hatcher and Dunn 2011). One aspect of host-parasite ecology that has recently received considerable attention is the extent to which parasite infestation of hosts can both influence and be influenced by the spread of invasive species (Torchin and Mitchell 2004; Hatcher and Dunn 2011). Parasites can impact the success of introduced species in multiple ways. The effects of host-specialists are easiest to predict and have received the most attention as components of “enemy release” (Cornell and Hawkins 1993; Kennedy and Bush 1994): introduced species likely leave behind specialist parasites from their native range and are likely avoided, at least initially, by specialist parasites in the introduced range due to a lack of shared evolutionary history. The dynamics involving introduced hosts and generalist parasites are less predictable. Exotic hosts may introduce generalist parasites to which

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they have high resistance but to which native species have limited or no resistance (Tompkins et al. 2003; Garner et al. 2006). Invasive species may also be more or less susceptible to generalist parasites in the introduced range, influencing the dynamics between hosts and parasites as well as the transmission of any disease-causing organisms transmitted by generalist parasites (Telfer et al. 2005; Miller et al. 2008; Kelly et al. 2009; Pisanu et al. 2010; Gendron et al. 2011; Poulin et al. 2011).

While various species of marine fishes have been introduced by human activities to new habitats worldwide, our understanding of the role of parasites in these invasions lags far behind freshwater systems (Vignon and Sasal 2009). One marine fish in particular, the Indo-Pacific lionfish, *Pterois volitans*, was listed in a recent review as one of the top 15 global conservation issues (Sutherland et al. 2010). Since their accidental or intentional release from aquaria off the coast of Florida in the mid-1980s, lionfish have undergone a population explosion and now range throughout the western tropical and subtropical Atlantic, Caribbean, and Gulf of Mexico (Whitfield et al. 2002; Schofield 2010). The invasion has had a significant effect on native coral-reef ecosystems, primarily via predation of native species (Morris and Akins 2009; Cure et al. 2012), causing considerable reductions in the recruitment and abundance of reef fishes (Albins and Hixon 2008; Lesser and Slattery 2011; Green et al. 2012) and subsequently, negatively affecting native piscivorous predators (Albins 2013). Greater local density (>390 fish/ha vs. 6 fish/ha) and maximum size (45 cm total length TL vs 38 cm TL) of lionfish in the invaded Atlantic relative to their native Pacific range (Green and Côté 2009; Kulbicki et al. 2012) suggests some level of ecological release from natural control mechanisms, including possibly parasitism (Berry et al. 1982; Morris Jr and Whitfield 2009; Kulbicki et al. 2012).

While most monogeneans infect a narrow range of hosts, the capsalid monogenean *Neobenedenia melleni* (MacCallum 1927) appears to infect a broad and lengthy list of marine reef fishes (Whittington and Horton 1996; Bullard et al. 2000). It is possible that *N. melleni* represents a complex of monogenean species (Whittington 2004), which would account for the expansive range and morphologic variation reported. *N. melleni* has been documented to infect captive and wild fish in the Caribbean Sea, Western Atlantic Ocean, Eastern and Mid-Pacific Ocean, Red Sea (Whittington and Horton

1996) and Australia (Deveney et al. 2001). However, the Caribbean appears to be the area of focus for this “species” (Whittington and Horton 1996; Bullard et al. 2000; Kohn et al. 2006), where it is the only noted species of *Neobenedenia* and is thought to be *N. paragueraensis* (Dyer et al. 1992). Thus far, this parasite has been found on 59 Caribbean/tropical western Atlantic fish species, from 22 families (Kohn et al. 2006; Carvalho and Luque 2009; Sikkil et al. 2009; Roumbedakis et al. 2013; Silva et al. 2014; McCammon et al. submitted), and has even been shown to infest seawater-reared tilapia (Cowell et al. 1993).

Most studies of parasites infecting lionfish in their introduced range have been opportunistic, and no published studies have reported *Neobenedenia* on wild-caught lionfish. Recently, Ramos-Ascherl et al. (2015) conducted a 4-year study of lionfish parasites that included 326 specimens from among three different island groups in the northeast Caribbean region. Although they found 27 parasite taxa, including three species of monogenean, no *Neobenedenia* were found. Given that specimens were collected from areas in which *N. paragueraensis* is known to occur, these findings suggest that invasive lionfish are not highly susceptible to Caribbean *Neobenedenia*. However, we cannot rule out the alternative possibility that lionfish tend to occupy microhabitats with low numbers of infective stages. Thus, the goal of this experimental study was to test the hypothesis that invasive lionfish are not highly susceptible to generalist *N. paragueraensis* in the Caribbean by exposing them to high concentrations of infective stages in standardized environments.

Materials and methods

Study site

Fish used in the experiment were collected from Brewers Bay, St. Thomas (18°20'26"N, 64°58'42"W), and Great Lameshur Bay, St. John US Virgin Islands (18°18'53"N, 64°43'22"W). The experiment was conducted in the overflow trough that surrounds the circular Coral Reef Exhibit (CRE) at Coral World Ocean Park, St. Thomas, U.S. Virgin Islands during May–July 2012 and 2013. This facility was used because it receives unfiltered and untreated seawater from the ocean and contains high levels of *N. paragueraensis* that infect multiple fish species in the exhibit (D. Nemeth pers. comm).

The trough is 45 cm wide×70 cm deep and has been used in previous experiments on *Neobenedenia* infection by our research team (McCammon et al. 2010).

Subjects

A total of 24 lionfish were used in the experiment, eight in 2012 and 16 in 2013. A total of 19 blue tang, *Acanthurus coeruleus*, 14 in 2012 and five in 2013, were used to confirm the presence of *N. pargueraensis* in the trough. This native fish species was chosen because it is known to be infested by *N. pargueraensis* both in the wild and in our experimental enclosures (Sikkel et al. 2009; McCammon et al. 2010). All fish were collected by divers and snorkelers and held in 3000-L tanks for 24 h before being transported to Coral World in aerated 19-L buckets.

Experimental protocol

Plastic coated hardware cloth was used to partition enclosures within the trough to facilitate maintenance and retrieval of fish. Lionfish were placed individually in alternating 45 cm×91 cm sections with empty sections partitioning lionfish enclosures to ensure lionfish did not interact with one-another, as required by permit. Because they tend to swim in groups, five to seven blue tang were placed together in larger 45 cm×152 cm enclosures.

Upon arrival at Coral World, each fish was dipped in two liters of dechlorinated fresh water for 5 min and gently rubbed with small paintbrushes to dislodge any preexisting parasites. This method is widely used as a prophylactic against and treatment for parasite infections of captive marine fishes and is particularly effective for killing soft-bodied external parasites such as monogeneans that quickly absorb water through osmosis, die, and dislodge from the host (Thoney and Hargis 1991; Stoskopf 1993; Noga 1996). It has also been used in other recent studies on coral reef fishes to remove and quantify monogeneans and other ectoparasites (e.g., Becker and Grutter 2004), including blue tang (Sikkel et al. 2009; McCammon et al. 2010) and lionfish (Ramos-Ascherl et al. 2015). *Neobenedenia* immersed in fresh water become opaque and thus easy to see and remove from dark-bodied species like blue tang (Fig. 1). Following this procedure, fish were placed in the experimental enclosures for 14 days. All fish were fed squid meal and algal gelatin daily by Coral World staff. To



Fig. 1 Blue tang removed from experimental enclosure after 1 min in fresh water. Note the opaque “coloration” of the *Neobenedenia* is the result of lethal osmotic water uptake. While all blue tang were infected with multiple *Neobenedenia* post-removal, only a single *Neobenedenia* was found on a single lionfish after 2 weeks’ exposure to infective stages

increase our sample size for studies on ectoparasites of wild-caught lionfish, filtrate from lionfish dip was later examined under a dissecting scope.

At the end of each trial, individual fish were removed from their enclosure and placed in their own respective buckets of seawater for transport to the processing station below the trough. Fish were then subject to freshwater dip and brushing as described above to dislodge monogeneans. All fish were measured for fork length and lionfish were humanely sacrificed, per permit requirements, by severing the head. Blue tang were placed in a “recovery bucket” of aerated seawater with Stresscoat® and later released to the original capture location. All contents from the freshwater dip was poured through 55 µm mesh to collect any monogeneans that were dislodged during the cleaning process. This filtrate was later examined under a stereomicroscope at both 10 and 40× magnification. Where monogeneans were present, they were counted and preserved in 70 % ethanol.

Results

While some *N. pargueraensis* were visible on and removed from blue tang during freshwater dipping prior to the experiment, none were seen on lionfish and no ectoparasites were later found upon examination of the filtrate. At the time of retrieval from the enclosure, all 19 blue tang were infected with an average of 9.74 (sd=

3.45, range=1–28) *Neobenedenia*. In contrast, only a single *N. pargueraensis* was found among the 24 lionfish (Table 1).

Discussion

In a survey of 82 species of native Caribbean reef fish, we found *N. pargueraensis* on 33 species from 17 families (A. McCammon and P. Sikkell unpublished data), increasing the number of known hosts for this parasite from 39 to 59. Moreover, among the 19 species for which the total sample size was 15 or greater, *N. pargueraensis* was found in 14 (74 %), and in 78 % of those with sample sizes of at least 25. Infections were found in ecologically similar species such as serranid groupers, holocentrid squirrelfishes, haemulid grunts, lutjanid snappers, and synodontid lizard fishes. Thus, given the nearly 400 lionfish examined by Ramos-Ascherl et al. (2015), and the 24 collected during this study from the same sites as the native fish collected in our previous study, we fully expected to find *N. pargueraensis* on at least some wild-caught lionfish specimens. However, this was not the case.

In our experimental macrocosm, all blue tang were infected, with an average of approximately 10 monogeneans, after a 2-week period, confirming the continued presence of high concentrations of infective stages. By comparison, we found infections in 72 % of blue tang collected among 4 Virgin Islands' sites, with an average of 7.9 *Neobenedenia* per infected host. Thus, in spite of the fact that infection levels for our blue tang standard were approximately 1.5 times higher in our experimental macrocosm compared to nearby sites where they and individual lionfish were collected, only a single *Neobenedenia* was found among the 24 experimental lionfish after the 2-week period. These results suggest

that lack of exposure to infective stages does not explain the absence of this apparent generalist ectoparasite among our wild-caught lionfish. Given that exposure to freshwater kills and removes soft-bodied monogeneans (and has been used for this purpose for over two decades), all fish used in the experiment should have been free of preexisting *N. pargueraensis*. It is thus highly unlikely that preexisting *N. pargueraensis* on wild-caught blue tang account for their presence following removal from the experimental macrocosm.

Although apparent generalist parasites such as *N. pargueraensis* infect a wide range of hosts, hosts vary in susceptibility. Such variation can be attributable to some combination of parasite preference/host "attractiveness" and host resistance. Monogeneans appear to use chemical cues to locate hosts (Kearn 1967; Whittington 1997) and attach to hosts using hooks and suction disks. Because blue tang were not placed directly adjacent to lionfish, our results cannot be attributed to simple preference between two available hosts. These results also cannot be attributed to the fact that lionfish are not normal hosts, as *Neobenedenia* infest and even kill other non-native hosts such as captive African tilapia (Cowell et al. 1993; EH Williams pers. comm.) and farmed pelagic fish species that would not otherwise come in contact with infective stages (Kerber et al. 2011). However, lionfish may differ from other host species in the quality or quantity of molecules they produce that are attractive to *Neobenedenia*. Host resistance can be influenced by the secretion of excess mucosal epithelium (Harris et al. 1998), shedding of scales (Helfman et al. 2009), or initiation of coagulation in response to ectoparasite attachment (Horton and Okamura 2003). Indeed, there is some evidence that lionfish may "slough" their skin in a manner similar to squamate reptiles (Fishelson 1973), which could dislodge ectoparasites. Skin toxins may also affect the attachment of ectoparasites on fishes (Munday et al.

Table 1 *Neobenedenia* infection rates following 14 days exposure in experimental macrocosm

Host	Year	Sample size	Forklength (cm)	Mean (\pm SD)	Prevalence % (CI%)	Mean intensity (\pm SD)	Range
<i>Acanthurus coeruleus</i>	Combined	19	14.5 (2.5)		100 (3.7)	9.7 (2.1)	1–28
	2013	5	14.8 (4.5)		100 (9.6)	9.2 (1.4)	1–28
	2012	14	14.4 (2.8)		100 (4.6)	11.2 (4.2)	2–22
<i>Pterois volitans</i>	Combined	24	21.2 (1.5)		4 (0.1)	1	1
	2013	16	21.9 (3.1)		12.5 (0.3)	1	1
	2012	8	21.5 (5.2)		0	0	0

2003). Lionfish do possess venom in the grooves of their dorsal, pelvic, and anal spines that likely deter predation by larger fishes (Halstead et al. 1955; Bernadsky and Goulet 1991). While the venom itself is not located on the skin or in the blood, the venom precursor is systemic (Wilcox and Hixon 2015). It would be worthwhile to determine whether this chemical deters ectoparasites.

Other recent studies suggest that lionfish may be somewhat resistant to certain ectoparasites in both their native and introduced ranges. Collections of 138 lionfish from Guam and the Philippines revealed no capsalid monogeneans (P.C. Sikkel, unpub. data), although *Benedenia epinepheli* have been reported from captive lionfish in Japan (Ogawa et al. 1995). In a recent experimental field study, Sikkel et al. (2014) found that while lionfish were susceptible to generalist gnathiid isopods, they were much less so than other species, in spite of their large surface area. The mechanisms underlying this apparent resistance deserve further study.

Most previous studies that have examined the ectoparasites infecting introduced fishes (including monogeneans) have been solely observational (e.g., Shakman et al. 2009; Vignon et al. 2009; Gendron et al. 2011), and therefore cannot separate the relative contributions of exposure and susceptibility. Considerable evidence suggests that introduced species tend to arrive in their new environments free from their natural parasites (Torchin et al. 2003; Prenter et al. 2004; Torchin and Mitchell 2004), which may enable them to more effectively establish and spread in their introduced habitat. In contrast, more generalist parasites might be able to exploit invasive species (Bauer 1991), which could reduce the fitness of infected individuals and thereby negatively affect the invasive species population (Mouritsen and Poulin 2002). Our results demonstrate that lionfish are not highly susceptible to infestation by one of the most common and damaging generalist ectoparasites in the Caribbean region. This, combined with their low susceptibility to generalist gnathiid isopods, suggests that these ectoparasites either are not highly attracted to or cannot effectively exploit lionfish as a host and therefore cannot be expected to negatively affect populations of invasive lionfish.

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