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Effects of host injury on susceptibility of marine reef fishes to ectoparasitic gnathiid isopods

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Abstracts The importance of the role that parasites play in ecological communities is becoming increasingly apparent. However much about their impact on hosts and thus populations and communities remains poorly understood. A common observation in wild populations is high variation in levels of parasite infestation among hosts. While high variation could be due to chance encounter, there is increasing evidence to suggest that such patterns are due to a combination of environmental, host, and parasite factors. In order to examine the role of host condition on parasite infection, rates of *Gnathia marleyi* infestation were compared between experimentally injured and uninjured fish hosts. Experimental injuries were similar to the minor wounds commonly observed in nature. The presence of the injury significantly increased the probability of infestation by gnathiids. However, the level of infestation (i.e., total number of gnathiid parasites) for individual hosts, appeared to be unaffected by the treatment. The results from this study indicate that injuries obtained by fish in nature may carry the additional cost of increased parasite burden along with the costs typically associated with physical injury. These results suggest that host condition may be an important factor in determining the likelihood of infestation by a common coral reef fish ectoparasite, *G. marleyi*.

Keywords Marine symbiosis · Host condition · Ectoparasite · Gnathiidae · Coral reefs

1 Introduction

Parasitism is the most common consumer lifestyle among organisms (Lafferty et al. 2008) and biological interaction in ecological communities (Hudson et al. 2006). Parasites can directly influence host physiology, growth rates (Finley and Forrester 2003; Hatcher and Dunn 2011), and behavior (Barber et al. 2000; Lafferty and Kuris 2002; Sato et al. 2012), and can indirectly affect hosts through transmission of disease-causing microorganisms (Davies and Johnston 2000; Davies and Smit 2001; Sukhdeo and Hernandez 2005). Consequently, parasites can impact host populations (Finley and Forrester 2003; Hudson et al. 2006) and thus community-level interactions and processes (Wood et al. 2007; Hatcher and Dunn 2011). Parasites have been shown to have significant impacts on trophic dynamics, and even the potential to dominate food web links, within their respective ecological communities (Panek 2005; Lafferty et al. 2006). Despite the abundance and ecological significance of parasites, parasite ecology remains a relatively understudied aspect of ecology (Marcogliese and Cone 1997; Wood et al. 2007; Johnson et al. 2010). This is particularly true in high biodiversity marine systems, such as coral reefs (Hatcher and Dunn 2011) where parasitic organisms may comprise over half of all species (Rohde 2002).

A common observation in studies on host-parasite interactions is the high variance in parasite loads among potential hosts, with a small percentage of individuals harboring many parasites while many others have few if any (Rózsa et al. 2000). Thus, an understanding of the effects of parasites at individual, population, and community levels requires an

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understanding of the factors that influence host susceptibility. However, these factors remain poorly understood for most host-parasite interactions. While parasite burden on hosts is often subject to environmental factors that influence the abundance of parasites in host environments (Rohde et al. 1998), hosts also exhibit a wide range of behavioral and physiological defensive measures (e.g., parasite avoidance and immunological response) that can decrease their susceptibility to parasitism. These defensive characteristics and behaviors may be energetically costly (Sheldon and Verhulst 1996), and thus depend on other aspects of host condition.

Parasites typically fall under one of two broad categories with respect to their site of attachment; ectoparasites live on external surfaces of hosts, and endoparasites reside within the interior cavities or in the viscera of a host. The former includes hematophagous (blood-feeding) parasites such as fleas, ticks and mosquitos that may also be considered micropredators because they are highly mobile and only temporarily infect their hosts (Kuris and Lafferty 2000; Lafferty and Kuris 2002). Gnathiid isopods are a marine equivalent to blood-feeding ticks, fleas and mosquitoes. They have a wide biogeographic distribution and diverse habitat affinities, from polar regions to the equator (Klitgaard 1997; Smit and Davies 2004; Tanaka 2007) and from shallow water coral reefs (Farquharson et al. 2012) to the deep-water abyss (Quattrini and Demopoulos 2016). However, they are perhaps best known in tropical reef communities where they commonly infest reef fishes (Grutter 1994; Arnal et al. 2001; Ferreira et al. 2009; Coile and Sikkel 2013) and are the primary food of cleaner fishes (Grutter 1996; Grutter and Poulin 1998; Arnal and Côté 2000; Whiteman and Côté 2002). Similar to their terrestrial counterparts, gnathiids only temporarily infest their hosts while feeding, disassociating and returning to the substrate between feedings, therefore qualifying as "micropredators" (Lafferty and Kuris 2002). The gnathiid life cycle consists of a parasitic larval phase (with 6 sub stages) followed by a non-parasitic, non-feeding adult stage (see Fig. 7–8 in Smit and Davies 2004). Juvenile gnathiids feed three separate times on three separate hosts, residing in the benthos between feedings. Unfed juvenile gnathiids are referred to as zuphea (Z's), while blood-engorged juveniles are referred to as pranizae (P's). The amount of time spent attached and feeding on hosts appears to vary among different species of gnathiids (hours to days) as does the amount of time juveniles spend in the benthos between feedings (days to weeks, depending on temperature; Smit and Davies 2004). After the third and final feeding stage, the pranizae (P3) return to the benthos and undergo a final metamorphosis into adult males or females. Females produce only a single brood of about 30 juveniles (Coile et al. 2014) and then die.

Gnathiids can impact hosts in multiple ways, including survival rates, stress levels, and overall host health. For example, heavy gnathiid loads can directly kill adult- fishes, presumably through blood loss (Hayes et al. 2011), and even a single gnathiid can kill a recently-settled larval fish (Artim et al. 2015). Gnathiids can also increase corticosteroid stress hormones (Triki et al. 2016), reduce host hematocrit (Jones and Grutter 2005), reduce host immune function (Manship et al. 2011), and facilitate infection through mechanical damage (González et al. 2004; Marino et al. 2004). Finally, gnathiids are suspected of transmitting blood parasites (Davies and Smit 2001; Smit and Davies 2004).

Growing appreciation for the roles that parasites play in marine ecosystems necessitates a better understanding of their patterns of host exploitation. Gnathiids are considered host generalists. For example *Gnathia marleyi* in the Caribbean has been found to infest over 20 different species of bony fish, including invasive Indo-Pacific lionfish (Farquharson et al. 2012; Coile and Sikkel 2013; Sikkel et al. 2014) and *G. auriomaculos* from the Great Barrier Reef has been shown to infest at least 18 species of bony fish (Ferreira et al. 2009). Ota et al. (2012) reported 25 different shark hosts for *G. trimaculata* off Japan. However, host species may vary in susceptibility (Jones et al. 2007; Coile and Sikkel 2013; Sikkel et al. 2014; Quattrini and Demopoulos 2016). Moreover, a common observation in studies of both wild-caught and caged host fishes is that, within species, some individuals are infested with large numbers of gnathiids (as many as 400), while others, in the same vicinity, have few or none (Sikkel et al. 2006, 2011, 2017). The influence of host behavior/physiology, parasite behavior/physiology, and environmental factors on observed infestation variations is poorly understood. Thus, a comprehensive assessment of the impacts that gnathiids have on their respective ecological communities requires an understanding of the forces that drive host selection and susceptibility. While host species, location, and time have all been determined to be significant predictors of gnathiid parasite loads for host fish (Sikkel et al. 2006; Nagel and Grutter 2007; Coile and Sikkel 2013), the factors that influence susceptibility of individual hosts remain poorly understood.

A common observation on coral reefs is the appearance of minor to moderate tissue injuries among fishes (Foster 1985), possibly as the result of escaped predation attempts and aggression among territorial species. It has also been suggested that attacks from micropredators cause significant tissue damage to host fish (Stepien and Brusca 1985; Marino et al. 2004). Regardless of their source, such injuries may have positive or negative effects on host susceptibility to parasitism. For example, given that gnathiids appear to rely heavily on olfactory cues to find hosts (Nagel and Grutter 2007; Sikkel et al. 2011) injured fish may be easier to detect (Stepien and Brusca 1985) and may therefore attract more gnathiids. Alternatively, the immune/clotting response to an injury may make hosts less attractive and more difficult to exploit as gnathiids likely depend on inhibited coagulation of host fish blood when feeding. Both trypsin inhibitors and anticoagulants have been identified in the saliva of juvenile gnathiids and may serve to suppress host immune functions such as blood coagulation and inflammatory responses (Manship et al. 2012). Thus, gnathiids may rely heavily on suppression of host immune system when feeding.

The purpose of this study was to determine whether injury influences susceptibility of host fishes to infestation by gnathiid isopods. We conducted an experiment that compared the probability of gnathiid isopod infestation between experimentally injured and uninjured hosts for three species of Caribbean coral reef fish. We hypothesized that injured hosts will demonstrate an increased susceptibility to infestation by gnathiid isopods and predicted that they would have a higher probability of infestation. If, however, the experimental injury does not increase susceptibility to infestation or has an inhibitory effect, then injured hosts would have equal or lower levels of infestation compared to uninjured hosts.

2 Methods

2.1 Field experiments

This study was conducted during the summer months (June–August) of 2009 and 2013 at four sites within the Lameshur Bay area of the Virgin Islands National Park, USVI (18° 19′ N, 65° 44′ W). Study sites were shallow (2–4 m depth) patch reefs located within 500 m of each other and where the gnathiid isopod, *G. marleyi* is present in high densities (Sikkel et al. 2006, 2009, 2011; Farquharson et al. 2012). Three species of reef fish hosts were selected for this study; French grunts (*Haemulon flavolineatum:* Haemulidae, FG), Longfin damselfish (*Stegastes diencaeus*: Pomacentridae, LFD), and Brown chromis (*Chromis multilineata*: Pomacentridae, BC). These hosts were selected based on their susceptibility to *G. marleyi* (Coile and Sikkel 2013) and abundance at the study site. Hosts were collected by free divers or scuba divers using modified cast nets and kept in 1500 L holding tanks with running seawater for 24–48 h.

A total of 30 trials were conducted at the three sites; West Lameshur Bay (WLB, *N* = 17), East Lameshur Bay (ELB, *N* = 8), and Saltpond Bay (SPB, *N* = 3) (Fig. 1). For each experimental trial, host fish were separated into size-matched conspecific pairs. Within each pair, individual fish were randomly assigned to either the injured or control treatments. The "injury" was created by removing a 3 × 3 patch of scales (9 total) from the rear dorsal area of the body, using a scissor blade. The size of injuries was based on observations of minor injuries of approximately the same size among fish we observed at our study sites. By standardizing the number of scales removed per fish, we were able to control for variations in body size within species of host (scale size differs among species). Because the entire process required approximately 20 s to complete, no anesthesia was used. Scale loss has been associated with naturally occurring physical trauma (Rottmann et al. 1992; Bereiter-Hahn and Zylberberg 1993; Deveney et al. 2001) and anthropogenic interactions, mainly catch and release fishing (Butcher et al. 2009; Davis 2002). Our method of injuring the host fish is based on the approach used to collect scale tissue samples of captive French grunts, and all procedures performed on these animals were in accordance with the ethical standards of Arkansas State University. Small injuries such as these have been commonly observed among coral reef fishes and appear to be non-fatal, possibly due to the role that cleaner organisms play in preventing wound infection (Foster 1985). While larger wounds are sometimes observed, they are less common than these smaller abrasive injuries (Foster 1985). Additionally, laboratory studies on the effect of scale removal from fish indicate that this is an effective way to experimentally injure fish (Bereiter-Hahn and Zylberberg 1993).

Gnathiid infestation was quantified using cylindrical cages constructed from black plastic mesh (1.5 cm mesh width) that ranged in length from 50 to 100 cm depending upon fish size, as described in previous studies (Sikkel et al. 2006, 2017; Coile and Sikkel 2013). Cages (10 to 30 per experimental trial, depending on number of host fish that could be caught that day) were deployed at dusk in mixed reef and sand habitat. Fish from each size-matched pair were placed 0.25 m from each other, and at least 2 m from other replicate treatment pairs. This ensured that injured and control fish were subject to similar populations of active gnathiids. Infestation of gnathiids on host fish at our study site peaks near midnight (22:30–23:30) and again at dawn (05:00–06:00) (Sikkel et al. 2006, 2009) and cages were retrieved from the reefs during these peak activity times. Retrieval was conducted by slowly swimming the cages up from the reef, being careful not to disturb the host fish and/or feeding gnathiids, and then transferring the cages, with fish inside, into individual 19 L buckets (standard hardware store buckets) with seawater. Fish remained in their buckets until all attached gnathiids finished feeding and dislodged, and were then transferred back to the holding tanks for recovery and eventual release. Data were excluded in cases where the host fish died while deployed or was lost (due to escape, removal by large predator or if cage with fish was lost).

Gnathiids were collected by sieving the contents of the buckets through 53 μm plankton mesh. The filtrate from each fish's bucket was examined under a dissecting scope and total number of gnathiids was recorded for each individual host fish.

2.2 Data analysis

Parasite abundance data were analyzed using the R Core Team (2017) statistical program. Data were initially fitted to a

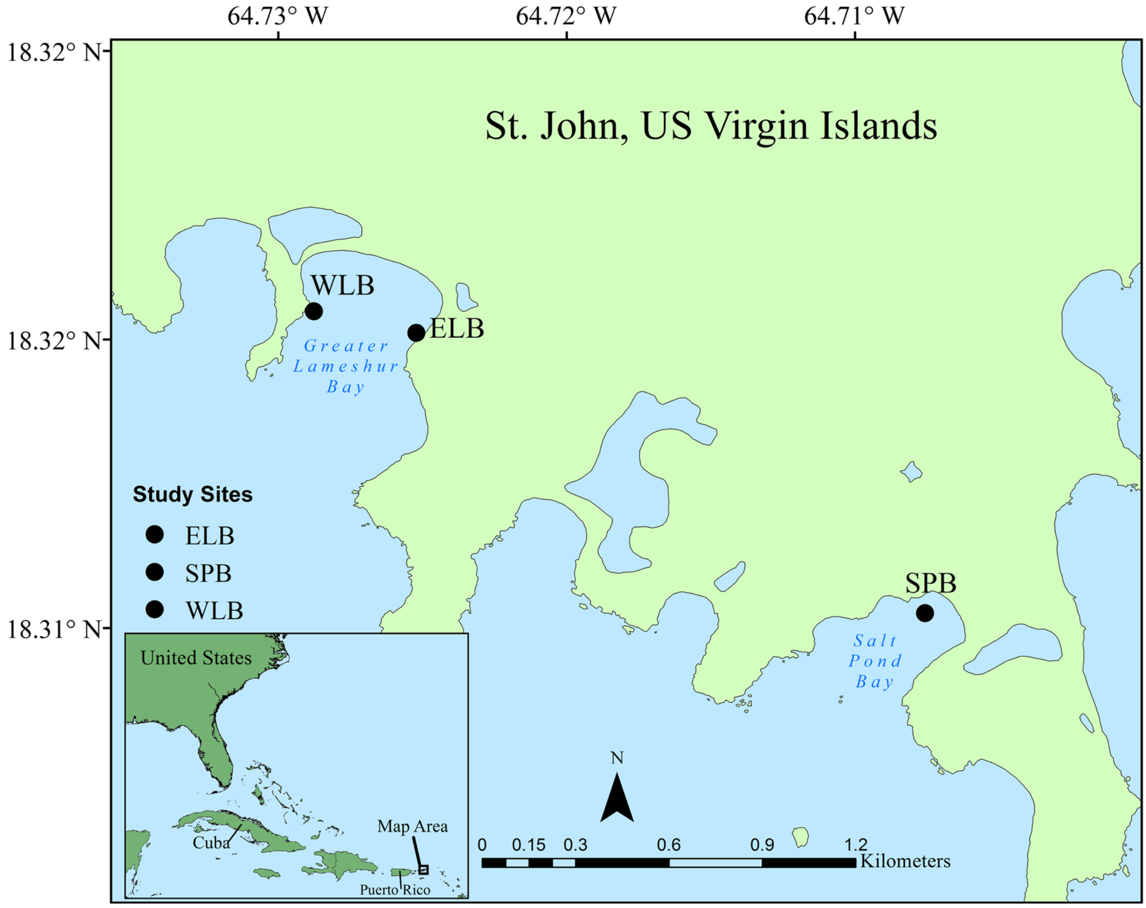

Fig. 1 Map of study sites within the Greater Lameshur Bay area, St. John, United States Virgin Islands. Sampling occurred at the following sites: West Lameshur Bay (WLB), East Lameshur Bay (ELB), and Saltpond Bay (SPB)

Poisson generalized linear model, but due to a high degree of overdispersion in the initial model (residual deviance of 10,943 on 300 degrees of freedom), a negative binomial distribution was instead used (residual deviance of 286 on 300 degrees of freedom). The negative binomial distribution was used in a zero-inflated model (ZINB) to account for the high occurrence of zeros in the parasite count data (147 out of 300 total observations, see Table 1 and Fig. 2). This decision was supported by the results of a likelihood ratio test ($p < 0.05$) and results of a Vuong test (Zeileis et al. 2008) of the non-nested zero-inflated and standard negative binomial models ($Z = 2.693$, $p = 0.004$). The final zero-inflated model included host injury status as the primary predictor with host species, location, and collection time as additive predictors. Interaction effects of host species and location on host injury status were tested for using the Wald's test of nested models, the results of which indicated that there were no significant interactions ($X^2 = 8.20$, $p = 0.08$ and $X^2 = 0.55$, $p = 0.76$ respectively). Confidence intervals for the coefficients were obtained using the likelihood profiling method on the final model selected.

3 Results

Instances of zero parasite counts (i.e., no infestation) were higher for the uninjured hosts (Table 1, Fig. 2), indicating a greater likelihood that uninjured hosts would have no observable gnathiids. In the logistic aspect of the ZINB model, injury status was the only significant predictor of the probability of zero gnathiid counts for individual hosts. The coefficient for uninjured hosts was 1.29 ($p = 0.01$) with the baseline being injured hosts. The logistic portion of the model is estimating the probability of a zero count so the uninjured coefficient is interpreted as uninjured hosts having a higher probability than the injured hosts of having no parasites. Inverse logit transformation of the uninjured coefficient provided the odds ratio, which was estimated to be 0.78, indicating that the odds of having zero parasites increases by 0.78 for the uninjured hosts. On average, there was also a trend for injured fish to have higher parasite loads than uninjured hosts (see Table 1.). While the logistic portion of the model (i.e., presence/absence) indicated that the probability of parasitism by gnathiids was significantly higher when hosts were injured, the negative binomial portion of the ZINB model, failed to demonstrate

Table 1 Sample sizes, mean parasite count, calculated proportion of zero counts, and maximum parasite count for each treatment, host species (French grunt 'FG', Longfin damselfish 'LFD', Brown chromis 'BC'), sampling location (East Lameshur Bay 'ELB', Saltpond Bay 'SPB', West Lameshur Bay 'WLB'), and sampling time

Category		Sample Size	Mean Parasite Count	Proportion Zero Count	Max Parasite Count
Treatment	Injured	150	23	0.35	654
	Uninjured	150	13	0.54	184
Species	FG	56	61	0.09	654
	LFD	214	8	0.57	204
	BC	30	8	0.23	38
Location	ELB	130	30	0.28	19
	SPB	48	20	0.38	204
	WLB	122	6	0.63	654
Time	Dawn	222	22	0.39	654
	Night	78	6	0.60	67

any significant relationship between host injury status and the total number of parasites observed (i.e., parasite load) on infected hosts (Table 2, $p = 0.76$). Thus, statistically, injured hosts had a greater probability of becoming parasitized, but among parasitized hosts there was no difference in parasite abundance between the injured and uninjured hosts.

Host species, location, and time were significant predictors of observed gnathiid parasite loads (i.e. parasite counts per host) and were included in the model to improve model fit (see Table 2). The significance of host species on parasite load was demonstrated by a coefficient of 2.01 ($p < 0.01$) for French grunts relative to the baseline species used in the model (Brown chromis). Longfin damsels, on the other hand, did not provide a significant variation from the baseline ($p = 0.83$). Within the study sites, only the location coefficient SPB was significant, relative to the location baseline (ELB), with a coefficient value of 1.58 ($p = 0.01$). Significance of the time of collection (dawn vs. night) was demonstrated by the coefficient for night (−0.46. $p < 0.01$) indicating lower levels of parasitism during the night collections relative to the baseline (dawn).

4 Discussion

The results indicate that although the intensity of gnathiid isopod infestation among infested hosts was not affected by the presence of the experimental injury, the probability of gnathiid isopod infestation was higher for injured hosts, indicating a higher susceptibility to initial infestation by gnathiids. Many external parasites and micropredators rely at least in part on chemical cues from hosts. Mosquitos have been shown to be attracted to human sweat and carbon dioxide (Eiras and Jepson 1991) and hedgehog ticks are attracted to fecal odors unique to sick hosts (Bunnell et al. 2011). It is thus possible that the observed increase in the likelihood of infection for injured hosts is the result of injured hosts being easier to locate through olfactory cues than uninjured hosts. Detection of hosts by *G. marelyi*, as well as by other species of gnathiid isopods, appears to depend heavily on olfactory cues (Nagel et al. 2008; Sikkel et al. 2011). Other species of isopods that feed as scavengers are known to be attracted to chemicals released by injured fish (Stepien and Brusca 1985), so it is possible that the experimentally injured hosts in this study were releasing similar compounds allowing for better detection by nearby gnathiids.

The lack of statistical variation in observed number of parasites between the injured and uninjured hosts may be a function of the amount of damage caused when gnathiids feed. Initial infection of hosts by gnathiids may have facilitated further infection by causing hosts to release detectable chemical cues. For example, Stepien and Brusca (1985) observed micropredatory cirolanid isopods exploiting fish hosts only after an initial feeding by swarms of micropredatory ostracods. In laboratory studies, the cironalid isopods demonstrated a significant chemical attraction to injured hosts. When feeding on hosts, gnathiids use piercing mouth parts to penetrate the host flesh (Farquharson et al. 2012) and cause significant tissue damage to their hosts (Marino et al. 2004) with heavily infested hosts displaying bloody lesions (See Fig. 3). The damage caused by gnathiids feeding on hosts may be quite similar to the damage caused by the feeding ostracods in Stepien and Brusca (1985), and the physiological responses of the host to gnathiid micropredation may result in detectable chemical responses by the hosts, which in turn may facilitate further infestation by other gnathiids. This is supported by evidence that the presence of gnathiids causes an acute stress hormone response in fish (Triki et al. 2016). If initial gnathiid infestation results in a release of chemical cues that stimulate further gnathiid infections, then uninjured hosts, which are suffering from micropredation, may be releasing the same chemical attractants as the injured hosts. If this is the case, then among infected hosts, the difference between injured and uninjured hosts is negated by the damage caused by feeding gnathiids. However, removal of scales and initial infection by gnathiids

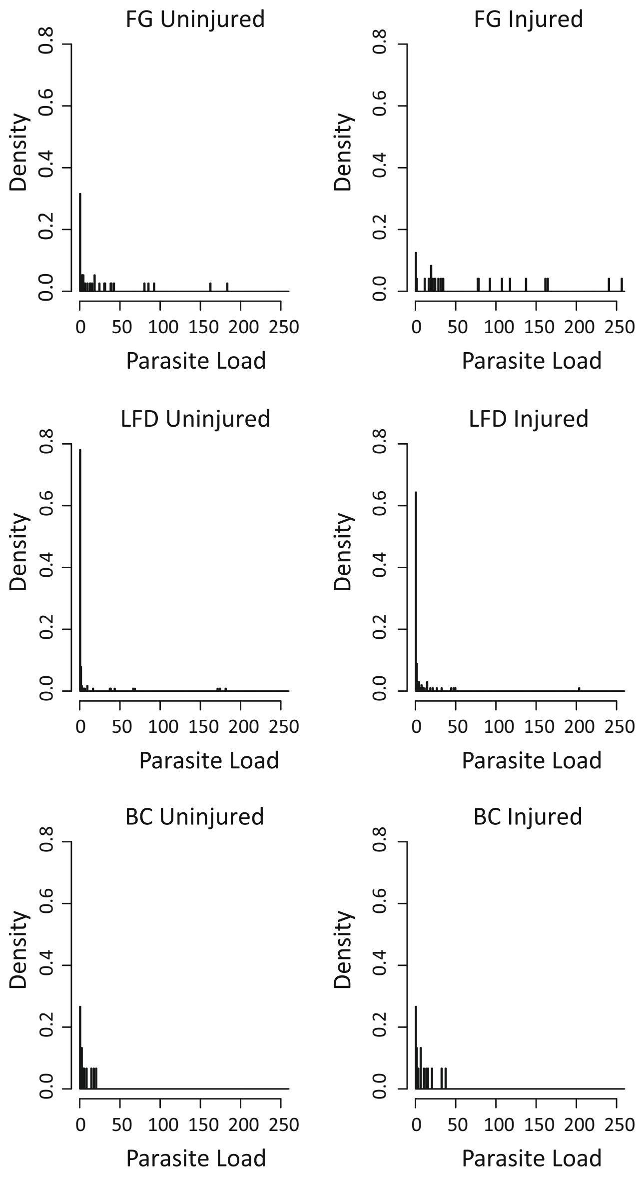

Fig. 2 Relative frequency distribution of parasite loads for each of French grunt (FG), Longfin damselfish (LFD) and Brown chromis (BC) for injured and uninjured treatments

may illicit different host physiological responses, which may then result in different patterns of susceptibility to gnathiids. The removal of scales in this study created a much larger wound physically than would be caused by a single gnathiid. It should also be noted that in laboratory studies with other teleost fish, experimental wounds began healing within minutes of scales being removed (Bereiter-Hahn and Zylberberg 1993). As such, it is possible that the removal of scales only caused a short-term physiological response from the host and that any chemical cues being produced by the host may have no longer been present by the time of deployment. Additionally, larger wounds than those that were experimentally inflicted on the hosts were observed among fish in the study sites and among other coral reef fish communities (Foster 1985) and it is possible that the size of injury may affect gnathiid infestation. Further investigation into the role that fish scales and the size of injuries play on host susceptibility to gnathiid micropredation is warranted.

In terrestrial host-parasite systems, variations in instances of parasitism, similar to what is observed with gnathiid isopods and their hosts, have been observed (Anderson and May 1978; Anderson and Gordon 1982) and it has been suggested that these variations might be due to varying levels of attractiveness of hosts to their parasites (Zuk and McKean 1996; Poulin 1998; Krasnov et al. 2004). It is possible that differences in host condition (specifically host nutritional and/or immune system status) play a significant role in how attractive a host is and greatly influence host exploitation by parasites (Keymer et al. 1983; Blanco et al. 1997; Dawson and Bortolotti 1997). However, what constitutes an "ideal host" in terms of host condition appears to vary between different host-parasite systems (Krasnov et al. 2005; Tschirren et al. 2007).

Injured and uninjured hosts may differ in physiological traits associated with immune system responses affecting their suitability as hosts for gnathiids. These traits include external barriers that influence the ability of the parasite to penetrate the host (Grutter et al. 2011), and internal controls, including blood coagulation, that affect the ability of the parasite or micropredator to obtain a meal (Horton and Okamura 2003). While injured hosts may have their external barriers compromised (e.g., scale removal), they may also increase production of blood coagulants in response to the injury, which would likely inhibit gnathiid feeding success. The role that host physiology plays in host susceptibility to, and its ability to defend against, gnathiids require further investigation. If different conditions of host physiology allow for easier infestation by gnathiids, those conditions may increase susceptibility.

There is evidence that gnathiids prefer to feed on hosts that provide certain, yet unquantified, nutritional advantages and increase overall parasite fitness. Gnathiids that fed on more susceptible host fishes produce larger offspring (Coile et al. 2014) and reach adult stages quicker (Nagel and Grutter 2007) than those that fed on non-preferred hosts. Selection of different fish hosts, and corresponding differences in offspring size and rate of maturity of gnathiids may be associated with the nutritional value of blood meals. There is, however, evidence that gnathiids may only be preferential opportunists, feeding on preferred hosts when available, but acting as generalists when suitable hosts may not be available (Jones et al. 2007). If host susceptibility to gnathiids correlates with nutritional advantages to the parasite, then this study suggests that injured hosts may offer some nutritional benefit over hosts that are in better condition.

The results of this study suggest the presence of host injury increases the probability of gnathiid micropredation, and, consequently, has the potential to alter ecological communities.

Table 2 Variables, coefficients, *p*-values, and calculated incident rates (IR, for log-link model) and odds ratios (OR, for logit link model), from the zero-inflated negative binomial (ZINB) model. The ZINB model is a two-part model with a negative binomial with log link model (estimates mean parasite count) and a zero-inflation binomial with logit link model (estimates probability of zero count). Species included in the "Species" variable were French grunt (FG), Longfin damselfish (LFD), and Brown chromis (BC). The variable location included the sampling locations: East Lameshur Bay (ELB), West Lameshur Bay (WLB) and Saltpond Bay (SPB). The variable Time included the two times at which gnathiid sampling took place; dawn (05:00–06:00) and night (22:30–23:30)

	Variable	Variable levels (Injury status, Species, Location, Time)	Coefficient	IR/OR	P
Count Model (negative binomial, log link)	Intercept	Injured, Brown chromis, ELB, Dawn	2.13	8.4	≤ 0.01
	Treatment: Uninjured	Uninjured, Brown chromis, ELB, Dawn	−0.09	0.92	0.76
	Species: FG	Injured, French grunt, ELB, Dawn	2.01	7.44	≤ 0.01
	Species: LFD	Injured, Longfin damsel, ELB, Dawn	−0.14	0.87	0.83
	Location: SPB	Injured, Brown chromis, SPB, Dawn	1.58	4.84	0.01
	Location: WLB	Injured, Brown chromis, WLB, Dawn	0.59	1.81	0.28
	Time: Night	Injured, Brown chromis, ELB, Night	−0.46	0.63	≤ 0.01
Zero-inflation model (binomial, logit link)	Intercept	Injured, Brown chromis, ELB, Dawn	−13.23	≤ 0.01	0.94
	Treatment: Uninjured	Uninjured, Brown chromis, ELB, Dawn	1.29	0.78	≤ 0.01
	Species: FG	Injured, French grunt, ELB, Dawn	−1.58	0.17	1.00
	Species: LFD	Injured, Longfin damsel, ELB, Dawn	12.45	0.99	0.95
	Location: SPB	Injured, Brown chromis, SPB, Dawn	−0.94	0.28	0.22
	Location: WLB	Injured, Brown chromis, WLB, Dawn	0.01	0.5	0.99
	Time: Night	Injured, Brown chromis, ELB, Night	0.18	0.54	0.71

When considered as predators (albeit micropredators), gnathiids and other similar ectoparasites appear to be significant forces in driving species richness of ecological communities (Raffel et al. 2008; Freestone et al. 2011). Studies that have examined the role that parasites play in food webs have provided evidence that they play an integral role in food web stability (Hudson et al. 2006; Wood et al. 2007), connectivity (Lafferty et al. 2006), energy dynamics (Marcogliese and Cone 1997; Johnson et al. 2010), and the transfer of vector borne pathogens (Johnson et al. 2010). As such, anthropogenic activity and other disturbances that affect the condition of host fish may have broad ecological implications. For example, loss of fish scales and tissue damage occurring during catch and release of fish (Butcher et al. 2009) may have long lasting ecological effects if those fish then experience micropredation, altering natural host-parasite dynamics.

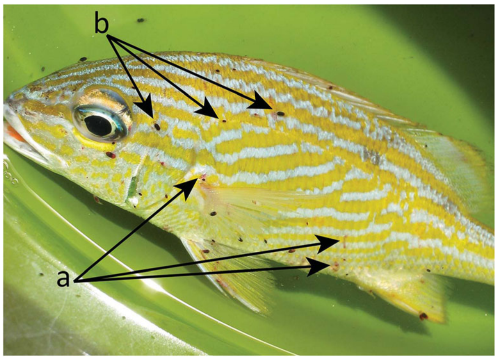

Fig. 3 Bloody lesions (**a**) characteristic of a fish heavily infested with gnathiid isopods (**b**). Photo credit Elizabeth Brill

Previous studies have shown that the costs of injury in reef fishes include increased susceptibility to infection and disruption of osmotic balance (Rottmann et al. 1992), along with increased risk of attack by scavenging crustaceans. Our findings indicate that increased infestation by blood-feeding gnathiid isopods may represent an additional cost. However, the energetic significance of this additional cost cannot yet be determined. Moreover, it is unclear to what extent injuries influence the risk of infestation by other fish ectoparasites such as copepods, monogeneans, and cymothoid isopods. Additional research on the effect of injury on infection risk would be needed to determine if our results are generalizable to other fish ectoparasites.

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Compliance with ethical standards

Conflict of interest W. Jenkins, P. Sikkel, and A. Demopoulos declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of Arkansas State University.

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