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An experimental field test of host-finding mechanisms in a Caribbean gnathiid isopod

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Abstract Field experiments were conducted from dusk to dawn off St. John (18° 18′ 59.32″ N, 64° 43′ 24.5″ W) and Guana Island (18° 28″ 28.31″ N, 64° 34′ 30.83″ W), Virgin Islands from June through August 2008-2010 to assess the sensory cues used by the nocturnal/crepuscular fish-parasitic gnathiid isopod, *Gnathia marleyi*, to locate fish hosts. Experimental traps providing both visual and olfactory cues from live French grunts (*Haemulon flavioliniatum*) attracted significantly more gnathiids than traps providing only visual cues or control traps (empty or with a rock), which were not significantly different from each other. In another experiment, traps providing both cues and only olfactory cues attracted significantly more gnathiids than empty control traps, but were not significantly different from each other. Our findings suggest that during nocturnal and crepuscular periods, visual cues provided by resting or slow-moving fish are not alone sufficient to attract gnathiids, while olfactory cues alone are. The traps designed for this study offer a new method of sampling free-living gnathiid isopods.

Introduction

Although parasites constitute the majority of marine organisms, their behavior and ecology remain poorly studied compared with other groups of marine organisms or with terrestrial parasites (e.g., Rohde 1993, 2002). Parasites have been found to dominate food-web links (Lafferty et al. 2006, 2008) and to be useful indicators of aquatic environmental conditions (MacKenzie 1999; Hudson et al. 2006; Sasal et al. 2007). They have also been shown to reflect the source population of fishes (MacKenzie 2002) and are a major source of disease, either through the injuries they cause or through their activity as vectors (Panek 2005), and can thus influence the population dynamics of reef fishes (Finley and Forrester 2003). An understanding of the biocomplexity of marine ecosystems therefore requires an understanding of the ecology of marine parasites.

One of the most important events in the life history of parasites is the detection, location, and ultimately exploitation of a suitable host, each of which may involve different sensory cues and behavioral responses. Selection in turn favors the evolution of traits that allow hosts to reduce detection and exploitation by parasites (Poulin 2007), and parasites may themselves face the risk of being eaten or parasitized while searching for a host (Grutter 2002). Thus, host–parasite dynamics will depend largely on the resolution of these opposing selective forces. However, little is known about the mechanisms marine parasites use to find their hosts.

Gnathiid isopods (Crustacea) are common ectoparasites on fish hosts in both temperate and tropical oceans (Smit and Davies 2004). They are unusual among parasitic arthropods in that only the larvae are parasitic (protelian parasitism). The larval phase consists of three stages (instars), ranging from approximately 0.5–3 mm in length which emerge from the substratum to find a host fish. When engorged on blood, they return to the substratum to molt into the next larval stage. The amount of time required for

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gnathiids to become engorged with host fluids varies among species and developmental stages, being longer for larger species and more advanced developmental stages (Grutter 2003; Smit et al. 2003; Smit and Davies 2004). After the final blood meal, third-stage larvae metamorphose into adults that live in the benthos and do not feed. Females retain eggs in a brood pouch (marsupium) until hatching of first-stage larvae that live in the benthos and begin seeking a fish host.

Gnathiids are of particular ecological importance on tropical reefs. They are the most abundant crustacean parasite of reef fishes, are believed to transmit protozoan blood parasites to host fishes (Davies and Smit 2001), and are the primary food item of cleaner organisms such as cleaner wrasses in the Indo-Pacific (Grutter 1996) and cleaner gobies in the Caribbean (Arnal and Côté 2000; Whiteman and Côté 2002).

At sites on the Great Barrier Reef and the Caribbean, where gnathiid ecology has been studied most extensively, gnathiid activity varies significantly during the 24-h diel cycle. Peak activity occurs at dawn and near mid-night, with lowest activity during midday (Grutter 1999; Grutter and Hendrikz 1999; Côté and Molloy 2003; Sikkel et al. 2004, 2006, 2009a). Thus, gnathiids on tropical reefs must typically locate hosts during times of low ambient light, when many hosts are immobile and/or under shelter. However, virtually nothing is known of the sensory mechanisms involved in locating hosts. Gnathiids have large, compound eyes that may enable them to see well at night. However, immobile hosts may still be difficult to locate when hidden. Gnathiids also have long antennae that may enable them to locate hosts using chemical cues (Nagel et al. 2008).

In this study, we used field experiments to better understand the mechanisms used by a recently described gnathiid isopod (*Gnathia marleyi*) common to shallow reefs of the northeastern Caribbean to locate hosts during nocturnal and crepuscular time periods. In the process, we develop a new method for estimating among-site differences in per capita risk of infection of fishes by gnathiids.

Methods

Experiment 1 dusk to dawn: visual cues

The first experiment was conducted between July 6 and July 27, 2008, in Lameshur Bay, St. John, US Virgin Islands (18° 18′ 59.32″ N, 64° 43′ 24.5″ W), White Bay, Guana Island (18° 28″ 28.31″ N, 64° 34′ 30.83″ W) on August 12–13, 2008, and south Haulover Bay, St. John on June 5–7, 2010 (see Sikkel et al. 2009b for map). This experiment was designed to test whether gnathiids were attracted to fish hosts using visual cues alone and consisted of four treatments, each using traps made of modified 20 cm diameter x 35 cm long PVC "T" sections (Figs. 1, 2). Treatments included (1) visual + olfactory cues from a fish; (2) visual cues alone; (3) rock control; and (4) empty control. The first treatment was included to verify the traps' effectiveness and to confirm that gnathiids were present. For all four treatments, the two ends of the tube were capped with transparent acrylic into which a 10-cm-diameter, clear plastic funnel with a 1.25-cm-diameter end spout had been glued. Thus, the traps' design was similar to emergence traps commonly used to collect benthic zooplankton (e.g., Alldredge and King 1977). To facilitate water filling and emptying of the tubes, two 2.5-cm-diameter holes were drilled on the bottom of the tube, approximately 6 cm from each end. These were sealed with rubber corks during deployment. Trap designs were similar for all treatments except that the traps used to isolate visual cues consisted of three separate chambers, two end chambers and a middle chamber, rather than one continuous chamber between the two end ports. The central chamber was created by gluing two transparent acrylic "walls" inside the tube on either side of the central port, into which a fish could be placed. The tubes were tested before deployment to verify that the central chamber was water tight. Objects in the central chamber could be clearly seen through the end ports. French grunts (*Haemulon flavioliniatum* Desmaret) approximately 20 cm in length were used as test fish. This species shoals near the substratum during the day and forages actively at night. It is abundant at our study sites, easy to maintain, and attracts large numbers of gnathiids when placed in mesh cages (Sikkel et al. 2009a). For the first treatment, fish were introduced into the trap from the top port, which was then covered with two layers of 50% shade cloth. For the second treatment, fish were similarly introduced into the central port that was sealed with 1-cm square black plastic hardware cloth to prevent fish from escaping through a 50-cm-long PVC "chimney" that was inserted into the central port to provide adequate water exchange to the fish in the central chamber. To avoid the attraction of gnathiids through the chimney, the chimney tube was oriented upward and away from the reef. For the third and fourth treatments (controls), we used either of the two trap designs but with a rock that was similar in size to the fish (rock control), or nothing at all (empty control), added through the central port.

The experiment was repeated three times at different localities within Lameshur Bay and at one locality each within White and Haulover Bays. For each experimental block, each of the four treatments was replicated 8–12 times. Traps were assembled and loaded with fish or rocks (as appropriate) from a dock or from shore and transferred

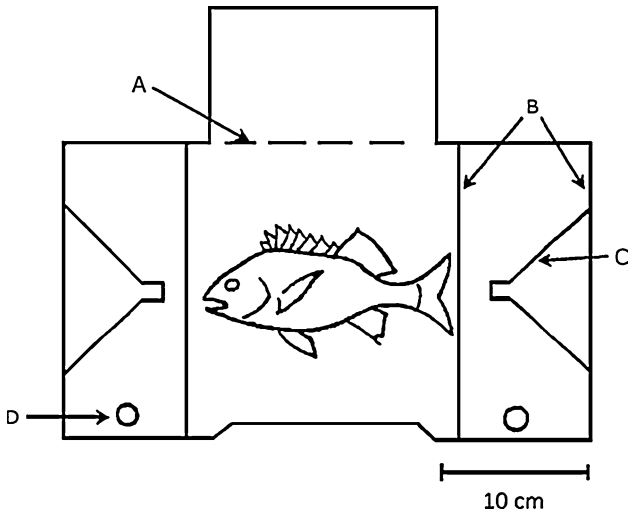

Fig. 1 Diagram of vision-only trap used in field experiment. Traps were made from white plastic PVC: *A* Plastic hardware cloth mesh to allow water circulation and prevent fish from escaping; *B* Transparent acrylic walls; *C* Transparent plastic funnel; *D* Holes for draining end chambers (sealed with rubber cork). A 50-cm-long tube was inserted in the top port as a "chimney" to direct odor away from the trap while providing the fish with adequate water circulation. The interior transparent walls were used to eliminate olfactory cues from the fish and thus were absent in traps that presented both cues or only olfactory cues. Visual cues were eliminated from the latter by covering the ends with dark plastic and lining the transparent funnel with silver tape

Fig. 2 Photograph of submerged trap (visual plus olfactory)

to snorkelers who placed them haphazardly on the reef near high rugosity substratum (e.g., dead or live coral and sponge) at 2–4 m depth. Traps were deployed near sunset and retrieved within 1 h after sunrise. Thus, they were exposed to the peaks in gnathiid activity at these sites (Sikkel et al. 2006). When first placed on the substratum, fish were observed moving rapidly between each end of the chamber. However, by the end of the approximately 30-min period required to place all traps, fish deployed at the beginning of the period were observed moving slowly and fish were also moving slowly at the time of retrieval.

Upon retrieval, traps were immediately placed in a plastic tub where they were drained and flushed with seawater to remove contents. For traps with a separate central chamber, water from the central chamber was drained first and processed separately from the end chambers, which were drained by removing the cork. Fish or rocks (depending on treatment) were carefully rinsed to dislodge any remaining parasites. Contents of each plastic tub were filtered through 55-μm plankton mesh and transferred to a Petri dish. Gnathiids were then counted under a dissecting (stereo) scope. A subset of gnathiids was reared in plastic cups containing seawater until their next molt. Resulting males were used for species identification and females for breeding.

Experiment 2 dusk to dawn: olfactory cues

The second experiment was designed to determine whether olfactory cues alone were sufficient to attract gnathiids. Thus, this experiment compared traps providing both visual and olfactory cues (as in treatment 1 above) with traps providing olfactory cues alone and empty control traps. For the olfactory-only treatment, the end ports were covered with blue plastic and the funnel was lined with silver tape. To prevent gnathiids from seeing through the nipple of the funnel, the end was sealed with a black rubber cork. An equal sized hole was drilled in the side of the nipple to allow odors to escape and gnathiids to enter the trap. The control traps were similar in design to the odor-alone traps but did not contain fish. This experiment was conducted at two sites in Lameshur Bay, St. John from August 4–9, 2008, and in White Bay, Guana Island from 13 to 15 August 2008. During each experimental block within Lameshur Bay, the vision + olfactory and olfactory-alone treatments were replicated 8–9 times and the empty control 6 times each. At the Guana Island site, all three treatments were replicated 12 times. Traps were deployed, retrieved, and processed as described earlier.

To determine whether vision-odor and odor-only traps were attracting different size/age classes of gnathiid, we randomly selected 305 gnathiids (5 from each of 23 olfactory-only traps and 35 vision + olfactory traps) and photographed them using a digital camera mounted on a microscope. We then measured the width of the head of each gnathiid using Image J (U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/; see Mott et al. 2010 for evaluation of effectiveness). Head width was used to compare size because it is not influenced by the volume of fluid in the gut and is less subject to photographic image distortion due to rotation of the body.

Experiment 3: morning to dusk

In an attempt to determine whether gnathiids that may be active during time periods with more ambient light (versus crepuscular or nocturnal periods) rely more heavily on visual cues to detect fish hosts, we repeated these experiments at two sites within Great Lameshur Bay during June and July 2009, setting 10 traps of each treatment at each site between 08:00 and 17:00 h.

Statistical analyses

There were many traps with no gnathiids, resulting in a large number of zero values. This meant that data did not meet the assumptions of ANOVA, even with transformation (Experiments 1 and 2), or were insufficient for statistical analysis (Experiment 3). For the first two experiments, we therefore analyzed data initially using chi-square analysis, comparing the presence versus absence of gnathiids in traps. For Experiment 1 (dusk to dawn: visual cues), chi-square analysis was followed by two-way ANOVA (with treatment and site as independent variables) on the number of gnathiids per trap (natural log + 1 transformed) for those traps that contained gnathiids. For Experiment 2 (dusk to dawn: olfactory cues), chi-square analysis was followed by ANOVA on all data after eliminating those treatments where the majority of traps contained no gnathiids (there were few empty traps in the remaining treatments). Two-way ANOVA was also used to compare head widths between treatments and sites in Experiment 2.

Results

Experiment 1 dusk to dawn: visual cues

Only one vision-only trap had any gnathiids (1) in the central chamber, suggesting that odors from the fish in the central chamber were not a significant source of attraction to traps in the vision-only treatment. All other gnathiids collected from this treatment were from the end chambers. At the Haulover Bay site, only 5 (all vision + olfactory) of 40 traps deployed contained gnathiids (1–3 each), indicating low availability of these parasites. Data from this site were therefore excluded from analyses. At the other four sites, most (70–100%) of vision + olfactory traps contained gnathiids (Table 1), whereas the majority of vision-only traps did not, and the majority of control traps did not contain gnathiids at three of four sites. Differences between treatments were statistically significant (X^2_3, all $P < 0.05$) at all but one site, as were differences pooled among sites ($X^2_3 = 27.05$, $P < 0.001$). However, no differences were significant when the vision + olfactory treatment was removed (all $P > 0.50$).

At two sites (Lameshur Bay site 1 and White Bay Guana Island), there were a sufficient number of traps with gnathiids in each treatment to allow for among-site comparison of gnathiids per trap (Fig. 3). For these two sites, there was a significant effect of treatment ($F_{3,41} = 14.12$, $P < 0.001$), but no effect of site ($F_{1,41} = 0.343$, $P = 0.561$) or the interaction between the two ($F_{3,41} = 0.142$, $P = 0.930$). Post hoc pairwise comparisons revealed that the vision + olfactory treatment was significantly different from all other treatments (all $P < 0.001$), which were not different from each other (all $P > 0.50$). Results were identical when data from all four sites were pooled.

Experiment 2 dusk to dawn: olfactory cues

At the two Lameshur Bay sites, only 1 of 6 and 2 of 6 (25% combined) of the empty control traps had any gnathiids, and only 2 of 12 (16.7%) at White Bay did so (Fig. 4). In contrast, 8 of 9 vision + olfactory at each of the two Lameshur Bay sites (88.9% combined) and 6 of 8 and 7 of 9 (76.5% combined) of the olfactory-alone traps from the Lameshur Bay sites did so. Similarly, 11 of 12 (91.7%) and 12 of 12, respectively, from White Bay did so. Combining similar results for both Lameshur Bay sites, the difference at both bays was highly significant ($X^2_2 = 14.91$ and 23.83, $P < 0.001$), but not when the olfactory-control treatment was removed ($P > 0.60$). In the few cases where the control treatment had gnathiids, the maximum number was three, compared with 19 and 23 (Lameshur Bay) and 347

Table 1 Sample size per treatment (percentage of traps with gnathiids) for Experiment 1 at Lameshur Bay, St. John (sites 1–3), and White Bay, Guana Island (site 4)

Treatment	Site			
	1	2	3	4
Empty control	9 (44.4%)	11 (27.3%)	8 (33.3%)	10 (80%)
Rock control	11 (45.5%)	6 (16.7%)	8 (14.3%)	10 (70%)
Fish (visual cue only)	12 (41.7%)	7 (14.3%)	7 (14.3%)	11 (36.4%)
Fish (olfactory + visual cue)	10 (70%)	8 (100%)	7 (85.7%)	10 (90%)

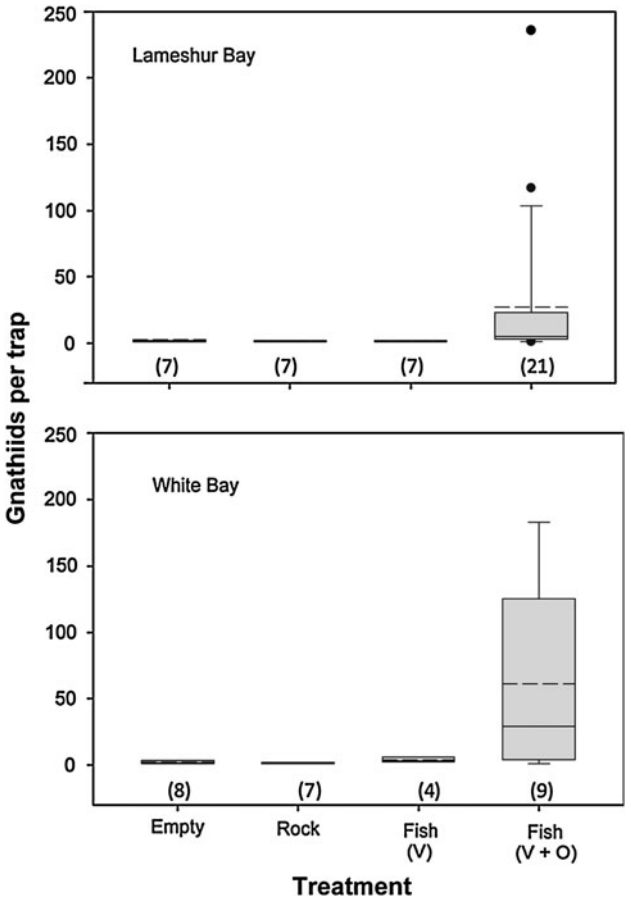

Fig. 3 Box and whisker plots (10th, 25th, 50th, 75th, and 90th percentiles) for those traps containing gnathiids from Experiment 1. Data are pooled for the three Lameshur Bay sites. Treatments as in Table 1: (V) = traps providing only visual cues; (V + O) = traps providing both visual and olfactory cues. Mean is represented by *dashed line* and extreme points by *dots*. *Numbers in parentheses* are sample sizes. One extreme value (236) from the V + O treatment at White Bay is not shown but was included in the analysis

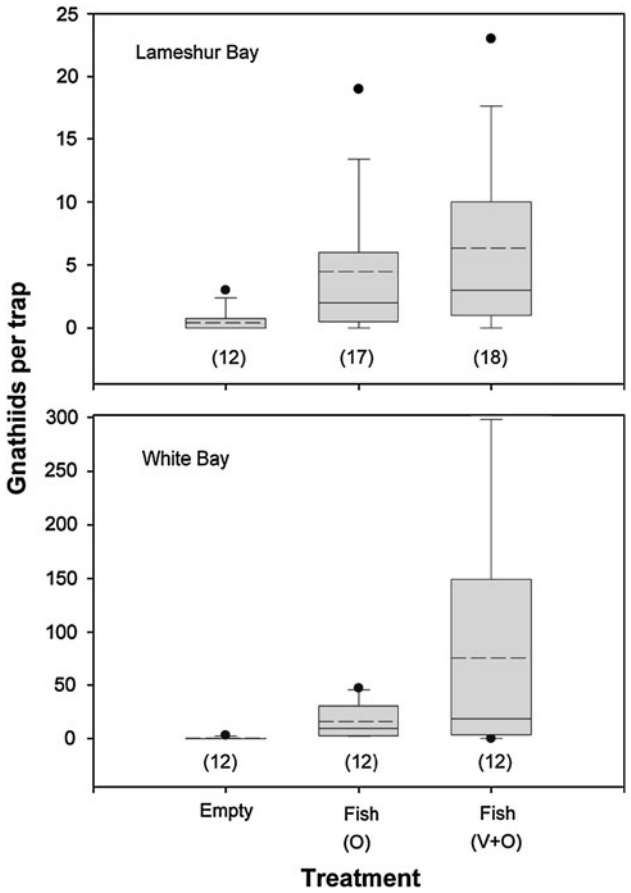

Fig. 4 Box and whisker plots (10th, 25th, 50th, 75th, and 90th percentiles), including data from traps with no gnathiids, showing results of Experiment 2 comparing traps with fish that provided only olfactory cues (O) with traps providing both olfactory and visual cues (V + O) and empty control traps. Data are pooled for the two Lameshur Bay sites. Mean represented by *dashed line* and extreme points by *dots*. *Numbers in parentheses* are sample sizes. Note differences in scale of ordinate axis. One extreme value (347) from the White Bay O + V treatment is not shown

and 47 (White Bay) for the olfactory-vision and olfactory-alone treatments, respectively. When comparing gnathiids per trap between vision-olfactory and olfactory-alone treatments, there was no significant treatment effect ($F_{1,53} = 1.58$, $P = 0.214$) and no site x treatment interaction effect ($F_{2,53} = 0.150$, $P = 0.861$), although there was an overall effect of site due to traps from White Bay containing more gnathiids than traps at the two Lameshur Bay sites ($F_{2,53} = 7.45$, $P < 0.001$, post hoc Tukey test: $P = 0.02$ and 0.002), which were similar to each other ($P = 0.761$; Fig. 4).

There was a small but significant effect of locality (bay) on head width, with gnathiids collected from Lameshur Bay averaging approximately 5% larger ($F_{1,301} = 6.04$, $P = 0.012$). However, there was no effect of treatment ($F_{1,301} = 0.448$, $P = 0.504$) or interaction between the two ($F_{1,301} = 0.034$, $P = 0.853$).

Experiment 3 morning to dusk

Among a total of 120 traps deployed during the daytime period, a total of only 5 gnathiids were recovered.

Discussion

Host-finding mechanisms in parasitic gnathiid isopods

To our knowledge, this is the first field study on host-finding mechanisms in gnathiid isopods or any other marine ectoparasite. Because of the difference in the dispersion and transmission of chemical versus visual cues, it is difficult to directly compare olfactory-only and vision-only treatments. However, the effect of the vision-only treatment was no different from empty or rock controls,

whereas traps that presented only olfactory cues were similar in effectiveness to traps that offered a combination of visual and chemical cues.

Because of the large size of their eyes relative to body size, we expected vision to play a more prominent role. In the only other study to examine the role of visual and olfactory cues by gnathiids, Nagel et al. (2008) recorded behavioral responses in aquaria of gnathiids collected during the day and night from sites on and near the Great Barrier Reef, Australia. Gnathiids were presented with fish mucus versus a control substance and separately with a moving versus still model of a fish. Although there was a tendency for nocturnal gnathiids to respond first to the mucus versus the control when tested at night, the difference was not significant due to the small sample size. Gnathiids collected during the day showed no such trend, regardless of the light level during testing, nor did nocturnally captured gnathiids tested during daylight. In contrast, only daytime-captured gnathiids tested during daylight showed a strong response to moving versus stationary fish models. Their laboratory findings suggest that the important sensory cues may vary among gnathiid species, depending on when they are typically active. Unlike diurnal fish species, the nocturnal host species used in this study is naturally active at night and moved slowly in traps, providing a moving visual cue. Thus, host immobility could not explain the extremely low numbers of gnathiids collected from traps providing only visual cues. However, it is also possible that a faster moving fish (i.e., free swimming) would have provided a stronger visual cue.

Nagel et al. (2008) limited their study to third-stage larvae but tested what appeared to be different species that are active at different times of the diel cycle. During the 3-year period over which this study was conducted, larvae collected at our study sites that have metamorphosed into adult males have all been identified as the same species (*G. marleyi*, currently being described: Farquharson et al. in prep). While other species have been described for the Caribbean region (e.g., Smit and Davies 2004), they have not been found at our shallow reef sites. Activity periods for gnathiids at our sites appear to change ontogenetically and differ between sexes (Sikkel et al. 2009a). The largest size class is most prevalent in nighttime collections (with larvae metamorphosing into females more common than males near midnight and vice versa closer to dawn), and the smallest size class is almost exclusively limited to daytime collections. However, the daytime-active individuals are most active at dawn, when light levels are still relatively low. In studies involving both caged fish and emergence traps, fewer gnathiids have been captured between sunrise to dusk compared with dusk to dawn (Sikkel et al. 2004, 2006). This was also the case in this study (where we used a different kind of trap), and thus, we cannot rule out the possibility that the small number of first- and second-stage larvae that are active between dawn and dusk rely more heavily on visual cues during that time of day and, of course, cannot rule out the possibility that other Caribbean gnathiids rely more heavily on visual cues.

Our olfactory-only experimental treatment effectively eliminated visual cues that could be used to find hosts while providing olfactory cues. It seems unlikely that any other cues could be used by gnathiids entering such traps and that could alternatively explain the large numbers captured. While fish produce electric fields, there is no evidence that crustaceans can detect those fields (Ruxton 2009). Some parasitic copepods can detect hosts by the pattern of water flow around them (Heuch et al. 2007). However, in our study, this cue would not be detectable until gnathiids were already inside the tube. Laboratory studies have found that other aquatic ectoparasites such as monogeneans also locate hosts using chemical cues (e.g., Kern 1986; Whittington and Kearn 1990), and many aquatic invertebrates utilize chemical cues to locate appropriate habitat (Pawlik 1992; Santagata 2004). Chemical cues may be more reliable as they provide a unique "signature" of the host. Even though gnathiids are generally regarded as generalist parasites, under low-light conditions, many objects (e.g., soft corals and algae) on a reef may resemble a fish. Gnathiids responding to any movement or "fish-like" cues may thus waste time and energy attaching to the wrong host. However, a broad host range would also necessitate the use of chemical cues that are found in a wide range of fish species. Not surprisingly, most of what is known about chemical cues used for host detection by crustacean parasites comes from studies on sea lice (Copepoda) that infect captive salmonids (e.g., Devine et al. 2000; Bailey et al. 2006; Pino-Marambio et al. 2007). These parasites appear to rely on different chemical compounds for different stages of host infestation: small lipophilic organic molecules to locate hosts (Ingvarsdottir et al. 2006) and non-volatile hydrophilic compounds to recognize hosts (Wyatt 2003). Fish in this study were held in confinement and may have therefore produced chemicals associated with stress. Given that some previous studies have found that injured fish become more heavily infected with certain kinds of ectoparasites (Stepien and Brusca 1985), it is possible that chemicals associated with stress or injury are also more attractive to gnathiids. Future research on host detection in gnathiids should focus on the actual chemical compounds used and how these may influence differences in infestation by gnathiids within and among fish species.

Implications for sampling of gnathiids and other small benthic/demersal organisms

Obtaining estimates of the potential levels of gnathiid infestation on reefs is complicated. Gnathiids are temporary parasites, abandoning hosts when satiated or when the

host is disturbed, and gnathiids on fish are eaten by cleaners. Thus, collecting free-living fish will tend to underestimate the number of parasites on a fish or the risk of infestation at the time of capture and does not allow estimates of cumulative infestations. Some of these problems can be reduced or eliminated by capturing fish quickly and placing them immediately in sealed containers (e.g., Grutter 1995; Sikkel et al. 2004) or with the use of cages that can be deployed and retrieved with minimal disturbance to the fish and prevent fish from seeking cleaners (Grutter 1999; Sikkel et al. 2006, 2009a). However, neither technique retains gnathiids that have dislodged from the host prior to the time of capture or retrieval, and thus, fish must be sampled throughout the day. Sampling during the nocturnal and crepuscular peaks may also be difficult or hazardous at many localities. Emergence traps used to sample benthic zooplankton are commonly used to sample gnathiids (Grutter et al. 2000; Côté and Molloy 2003; Sikkel et al. 2004; Jones and Grutter 2007). Once inside the sampling bottle at the top of the trap, gnathiids cannot escape. This allows for flexibility in deployment and retrieval time and sampling duration. However, the sample is limited to the area covered by the trap, and the percentage of gnathiids under the trap that are captured and the percentage of gnathiids caught in traps that are actually seeking hosts are unclear. Light traps have also been used to collect gnathiids (Jones et al. 2007) but will attract both fed and unfed individuals, again making it difficult to assess the number of active host-seeking gnathiids at any given time. The traps used in this study incorporate elements of the other three collecting methods. Because of the presence of a live fish, like cages, they attract gnathiids that are motivated to feed on a host from an area that is typical of a free-living host. However, like emergence traps and light traps, they retain gnathiids once they have fed and have dislodged from the host. Traps can therefore be set and retrieved once every 24 h to estimate the cumulative gnathiid infestation per fish at a particular locality. These traps can further be used to test for differences among hosts in their attraction of gnathiids or for sampling other benthic and demersal reef organisms, especially those that use olfactory cues for locating resources.

Implications for nocturnal refuge choice and habitat utilization

Diurnally active fishes seek refuge during the night. Most discussion concerning the benefits of shelter and the factors that influence choice of nocturnal shelter sites in these fishes has focused on the risk of being attacked by piscivorous predators (e.g., Hixon and Beets 1993; Steele 1999). However, parasitic crustaceans can be viewed as micropredators (e.g., Penfold et al. 2008). While being visually inconspicuous or in a "tight-fitting" refuge is effective in reducing predation by most piscivorous predators, it may be effective at reducing infestation by ectoparasites only inasmuch as it also reduces the amount of chemical cues emanating from the fish. Thus, for fishes lacking physiological mechanisms to reduce chemical detection or penetration by ectoparasites (e.g., parrotfishes: Videler et al. 1999; Grutter et al. 2010), choosing resting sites where gnathiids are not abundant may be more important than the nature of the shelter site itself. Indeed, gnathiid abundance appears to vary considerably within reefs over small spatial scales (Sikkel et al. 2000, 2004, 2006; Cheney and Côté 2003; Jones and Grutter 2007). Similarly, the ability of gnathiids to detect hosts at night using chemical cues may influence habitat utilization by nocturnal species. A nocturnally active fish that moves slowly close to the reef would be highly susceptible to infestation by gnathiids unless it was physiologically resistant. Thus, just as they appear to influence diel peaks in interactions with cleaners (Sikkel et al. 2004, 2005), gnathiids that are active at night and dawn could influence nocturnal foraging habitat, the height in the water column where nocturnal fishes feed, swimming speed, and the time at which they return to daytime resting sites. Future studies on gnathiid–host interactions should more carefully examine the relationship between gnathiid habitat preferences and nocturnal habitat utilization in both diurnal and nocturnal reef fishes.

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