



Nocturnal migration reduces exposure to micropredation in a coral reef fish

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ABSTRACT.—Tropical Atlantic reef fishes in the family Haemulidae (grunts) remain quiescent on reefs during the day and migrate to seagrass beds or sand flats at night. Hypothesized advantages of such nocturnal migrations are increased food availability and/or decreased predation risk. Here, we tested predictions of an alternative hypothesis that nocturnal migrations of French grunt, *Haemulon flavolineatum* (Desmarest, 1823), reduce exposure to blood-feeding gnathiid isopods. The departure of grunts from the reef coincides with increasing gnathiid activity. In field experiments, subadult fish placed in cages and deployed on the reef at night harbored significantly more gnathiids than those placed in the seagrass habitat. However, this was not the case during the day when gnathiid activity in all habitats is low. In another experiment, the timing of return to the reef was determined to coincide with the postdawn decrease in gnathiid activity. Estimates of cumulative gnathiid exposure at two sites revealed that grunts remaining in reef habitat at night would experience an average of 3 and 44 times more gnathiids than if they spent the night in the seagrass bed, and could reach more than 300 gnathiids on a single fish. In a final field experiment, even recently-settled (<2 cm) juvenile grunts were infested by gnathiids, supporting previous laboratory experiments showing that a single third-stage gnathiid will infest and kill grunts of this size. Combined, these findings suggest that nocturnal feeding migrations of French grunts and ecologically similar fishes result in reduced exposure to blood-feeding gnathiid isopods.

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Many animals undergo daily or seasonal migrations between habitats (Rubenstein and Hobson 2004, Møller and Szép 2011, Poulin et al. 2012). Given the costs of travel, evolutionary ecologists seek to understand the net benefits of migration, while community and population ecologists are interested in the ecological consequences of

migration. Studies on benefits of migration focus primarily on increased food availability (e.g., Owen-Smith et al. 2010) for and decreased predation on adults and/or offspring (e.g., Hebblewhite and Merrill 2009). For example, a study on the foraging and movement patterns of bottlenose dolphins, *Tursiops aduncus* (Ehrenberg, 1833), documented a potential seasonal trade-off between foraging efficiency and predation risk, as bottlenose dolphins were observed to forage in less productive areas when tiger shark, *Galeocerdo cuvier* (Péron and Lesueur, 1822), predators were present (Heithaus and Dill 2002). Migrating animals may also benefit through reduced exposure to parasites and micropredators (reviewed by Shaw and Binning 2016). For example, the migratory grounds that birds (Møller et al. 2004, Møller and Szép 2011), ungulates (Folstad et al. 1991, Ezenwa 2004), insects (Dumont and Hinnekint 1973, Bartel et al. 2011), and fish (Poulin et al. 2012) inhabit seasonally may have fewer or lower density of parasites than the grounds from which they originated, and ticks may increase the benefit of partial migration for European cervids, as tick, *Ixodes ricinus* (Linnaeus, 1758), density is lower in the migratory summer grazing areas (Qviller et al. 2013).

Many coral reef fishes undergo daily migrations between resting and feeding sites. The resulting day-night changeover is one of the most conspicuous and dynamic events on coral reefs (Burke 1995, Danilowicz and Sale 1999, Sale 2013). A major part of this changeover in the tropical western Atlantic Ocean is the diel migration of some species between daytime resting sites on the reef and nocturnal feeding sites in seagrass beds or sandflats. Such migrations occur over several to hundreds of meters (Appeldoorn et al. 2009, Luo et al. 2009, Hitt et al. 2011), depending on species and locality. Among the most common of these tropical western Atlantic migratory species is the French grunt, *Haemulon flavolineatum* (Desmarest, 1823) (e.g., Helfman et al. 1982, McFarland and Wahl 1996, Nagelkerken et al. 2000, Clark et al. 2009), which is perhaps the best studied of any tropical Atlantic reef fish (McFarland 1980, Meyer and Shultz 1985, Rooker and Dennis 1991, Hein 1996, Munro 2000). The majority of French grunt leave their daytime resting sites en masse at dusk (e.g., Ogden and Ehrlich 1977, McFarland et al. 1979, Welicky and Sikkell 2015) and travel from 50 to 300 m (reviewed in Appeldoorn et al. 2009) to seagrass beds and sand flats, returning to the same site of origin at dawn. Migrations occur in all postsettlement sizes, from newly settled (approximately 100–150 mm) to adult (>1500 mm) (Appeldoorn et al. 2009). Two hypotheses have been proposed to explain the benefits of nocturnal migration in this and related species (Appeldoorn et al. 2009, Hammerschlag et al. 2010). First, nocturnal migration could increase foraging efficiency because of greater prey availability and/or decreased competition (e.g., Burke 1995). Second, leaving the reef at night may reduce exposure to reef-based predators (McFarland et al. 1979, Danilowicz and Sale 1999). A third alternative that has not previously been proposed is reduced risk of parasitism.

Gnathiid isopods are small (1–3 mm), highly mobile crustaceans that feed on fish blood and body fluids. While gnathiids are found in all ocean habitats from the Arctic Ocean to the Antarctic Ocean, and rocky intertidal to the abyss (e.g., Klitgaard 1997, Ota et al. 2016, Quattrini and Demopoulos 2016), they are perhaps best known in coral reef habitats where they are the most common external parasite of reef fishes and the most common food item for cleaner fishes (Grutter 1996, 1999, Arnal and Côté 2000, Whiteman and Côté 2002). Larval gnathiids emerge from benthic substrate and find a host fish, and when engorged on blood and body fluids, return to the

substrate and molt into the next larval stage (Smit and Davies 2004, Tanaka 2007). 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 the hatching of postembryonic first stage juveniles that live in the benthos and begin seeking a fish host (Manship et al. 2011). Like blood-feeding terrestrial arthropods, such as ticks (Ixodoidea), mosquitoes (Culicidae), and fleas (Siphonoptera), gnathiids associate only temporarily with hosts. Because they feed from multiple hosts during their three larval stages, they may be considered “micropredators” (Raffel et al. 2008). However, more like parasites, they appear to feed on only a single host during each of the three stages.

Gnathiids can have multiple impacts on their hosts. Although small in size, high gnathiid loads in adult fish can decrease hematocrit (Jones and Grutter 2005), and even cause death (Hayes et al. 2011). Their piercing structures can cause tissue damage that can lead to secondary infection (Bunkley-Williams and Williams 1998), and, like terrestrial blood-feeding parasites, they are known or suspected to transmit blood parasites, such as haemogregarine or haemogregarine-like apicomplexans, filarial nematodes, flagellates, fungal structures, and viruses (e.g., Smit and Davies 2004, Davies et al. 2009, Curtis et al. 2013). More recently, gnathiids have been shown to infect and kill newly-settled juvenile reef fishes (Jones and Grutter 2008, Penfold et al. 2008, Grutter et al. 2011a, Sun et al. 2012, Artim et al. 2015).

Although regarded as host-generalists, differences in some combination of preference of the parasite, resistance by the host, and differences in the behavior of parasite and host that influence encounter rate can cause variation in host infestation (Coile and Sikkel 2013, Sikkel et al. 2014). Gnathiids on coral reefs overall appear more active between dusk and dawn and exhibit size-specific variation in activity peaks (Grutter 1999, Sikkel et al. 2006, 2009). At least in the eastern Caribbean Sea, this reflects an ontogenetic niche shift in time within a single species (Sikkel et al. 2009). First stage *Gnathia marleyi* Farquharson, Smit and Sikkel, 2012 are most active at dawn with low levels of activity during the remainder of the day. In contrast, larger gnathiids dominate the night peak. Thus, fish at night are exposed to both more and larger gnathiids.

Gnathia marleyi infests at least 20 different host species (Farquharson et al. 2012, Coile and Sikkel 2013). In field experiments, species of grunts and snappers were shown to be most susceptible (Coile and Sikkel 2013), and female gnathiids that metamorphosed after feeding on these hosts produced larger (but not more) offspring compared to those that metamorphosed after feeding on some other hosts (Coile et al. 2014). Moreover, a single third-stage gnathiid can kill a recently-settled French grunt (Artim et al. 2015). Curiously then, the most susceptible hosts are typically off the reef at night. The goal of the present study was therefore to test predictions of the hypothesis that nocturnal migration away from the reef reduces exposure to ectoparasitic/micropredatory gnathiid isopods. Specifically, we tested whether adult and subadult-size fish that remained on the reef at night would experience higher infestation by gnathiids, and whether the dawn return of grunts to the reef coincided with the postdawn decline in gnathiid activity. We further tested the assumption that gnathiids would infest recently settled grunts (that also migrate) in the field.

METHODS

The present study was conducted between April and August 2011–2015, and June and July 2016 in shallow reef-seagrass habitat in: White Bay, Guana Island, British Virgin Islands (18°28'26"N, 64°34'33"W); Lameshur, Salt Pond, and Maho Bays, St. John, United States Virgin Islands (18°19'1"N, 64°43'25"W; 18°18'28"N, 64°42'21"W); Brewers Bay, St. Thomas, United States Virgin Islands (18°20'28"N, 64°58'44"W); Tamarindo Bay, Culebra, Puerto Rico (18°19'4"N, 65°19'6"W); and Enrique Reef, La Parguera, Puerto Rico (17°57'14"N, 67°03'7"W). Not all experiments were conducted at all localities. Fish were collected by free-divers using modified cast nets at or near the site where they were used. For St. Thomas and St. John sites, colonies of fish were maintained in 1500 L circulating seawater tanks and fed approximately 10% their body weight of squid daily. For each field trial, fish were selected haphazardly from the "pool" of captive fish until all fish had been used for a given experiment. Fish were never reused for the same experiment. For the other sites, fish were captured as needed for experiments and maintained for >2 d in submerged mesh cages or large plastic tubs equipped with portable aerators, and were never used more than once for the same experiment. Fish were returned to the location from which they were collected.

With the exception of the juvenile experiment (see below), all fish used in our study were within a narrow, subadult to small-adult size range [mean fork length = 12.21 (SD 2.1) cm]. Moreover, for each field trial, fish in each treatment were matched for size to ensure that body size was not a confounding factor.

EFFECTS OF HABITAT ON GNATHIID INFESTATION: REEF VS SEAGRASS.—To determine whether fish leaving the reef at night are exposed to fewer gnathiids than if they were to remain on the reef, French grunt were deployed in cages at 18 different "sites" among the study localities. All sites consisted of reef with nearby seagrass beds and included aggregations of grunts. No site was closer than 200 m from any other site. At each site, a set number (5–8) of caged fish was placed in reef or seagrass habitat at dusk. Cages were cube-shaped, and constructed of thick plastic. They measured approximately 30 cm on each side, allowing fish to turn around inside the cage, and included multiple 2 cm diameter holes allowing passage of water and gnathiids, but preventing the fish from escaping. For reef sets, cages were placed 3–5 m apart from one another. Cages were similarly arrayed for seagrass sets, but were placed 50–60 m into the seagrass bed where grunts had been observed feeding at night, such that they were perpendicular from the reef set.

Cages were retrieved approximately 40 min before sunrise, shortly before free-living grunts returned to the reef. Upon retrieval, each fish was removed from its cage and placed in a 10-L plastic container with fresh seawater and an aerator. The fish remained in the container for approximately 2 hrs, allowing for gnathiids to consume their blood meal and dislodge naturally from their host. Fish were subsequently transferred to a "recovery" container where they were treated with StressCoat® to aid in replenishment of mucous and then transferred to the holding facility. The 10-L seawater containers were then filtered using 100-µm mesh to filter and collect the gnathiids that had dislodged from the fish. The number of gnathiids collected per fish was then enumerated using a stereoscope.

Even in areas of high abundance, the number of gnathiids collected in traps exhibited high variance, with a high proportion of traps having zero gnathiids. This

pattern has been found in our previous studies employing a variety of trapping techniques, including live fish-baited traps. (e.g., Sikkel et al. 2006, 2011b, Artim and Sikkel 2013, 2016). Therefore, as the dependent variable, we used the total number of gnathiids collected among the set of fish deployed in each habitat at each site divided by the number of fish in the set (mean gnathiids per fish). We then compared the two values (one for each habitat type) at each of the 18 sites using a matched-pairs *t*-test.

Gnathiids collected from pre-dawn retrieval reflected (to some degree) night accumulation up to the time of retrieval. However, because gnathiids dislodge after feeding, collections were dominated by the most recently (i.e., postmidnight) attached gnathiids. To test the assumption that differences between reef and seagrass reflected in the pre-dawn retrieval also occurred during the earlier part of the night, we conducted another set of trials at six sites in which we set cages at dusk and retrieved them at midnight.

Our previous studies have found consistently low gnathiid activity during the day, regardless of trapping technique (e.g., Chambers and Sikkel 2002, Sikkel et al. 2006, 2011). However, all previous studies have been conducted in reef habitat. Given that the gnathiid species in seagrass at our sites is the same as that found in the reef (*G. marleyi*), it seems likely that diel activity in seagrass beds and sand flats is similar to that on the reef. Nevertheless, it remains possible that daytime gnathiid activity in seagrass beds is higher than on the reef and that refuging in reef habitat during the day is actually an “escape” from high gnathiid activity. Therefore, to test the assumption that daytime gnathiid activity is similarly low in both reef and seagrass habitat, we conducted a series of daytime sets (08:00–16:00 hrs) at 10 sites. Analyses for mid-night and daytime sets were the same as those used for pre-dawn sets.

Our sampling protocols described above did not allow us to assess precisely how gnathiid densities change with distance from the reef. As a preliminary assessment, we conducted a series of five sets in which we placed cages in reef, seagrass, and the sand-patch interface between reef and seagrass. The sample sizes for this repeated measures design were not sufficient for a formal statistical analysis.

DAWN RETURN TO REEF.—Returning to the reef at dawn could expose grunts to high gnathiid loads associated with the dawn peak (Sikkel et al 2006), and thus reduce the benefits of off-reef nocturnal migration. Thus, to determine how the timing of grunt return compares to the changes in gnathiid activity at dawn, an additional caging experiment was conducted. At each of 13 sites, we determined the time grunts return to the reef by observing their daytime resting site, starting 30 min before first light, and recording the time the fish arrived. The following day, five caged French grunt were placed on the reef 30 min before the return time and retrieved at the time of return. Another set of five fish was placed nearby at the time of return and retrieved 30 min later. Fish were processed and gnathiids collected and counted as described above. Mean gnathiid loads per fish before and after the return time were compared using a paired *t*-test.

ESTIMATES OF CUMULATIVE PARASITE LOADS: REEF VS SEAGRASS AND INTERFACE.—The experiments described above allow for comparison of gnathiid infestation during limited time periods and thus do not allow estimates of differences in cumulative exposure between habitats. However, the latter is far more labor-intensive. We therefore estimated cumulative gnathiid infestation by setting 5–7 cages for approximately 2-hr time blocks in each habitat (reef, seagrass, and

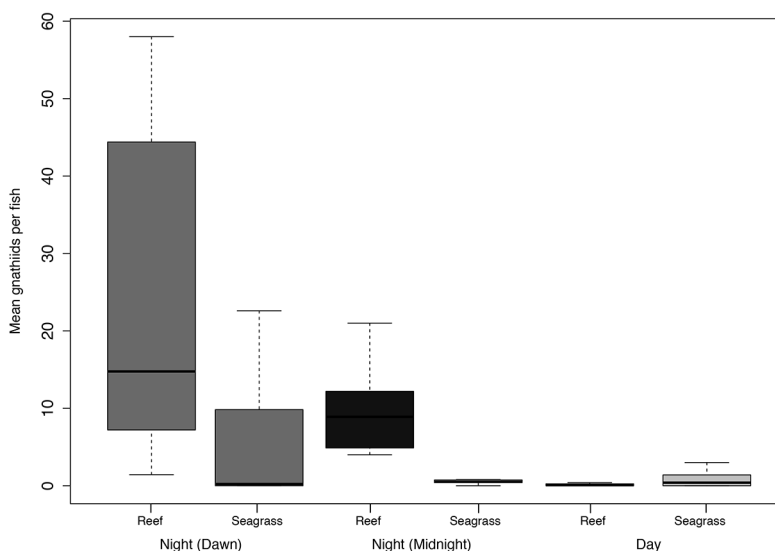


Figure 1. Box and whisker plots summarizing results of three field experiments comparing gnathiid loads on french grunt (*Haemulon flavolineatum*) in reef habitat, where fish typically spend the day but leave at night, and seagrass where fish typically spend the night. Experiments were conceived and conducted sequentially. In the first experiment ($n = 18$ sites), cages were set at dusk and retrieved pre-dawn before grunts returned to the reef. The second experiment ($n = 6$ sites) was conducted to test the assumption that nocturnal differences between reef and seagrass were not dependent on time of cage retrieval. The third experiment ($n = 10$ sites) tested the assumption that gnathiid activity during the day is low in both reef and seagrass habitat. Each data point used represents the mean number of gnathiids among 5–8 fish set and retrieved from the same site and during the same time of day. Box plots depict the 25th and 75th percentile. Dark horizontal bar represents the mean. Whiskers extend $\pm 1.5 \times$ interquartile range.

the interface between the two) distributed over a 24-hr time period. “Night-time” hours were approximated using the trap sets retrieved between 17:15 and 05:30. We calculated mean trap counts (gnathiids per fish per hour) by retrieval time. The R function “AUC” from package DescTools (Signorell 2016) was used to approximate the area under the count function. The 95% confidence intervals (CI) for these load estimates were determined using 10,000 bootstrap iterations. The individual counts were sampled with replacement, the mean of this resampling taken, and the resulting 10,000 means used to calculate 95% confidence limits using the quantile function from package stats (R Core team 2015). The 24-hr and nighttime load 95% lower- and upper-limits were then estimated using additional calls to the AUC function, as previously described. This procedure was performed for both the West Lameshur Bay and Tamarindo Bay sites.

JUVENILE INFESTATION.—Gnathiids in the lab infest and can kill recently-settled French grunt (Artim et al. 2015). To test the assumption that gnathiids will also infest recently-settled French grunt in the field, 10–20 French grunts (1–1.5 cm TL) were set in small (10 cm long $\times$ 8 cm diameter) mesh cages at each of four sites (Lameshur and Maho Bays, St. John, Brewers Bay, St. Thomas, and White Bay, Guana Island). Fish were set at dusk and retrieved at dawn, and a plastic crate was used to cover the small cages to reduce possible harassment by piscivorous fishes. Fish that survived

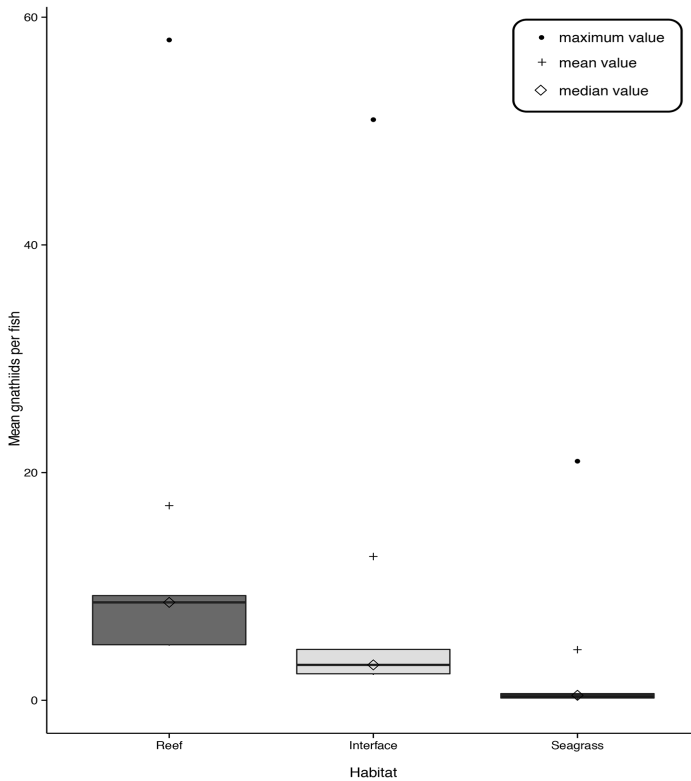


Figure 2. Comparison of mean gnathiid loads between reef, seagrass, and the interface between the two for each of five sites. Box plots depict the 25th and 75th percentile, the diamond depicts the median, the cross depicts the mean gnathiid load, and the filled circle depicts the maximum value.

the night (gnathiids will not feed on dead hosts), or did not escape from the cages, were examined for the presence of gnathiids.

RESULTS

EFFECTS OF HABITAT ON GNATHIID INFESTATION: REEF VS SEAGRASS.—Results for the three reef-seagrass comparisons are summarized in Figure 1. During the 18 paired sets retrieved at dawn, the mean number of gnathiids infesting fish was five times greater on reef (mean = 25.317) than seagrass (mean = 5.478) (t -test: $df = 14$, $t = -4.429$, $P = 0.001$). For the six sets retrieved at midnight, the mean number of gnathiids infesting fish was 9.980 on reef, significantly greater compared with 0.496 on seagrass ($df = 5$, $t = -3.868$, $P = 0.012$). For the 10 pairs of daytime sets, the mean number of gnathiids infesting each fish was <1 gnathiid regardless of environment type (reef = 0.759 gnathiids, seagrass = 0.140 gnathiids). Accordingly, during daytime there was no significant difference in fish gnathiid load between environments. For the five trials in which cages were set in reef, seagrass, and interface habitat, gnathiid loads in interface habitat appeared intermediate between reef and seagrass (Fig. 2).

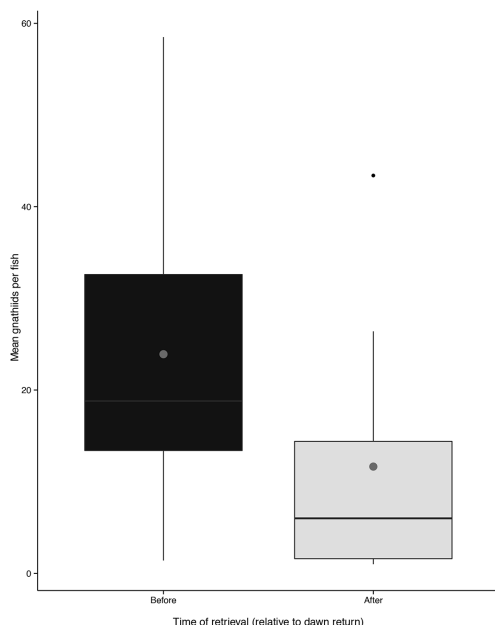


Figure 3. Comparison of gnathiid loads for caged grunts placed on the reef 30 min before expected return and retrieved at the time of return vs those set at the time of return and retrieved 30 min later. Paired comparisons were conducted at 13 different sites. Data points are the mean per fish among 5 fish per set. The large filled dots depict the mean among data points for that interval. Whiskers extend $\pm 1.5 \times$ interquartile range with outliers depicted as points beyond the whiskers.

DAWN RETURN TO REEF.—On average, among the 13 comparisons, the number of gnathiids collected from 30 min before grunts returned ($\bar{x} = 23.909$) was approximately double and significantly different from the number collected 30 min after ($\bar{x} = 11.646$; $df = 12$, $t = -2.300$, $P = 0.041$; Fig. 3).

ESTIMATES OF CUMULATIVE PARASITE LOADS: REEF VS SEAGRASS AND INTERFACE.—Estimated mean (95% CI) cumulative gnathiid loads for grunts from dusk to dawn at the West Lameshur Bay site were as follows: reef = 66.1 (29.9–112.1), interface = 51.8 (27.4–77.8), seagrass = 21.1 (10.1–34.5). Values for Tamarindo were: reef = 170.1 (49.5–316.2), interface = 40.1 (25.2–58.2), seagrass = 3.8 (0.3–8.2) (Fig. 4). As expected, daytime values were much lower, with mean values at West Lameshur of: reef = 18.5 (6.6–33.0), interface = 20.68 (10.9–30.2), and seagrass = 5.8 (1.4–11.6); and for Tamarindo of: reef = 6.7 (2.6–11.4), interface = 5.2 (1.8–8.9), and seagrass = 0.5 (0.0–1.0) (Fig. 4).

JUVENILE INFESTATION.—Of the total 43 juvenile fish retrieved alive from reef or sand-patch habitats, 11 had gnathiids, with at least two fish infected from each of the four sites. None of the 26 fish retrieved alive from seagrass had gnathiids.

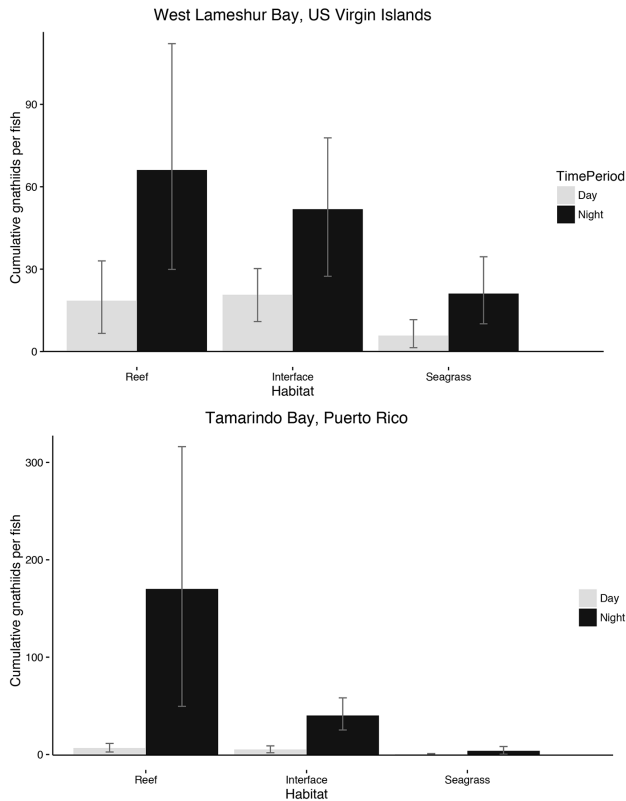


Figure 4. Cumulative gnathiid loads in relation to habitat and time of day for each of two sites. Error bars depict the 95% confidence interval.

DISCUSSION

By migrating off reef at dusk and returning just after the dawn spike in gnathiid activity, grunts significantly reduced exposure to gnathiids, consistent with a novel hypothesis/explanation for nocturnal migration for this and related, ecologically similar, species. While the expected cumulative gnathiid loads are unlikely to be fatal to subadult and adult grunts, over the course of many nights, the resulting blood loss could impose high energetic costs. Moreover, loads approaching the upper 95% CI for reef habitat at night would likely be lethal; in our experience, caged fish of the size used for this study with more than 200 gnathiids nearly always die within 24 hrs (PC Sikkel, Arkansas State University, unpubl data).

We did not test predictions of competing hypotheses (which are not mutually exclusive). Subadult and adult grunts feed primarily on infauna in sediment. However, these organisms also exist in sand patches in reef habitat and in the reef-seagrass interface. The biggest challenge to the “feeding hypothesis” is that small juvenile grunts feed on plankton during the day (Appeldoorn et al. 2009), but still migrate away from reef habitat at night. Laboratory experiments have shown that a single third-stage gnathiid can kill a small juvenile grunt (Artim et al. 2015), and the field

experiments reported here suggest that even grunts from the smallest size class are susceptible to gnathiids in the wild.

While some tethering studies have suggested that predation from piscivores is greater on reef than seagrass habitat (Danilowicz and Sale 1999), and greater in mangrove-seagrass interface than more distant seagrass habitat (Hammerschlag et al. 2010), differences found in such studies could be due at least in part to parasitic/micropredatory isopods. For example, heavy gnathiid loads produce visible “wounds” and wounded fish are susceptible to attacks by other, larger, microcarnivorous isopods (Stepien and Brusca 1985).

In the eastern Caribbean Sea, grunts and snappers are more susceptible to gnathiid infestation than are diurnal reef fishes that spend the night on the reef, and more susceptible than other nocturnal species that are active near the reef at night and even feed on gnathiids (Coile and Sikkell 2013). Moreover, gnathiids that feed on grunts and snappers experience fitness benefits over those that feed on some other host species (Coile et al. 2014). While the underlying mechanisms are unclear, these findings suggest that high susceptibility to gnathiids is either an underlying evolutionary cause or is a consequence of off-reef migration. If certain anatomical or physiological features, such as scale thickness, mucous properties, or the quality of blood meal they provide (e.g., Arnal et al. 2001, Nagel and Grutter 2007, Eckes et al. 2015), make grunts and snappers more susceptible to exploitation by gnathiids, and gnathiids are more abundant near reefs at night, this could provide a strong selective force for off-reef migration at night, allowing fish to both recover from and escape gnathiid infestation (Shaw and Binning 2016). Alternatively, if other ecological factors, such as food availability or predation risk, provide strong selective pressure to move off reef at night, then there would be less selective pressure to develop defense systems against gnathiids. In contrast, given the high level of gnathiid activity at night, fish that remain on the reef at night would be under strong selection to evolve effective defense systems against gnathiids and other micropredators, such as the mucous cocoons found in some parrotfishes (Grutter et al. 2011b). Our data do not enable us to rigorously test these alternatives.

Although we found large, statistically significant differences between reef and seagrass habitat, the magnitude of the difference varied. The factors responsible for the difference are unclear, but attributes of reef community and parasite-to-host ratio may explain some of the variation. There is increasing evidence that live coral is not suitable habitat for gnathiids (Artim and Sikkell 2013). Coral cover in the Caribbean region is declining (e.g., Gardner et al. 2003, Perry et al. 2013), and at our sites it is estimated to be <10%. Thus, grunts and snappers may have evolved under higher coral conditions with lower gnathiid exposure.

While French grunt typically leave the reef at dusk, some adult-size individuals remain near the reef and feed in sand patches. The reasons for this are unclear; however, recent studies on French grunt infected by the large parasitic isopod *Anilocra haemuli* L. B. Williams and E. H. Williams, 1981 have reported that the majority of infected individuals do not depart the reef at dusk with uninfected conspecifics (Welicky and Sikkell 2015). This may be related to infected fish being in poorer condition and having reduced swimming capacity as compared to uninfected conspecifics. *Anilocra haemuli* infection, coupled with spending nocturnal hours on the reef where gnathiid abundance is greater, may put *A. haemuli*-infected French grunt at higher risk of gnathiid infection, thereby further reducing their overall condition

and survival. Considering the significant role that French grunt serve as transporters of biomass between reef and seagrass systems (Meyer and Schultz 1985, Nagelkerken et al. 2000, 2008, Nagelkerken and van der Velde 2004, Clark et al. 2009), reductions in French grunt populations as a direct or indirect consequence of parasitism may indirectly alter trophic connectivity.

Although grunts reduce exposure to reef-based gnathiid isopods by leaving the reef at night, they do not entirely eliminate it. As a consequence, gnathiids can serve as one component of trophic transfer. Grunts depart the reef at dusk, just as gnathiid activity is increasing, and may have gnathiids attached to them. These gnathiids could thus feed on migrating hosts and then dislodge and become deposited in seagrass beds. They could in turn return gnathiids to the reef, although the low density of gnathiids in seagrass would result in less transfer. Upon returning to the reef at dawn, they would be fed upon by gnathiids during the decline of the dawn peak in gnathiid activity. Quantifying the role of ectoparasites and micropredators in fish-mediated trophic connectivity, relative to the better understood processes of waste-deposition and predation, is highly deserving of future study.

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