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Contribution to the Theme Section 'Marine functional connectivity'

Diel fish migration facilitates functional connectivity of coral reef and seagrass habitats via transport of ectoparasites

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ABSTRACT: Connectivity between habitats and ecological communities is a critical component of trophic structure. Coral reef systems include reef, seagrass, and mangrove habitats, and the movement of fishes is a key component of habitat connectivity among them. Fishes that undergo diel migrations between habitats are among the best-studied functional groups. Studies on their role in energetic connectivity between adjacent habitats have not considered the possible contribution of parasites. Some diel-migratory species are both highly susceptible to and disproportionately exploited by gnathiid isopods, temporary, tick-like parasites of marine fishes. By leaving the reef at night, diel-migratory fishes reduce their overall exposure to gnathiids, which are more active at night and more abundant in reef habitat. Here we show that for sites in both the Caribbean and the Great Barrier Reef, gnathiids are attached to diel-migratory fishes at the time they depart reef habitat. Because gnathiids associate temporarily with host fishes, they can be acquired by hosts in one habitat and can become dislodged and deposited in another. Field experiments in the Caribbean show that gnathiids from reef habitat dislodge in seagrass habitat, where they likely remain until their next feeding. Sequencing blood meals from free-living gnathiids in seagrass beds, where they are least abundant, shows that diel-migratory and other transient fishes are the most frequently exploited hosts, confirming that deposition of gnathiids in seagrass is facilitated mainly by migratory hosts. These findings have important implications for trophic, population-genetic, and disease connectivity involving gnathiid isopods and potentially other external parasites.

KEY WORDS: Trophic connectivity · Seagrass · Haemulidae · Lutjanidae · Apogonidae · Gnathiid isopod · DNA barcoding

1. INTRODUCTION

Ecosystem stability and function rely on the trophic connections that control the transfer of energy within the system (Saint-Béat et al. 2015). Among the suite of factors that impact energy flow are species abundance and diversity (Duffy & Stachowicz 2006, Coll et al. 2008, Durante et al. 2022), habitat composition (Docile et al. 2016), energy transfer efficiency (Eddy et al. 2021), nutrient input sources (Masese et al. 2018), the

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composition and strength of consumptive interactions within the network (Sentis et al. 2014), and connectivity to adjacent habitats (Unsworth et al. 2008). These variables are tightly linked, such that slight shifts in one have the capability to alter the rest, in addition to impacting overall trophic structure (Haddad et al. 2009, Hollings et al. 2014, Durante et al. 2022).

Trophic connectivity between communities can involve both physical and biological drivers. For example, on land, wind can move nutrients and even entire organisms between habitats (Visser et al. 2005, Damschen et al. 2014). In freshwater systems, transport can occur via streams and rivers, and in the ocean via ocean currents (Guest et al. 2006, Viana et al. 2013). Biological transfer can occur via the movement of organisms between habitats. For example, many terrestrial animals act as vectors of seed dispersal (Corlett 1998, Gosper et al. 2005), and in the ocean, upwards of 50% of fishes utilize multiple habitats (Berkström et al. 2012) and are responsible for substantial nutrient flux (Clark et al. 2009, McCauley et al. 2012, Pittman et al. 2014, Williams et al. 2018, Dunne et al. 2023).

Among consumer strategies, parasitism is the most common (Poulin 1999, De Meeûs & Renaud 2002, Holmstad et al. 2005, Hudson et al. 2006, Lafferty et al. 2008, Weinstein & Kuris 2016). Historically, parasites have long been omitted from both theoretical and empirical analyses of ecological food webs and trophic connectivity. However, reviews and commentaries by some ecologically-minded parasitologists have called attention to this gap (e.g. Marcogliese & Cone 1997, Wood et al. 2007, Lafferty et al. 2008, Byers 2009, Sukhdeo 2010) and made clear that a complete understanding of trophic ecology requires an understanding of the role parasites have in the system.

Parasite biomass can rival that of top predators (Kuris et al. 2008), and parasites can influence trophic linkages in many ways. Directly, they consume host tissue and, collectively, over time may contribute more to a host's carbon transfer than any other source (Preston et al. 2021). Moreover, the physiological responses to parasitism, including immune system responses and tissue repair, increase energetic demands of hosts and reduce host fitness (Holmstad et al. 2005, Hudson et al. 2006, Hatcher et al. 2012, Wood & Johnson 2015, Zhou et al. 2020). Indirectly, parasites may also influence trophic linkages by altering aspects of host behavior such as movement patterns and habitat use (Sikkel et al. 2005, Sato et al. 2012, Welicky & Sikkel 2015, Reisinger & Lodge 2016, Vale et al. 2018), and by increasing host susceptibility to predation (Ebert 2005, Johnson et al. 2010, Lopes et al. 2021).

Coral reef systems are the most diverse and trophically complex ecosystems in the ocean (Bellwood & Hughes 2001, Hoey & Bellwood 2009, Plaisance et al. 2011). Yet, despite decades of research, trophic dynamics of coral reef systems are still poorly understood relative to terrestrial and freshwater systems (Link et al. 2005, Marina et al. 2018, Eddy et al. 2021). Two of the most recent advances in our understanding of trophic dynamics in coral reef systems are the importance of nutrient inputs from external sources (Morais & Bellwood 2019), as well as those from small and inconspicuous 'cryptofauna' (Brandl et al. 2019a,b, Xie et al. 2021). However, the degree to which cryptofauna, including parasites, contribute to the import and export of nutrients is still relatively unexplored. This is unsurprising, as small organisms generally do not move between habitats on their own (Pagán et al. 2022).

Many fish species undergo diel migrations from reef habitat to adjacent habitats and are key components of the crepuscular 'changeover'. Some species 'rest' on the reef during the day and depart at dusk, returning to the same location the following dawn. Examples include haemulid grunts and lutjanid snappers (Beets et al. 2003, Clark et al. 2009, Welicky & Sikkel 2015, Sikkel et al. 2017), as well as some apogonid cardinalfishes (Marnane & Bellwood 2002, Azzurro et al. 2007, Collins et al. 2023). While these diel-migratory fishes disperse during migration, during resting periods they account for a disproportionate amount of local biomass and have long been recognized for their potential as trophic connectors between reef and adjacent habitats (Clark et al. 2009, Pittman et al. 2014). Other species take refuge on the reef at night and migrate during the day. Examples of these include many zooplanktivorous fishes that feed in the water column (e.g. Hamner et al. 2007, Siqueira et al. 2021). Some more solitary species such as sphyraenid barracudas, carangid jacks, and serranid groupers may also 'roam' during the day and/or night among different habitats (Popple & Hunte 2005, Meyer et al. 2007a,b) and still others may undergo lunar or seasonal spawning migrations (Van Sant et al. 1994, Meyer et al. 2007a). Research on the role of these transient species in trophic connectivity has focused on biomass transfer via predation and waste products (Ogden & Ehrlich 1977, Hemminga et al. 1994, Nagelkerken & van der Velde 2004). However, even though these fishes harbor a variety of parasites that could also play a significant role in the trophic transfer, there are currently no studies that have investigated this possibility.

Gnathiid isopods are hematophagous arthropods that live in the benthic substrate and emerge to feed on a fish host, with peak activity at dusk, dawn, and midnight (Grutter 1999, Sikkel et al. 2006, Santos & Sikkel 2019, Pereira et al. 2023). Once engorged, they return to the benthos (Smit & Davies 2004, Tanaka 2007). This occurs during each of 3 larval instars, with a molt in between each phase. Gnathiids tend to parasitize a wide range of fish hosts (Jones et al. 2007, Nagel & Grutter 2007, Coile & Sikkel 2013, Coile et al. 2014, Hendrick et al. 2019), and following their final meal, individuals will metamorphose into the final adult stage and will not feed. Because of their temporary association with hosts and unique life history, they have been referred to variously as temporary ectoparasites, protelean parasites, and 'micropredators' (Lafferty & Kuris 2002). These life history attributes create high potential for transfer between habitats by mobile hosts. Even so, the ambiguity surrounding their consumer strategy has contributed to gnathiids being overlooked by any researcher not targeting them.

Because animals that contribute to trophic connectivity through their movements are infected with parasites, parasites can indirectly impact trophic connectivity. However, parasites themselves can also be transported and relocated by their hosts and thereby have a direct impact on trophic connectivity (Morgan & Buckling 2004, Russell et al. 2005, Altizer et al. 2013). In this study, we hypothesized that, through transport via host fishes, fish-parasitic gnathiid isopods are a source of trophic connectivity between coral reef and associated habitats. From field experiments in the Caribbean and on the Australian Great Barrier Reef (GBR), we examined whether gnathiids: (1) are present on nocturnally migratory fishes at the time of departure from reef habitat, and (2) dislodge from hosts over time in the hosts' nocturnal foraging habitat. By collecting free-living gnathiids and sequencing their blood meals, we also examined (1) whether they are naturally occurring in both reef and seagrass habitats, and (2) patterns of migratory host use by gnathiids.

2. MATERIALS AND METHODS

2.1. Study sites

This study was conducted in the US and British Virgin Islands and Puerto Rico, Eastern Caribbean Sea, and at Lizard Island, GBR (~50 to 200 m off Casuarina Beach), Australia. Study sites at all locations included shallow (<5 m) reef habitat with adjacent (within 50 m) seagrass beds. A list of experiment and sample types by site is included in Table 1.

Table 1. Field experiment and blood meal identification sample type by region: PR: Puerto Rico; BVI: British Virgin Islands; USVI: US Virgin Islands; AU: Australia. Experiment types: RB: Reef–Bucket; RC: Reef–Commute; RS: Reef–Seagrass; SO: Seagrass-only. (See Section 2.3 for details of the experimental groups.) Blood meal identification sample types refer to samples collected on the reef (R) and in the seagrass (SG)

	Site location	Site name	Experiment/ sample type
Field experiment region			
Eastern Caribbean	Culebra, PR	Tamarindo Bay[a]	RB, RC, RS, SO
	Guana Island, BVI	White Bay[a]	RB
	St. John, USVI	Lameshur Bay	RB
		Leinster[a]	RB
		Round[a]	RB
	St. Thomas, USVI	Brewers Bay[a]	RB
Great Barrier Reef	Lizard Island, AU	Outfront Reef	RB
		Outfront Second	RB
		Beach Pipe	RB
Blood meal ID region			
Eastern Caribbean	Culebra, PR	Tamarindo Bay[a]	R, SG
	La Parguera, PR	Cayo Enrique[a]	R, SG
		San Cristobal	R, SG
	St. Thomas, USVI	Brewers Bay[a]	R, SG
	St. John, USVI	Lameshur Bay	R

[a]Biomass transferred was estimated

2.2. Study species

Work in the eastern Caribbean focused on French grunt *Haemulon flavolineatum* (Haemulidae), which is a well-studied and extremely common diel-migratory species in the western Atlantic (e.g. Helfman et al. 1982, McFarland & Wahl 1996, Nagelkerken et al. 2000, Clark et al. 2009). At dusk, French grunts leave the reef, where they rest during the day, and migrate to seagrass beds and sand flats (e.g. Ogden & Ehrlich 1977, Mcfarland et al. 1979, Welicky & Sikkel 2015). At dawn, they return to their original resting sites on the reef. All post-settlement size classes (from ~100 to >1500 mm total length) perform these nightly migrations (Appeldoorn et al. 2009).

On the GBR (Lizard Island), we focused on 2 species of lutjanid snap-

pers (*Lutjanus gibbus* and *L. carponotatus*) and 2 apogonid cardinalfishes (*Cheilodipterus macrodon* and *C. quinquelineatus*). These fishes were chosen because, like Caribbean haemulids, they are the predominant diel-migratory fishes present at our sites on the GBR. Most coral reef-associated lutjanids, including *L. gibbus* and *L. carponotatus*, are mostly quiescent and aggregate in shoals during the day. At night, they migrate individually or in small groups to adjacent seagrass beds to feed on fishes and a variety of invertebrates (Quéré & Leis 2010). Despite their small size, apogonids are the predominant nocturnal planktivores on Indo-Pacific reefs (Allen 1993) and comprise more than half of all nocturnal fish biomass production at Lizard Island (Collins et al. 2022). During the day, apogonids typically aggregate and rest in holes, caves, and branching corals mainly along reef slopes (Marnane & Bellwood 2002). At night, they travel away from the reef to feed over sandy lagoon substrata before returning to the same resting sites at dawn (Marnane 2000, Marnane & Bellwood 2002, Collins et al. 2023).

2.3. Field experiments

2.3.1. Transport of gnathiids between habitats during nocturnal migrations

To determine (1) whether gnathiids are present on diel-migrating fish as they depart the reef habitat at dusk, (2) the number of gnathiids transported per fish, and (3) whether gnathiids dislodge during the migration, we conducted an experiment in Tamarindo Bay, Culebra (18° 19′ 3.54″ N, 65° 19′ 5.06″ W; Table 1) from 21 June to 30 July 2014. This site is characterized by shallow patch reefs along the perimeter, some of which include aggregations of grunts, with an expansive seagrass bed in the center of the bay. The experiment included 3 primary treatments (Reef–Bucket, Reef–Commute, and Reef–Seagrass, Fig. 1), with each treatment being replicated at each of 7 different grunt aggregation sites within the bay, and a supplemental treatment (Seagrass-only, Fig. 1).

At each site (grunt aggregation), we collected 25–30 similar-sized fish from an aggregation during late

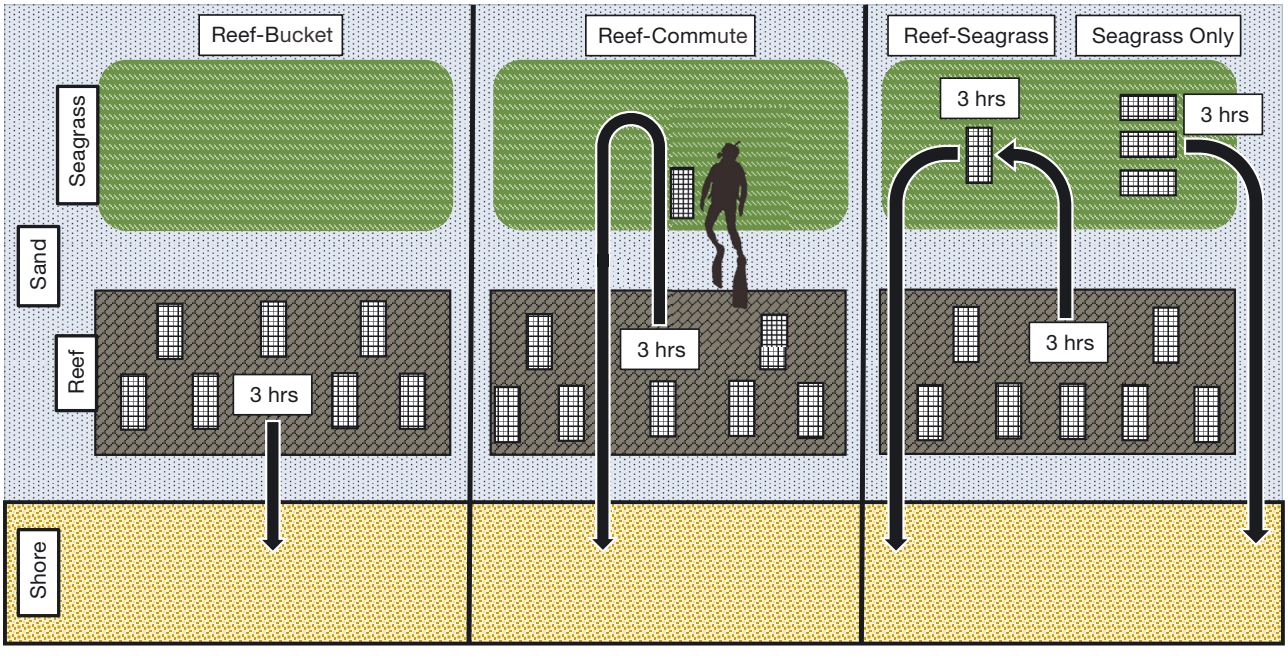

Fig. 1. Experimental design to test whether diel-migratory fish can transport parasitic gnathiid isopods between reef and seagrass habitat. For 3 treatments (Reef–Bucket, Reef–Commute, and Reef–Seagrass), fish in cages were placed in reef habitat for 3 h among the aggregation of fish from which they were collected. The linear placement of cages shown in the figure does not reflect the actual arrangement of cages but was done for clarity. A randomly selected subset of cages was assigned to each of the 3 treatments. At dusk, fish were either: (Reef–Bucket) — removed from the water and placed in buckets to assess the number of gnathiids on fish at departure; (Reef–Commute) — swum to the seagrass bed at approximately their normal swimming speed to estimate the number of gnathiids that dislodge during transit alone; or (Reef–Seagrass) — moved to the seagrass bed and deposited there for 3 h before returning to shore. The distance traveled for Reef–Commute and Reef–Seagrass treatments was approximately 95–142.3 m, depending on the location of the aggregation in which the cages were placed. This experiment was repeated at 7 different aggregations within Tamarindo Bay, Culebra. For 6 of the 7 aggregations, 7 fish were used per treatment. For the other, 8 fish per treatment were used. On 3 occasions, an additional treatment was performed (Seagrass-only) to assess the number of gnathiids that could have attached to fish in seagrass in the Reef–Seagrass treatment

morning, when gnathiid activity in the reef habitat is low (Chambers & Sikkel 2002, Sikkel et al. 2006, 2009). Fish were collected by free divers using modified cast nets (Coile & Sikkel 2013, Sikkel et al. 2017), then held in containers of fresh, aerated seawater for approximately 3 h before being placed in mesh cages. Any fish that was obviously larger or smaller than the others in the aggregation or showed signs of injury was immediately released. Cages followed the design of Coile & Sikkel (2013) and Sikkel et al. (2017). Each tube-shaped cage was constructed of black plastic hardware cloth (mesh: 6.35 mm) and measured 45 cm long, and 26 cm in diameter. This allowed the fish to move freely within the cage and allowed the cage to be placed inside an 18.5 L bucket upon retrieval (see below). A 1 kg lead weight was attached to the bottom of each cage to secure it in place. Each cage included a numbered label to identify it.

For each replicate set, cages were deployed with 1 fish per cage in the reef habitat during the late afternoon, at the same time within each replicate (15:30–16:30 h), or so-called 'trial day' (Fig. 1). Prior to loading, we rinsed each fish with a squirt bottle and gently brushed it to dislodge any gnathiids that might be attached, similar to the protocol by Grutter (1999). To load the fish, a cage was placed in a bucket of seawater, the fish was then collected in a fine-mesh net and gently placed in the cage, which was then sealed with cable ties. The fish was then swum by a snorkeler from shore to the deployment site (13.4 to 44.6 m). For the first replicate set, 24 cages were deployed, with 21 cages deployed for the remaining 6 sets. For each set, cages were placed on the substrate amongst the aggregation from which the caged fish were collected, at 2–3 m depth. We placed cages at least 0.5 m from any other cage.

At approximately 30 min before sunset, snorkelers began observing the aggregation of uncaged conspecifics to determine the beginning of the nocturnal migration. At the start of the migration, a pre-determined random subset of 7–8 caged fish was removed and immediately placed in a bucket of fresh seawater which was transferred to shore. This treatment (Reef–Bucket) allowed us to assess the number of gnathiids on fish at the time of departure. At this time, the remaining cages (14–16) were moved by snorkelers to the seagrass bed. The snorkelers followed the path and speed of the migrating fish. This was accomplished through practice from previous experience visually tracking departing grunts in the aggregations used in this study, and by using indirect lighting to keep pace with migrating grunts during the study. For these treatments (Reef–Commute and Reef–Seagrass), cages were tethered to a line that enabled the snorkeler to suspend the fish above the substrate (~0.5 m) while swimming. Following a commute from the reef to the seagrass bed (35–63.2 m), half of the cages were placed on the substrate at 3–4 m depth (Reef–Seagrass) and the remaining half (Reef–Commute) were brought back to shore and immediately transferred to buckets (Fig. 1). Reef–Seagrass fish remained in the seagrass bed for 3 h and were then retrieved and brought to shore and placed in buckets. The distance of the return trip from seagrass to the shore nearest the aggregation was 60–76 m. Thus, round-trip distances were 95–142.3 m. In effect, fish in the Reef–Commute and Reef–Seagrass treatments each 'swam' the same distance but with Reef–Seagrass fish spending 3 h in the seagrass between the outgoing and return trips. All distances were measured with a transect tape.

This experimental design relied on there being much lower gnathiid densities in seagrass beds compared to reef habitat to detect the net loss of gnathiids from fish transported from reef to seagrass. To assess this assumption, we determined the number of gnathiids that may have attached to fish while in the seagrass bed (Seagrass-only, Fig. 1). This involved placing 3 sets (on different days) of 7 fish each in the seagrass bed, near where the groups of Reef–Seagrass fish had been placed. As with the other treatments, we collected fish during late morning. We then placed the Seagrass-only treatment fish in temporary holding containers (20 l tubs). After approximately 3 h, we processed and placed them in cages as described above and deployed them in the seagrass bed in late afternoon (approximately 15:45 h). We then retrieved them at the same time as the Reef–Seagrass fish (approximately 22:30 h), swam them to shore, and placed them in individual buckets.

Our procedure for processing fish and retrieving gnathiids followed Coile & Sikkel (2013) and Sikkel et al. (2017). All fish remained in buckets for 2 h to allow gnathiids to complete feeding and dislodge, after which the fish were thoroughly rinsed with a squirt bottle and gently brushed to ensure all gnathiids had dislodged. The fish were then transferred to a holding enclosure and released at their aggregation site the following morning. We filtered water from the buckets through a 70 µm plankton mesh. We examined filtrate under a dissecting scope and counted gnathiids. For fish from 3 of the aggregations, we further categorized gnathiids according to developmental stage (size class). To confirm that

our randomly assigning fish to treatments resulted in similar-sized fish within each treatment, we measured (fork length, FL) all fish used in 3 (of 7) 3-treatment sets (trial days 1, 6, and 7), and 2 Seagrass-only sets.

2.3.2. Gnathiid loads on hosts at time of diel migration

To more broadly assess the number of gnathiids present on diel-migratory hosts at the time of departure, and thus the number of gnathiids that could be transported to seagrass habitat, we repeated the Reef–Bucket protocol (Table 1) at 4 sites (aggregations) within Lameshur Bay, St. John, US Virgin Islands (USVI) (18° 19′ 2.17″ N, 64° 43′ 21.09″ W) in July of 2013 (n = 15 fish), 4 in White Bay, Guana Island, British Virgin Islands (BVI) (18° 28′ 29.35″ N, 64° 34′ 34.54″ W) during July 2015 (n = 4–5 fish per set), and 9 within Brewers Bay, St. Thomas, USVI (18° 20′ 25.08″ N, 64° 58′ 39.77″ W) from June–August 2016 (n = 10–19 per set). We also repeated the Reef–Bucket protocol at 3 shallow reef sites in front of the Lizard Island Research Station, GBR, Australia (14° 39′ 59.47″ S, 145° 26′ 50.22″ E) in October 2016 and July 2017. Briefly, for the Reef–Bucket protocol, caged fish placed on the reef were immediately placed in individual buckets at the time of retrieval. At Lameshur and White Bays, we used a narrow (sub-adult) size range (10–15 cm) of French grunt. At Brewers Bay, we used a broader range to include juvenile grunts (4.5–15 cm). At Lameshur and Brewers Bays, we further categorized gnathiids according to developmental stage.

In 2016 at our GBR site, *C. macrodon* (n = 3), *L. gibbus* (n = 4), and *L. carponotatus* (n = 7) were set amongst conspecifics at a single reef-site ('Outfront Reef') at 15:30 h and retrieved shortly after sunset (18:35 h) when conspecifics departed. In 2017, fish in cages were set at each of 2 reef sites ('Outfront Second' and 'Beach Pipe'). Both included 5 *L. carponotatus* and 6 *C. quinquelineatus*. These fish were set between 15:23 and 15:45 h and retrieved at dusk, between 18:26 and 18:42 h.

2.3.3. Gnathiid biomass transferred

At 6 sites, we counted all *H. flavolineatum* within target size classes to estimate the biomass of gnathiid transfer at each site. At White Bay, all French grunts 10–15 cm were counted on a ~200 m^2 section of reef (~3000 m^2 total reef area). At all other sites, we counted all French grunts within a size range of 4.5–15 cm. At Leinster Bay (18° 22′ 1.36″ N, 64° 43′ 36.00″ W) and Round Bay (18° 20′ 47.90″ N, 64° 40′ 48.43″ W) (St. John, USVI), we performed 2 additional Reef–Bucket sets at each site and counted the number of French grunts in aggregations surrounding the area in which we placed the caged fish. In Tamarindo Bay and Cayo Enrique, all French grunts within 10 × 20 m plots (n = 3) at each site were counted. In Brewers Bay, we counted all French grunts within the entire bay (~1000 m diameter). These counts, along with the average number of gnathiids per fish and mass of third-stage, fed gnathiids (0.0004 g, M. D. Nicholson et al. unpubl. data), were used to calculate the biomass of gnathiids transported during nightly migrations. For White Bay, Tamarindo Bay, Cayo Enrique, and Brewers Bay, we estimated the gnathiid biomass transported for the entire site based on the area of reef surveyed and the total reef area within each bay. Thus, standard error was omitted from this estimate.

2.4. Statistical analyses

All analyses, unless otherwise stated, were conducted using the R environment version 4.0.2 (R Core Team 2022). See Section S3 in the Supplement (www.int-res.com/articles/suppl/m731p249_supp.pdf) for all final R code used. For all statistical analyses, we used a significance value (alpha) of 0.05, unless otherwise stated. For gnathiid abundance, generalized linear mixed models (GLMMs) with a negative binomial error distribution, with linear or quadratic parameterization, and without or with zero-inflation were tested, and the best-fitting model was selected using Akaike's information criterion (AIC). GLMMs were constructed using the function 'glmmTMB' in the package 'glmmTMB' (Brooks et al. 2017) and with an analysis of deviance test (Type II Wald chi-squared tests) using the function 'Anova' in the package 'car' (Fox & Weisberg 2019). Residual diagnostics analyses, tested using the R package 'DHARMa' (Hartig 2022), indicated that the assumptions of the final models were met. For all, a quadratic parameterization, using the function 'nbinom2(link='log')', provided the best fitting model. To test whether fish FL differed among treatments, a model using the function 'lm', in the R environment version 4.0.2 (R Core Team 2022), was used. Effect plots, constructed using the R package 'effects' (Fox 2003), were used to visualize results ac-

cording to the fixed factors tested; this package was also used to examine partial residuals of models. Some plots were also created in JMP® Pro version 16 (SAS Institute)

For the 4-treatment experiment in Tamarindo Bay (Table 1), we tested a model with gnathiid abundance as the response and cage 'treatment' as a fixed categorical effect and 'trial day' as a random effect; FL was not included in this main model because it was not available for all trial days (see Section 2.3.1 for processing); however, we also tested a reduced dataset for which FL was available (N = 66, instead of N = 150 samples), using an identical model as above but with FL as a fixed continuous effect. Only 3 (Reef–Bucket, Reef–Commute, and Reef–Seagrass) of the 4 treatments were included. 'Seagrass-only' was not included, as it was treated differently (fish cages were not placed on the reef first).

In a second analysis, we compared the proportion of fish with and without a gnathiid(s) between the Seagrass-only and the Reef–Seagrass treatments. We did this to determine whether the number of gnathiids on fish retrieved from Reef–Seagrass treatments could be accounted for by gnathiids attaching to fish while in the seagrass bed (Seagrass-only). We used the presence/absence of gnathiids because of the high number of zeros in the data (88 and 79% per treatment, respectively). GLMMs with a binomial error distribution, without or with zero-inflation, were tested, and the best-fitting model was selected using AIC (i.e. without zero-inflation); the same model, methods, and packages as for counts described above were used. Whether fish FL varied among all 4 treatments was tested using a linear model.

For locations in the Caribbean where only Reef–Bucket data were collected (Table 1), we tested a model with gnathiid abundance as the response, 'site' (Brewers, West Lameshur, White Bay) as a fixed categorical effect, fish 'FL' as a fixed continuous effect, 'trial day' as a random effect, and the interaction between the 2 fixed effects. This model was then simplified by dropping the interaction term that was non-significant (site × FL, $p = 0.131$), following Quinn & Keough (2002); both the initial full and final simplified models are presented. For the GBR (Lizard Island) data, gnathiid abundances in the Reef–Bucket treatment were summarized visually using boxplots according to sampling times, site, and fish species. Data were not analyzed further, as sampling involved only 1 treatment and was relatively unevenly balanced across times, sites, and fish species.

2.5. Host identification from gnathiid blood meals

2.5.1. Collection of free-living gnathiids

To confirm that gnathiids inhabiting seagrass beds feed on diel-migratory fishes under natural conditions, we collected free-living gnathiids from seagrass beds adjacent to shallow coral reefs known to have high densities of gnathiids. This includes reefs within Tamarindo Bay, Culebra, Puerto Rico (18° 19′ 3.54″ N, 65° 19′ 5.06″ W) and 2 locations along the coast of La Parguera in SW Puerto Rico (Cayo Enrique: 17° 57′ 17.59″ N, 67° 3′ 9.96″ W and San Cristobal: 17° 56′ 33.60″ N, 67° 4′ 41.02″ W). Gnathiids were also collected from patch reefs and seagrass within Brewers Bay, St. Thomas, USVI (18° 20′ 25.08″ N, 64° 58′ 39.77″ W) and Lameshur Bay, St. John (18° 19′ 2.17″ N, 64° 43′ 21.09″ W). However, due to the low number of successful sequencing reactions for gnathiids collected from the seagrass in St. Thomas and St. John, these samples were not included in our statistical analyses.

Lighted plankton traps were deployed within plots of reef habitat and along transect lines running into adjacent seagrass beds following the methods of Artim & Sikkel (2016) and Artim et al. (2020). Reef plots were divided into 66 evenly spaced points within a 10 m × 20 m grid. Transect lines were run perpendicular to each plot, starting from the reef edge and extending for 50–80 m into the seagrass, and traps were set every 5 m. For both reef and seagrass habitats, traps were set before dusk and collected the following morning. The contents of each trap were sorted under a stereomicroscope to remove fed gnathiids (pranizae), which were then preserved in 100% molecular grade ethanol. Gnathiids were stored at ≤–20°C prior to being shipped to Arkansas Biosciences Institute (Arkansas State University, Jonesboro, AR) for DNA extraction. All samples were kept at −80°C during long-term storage. Gnathiid collection from each site occurred between May and August of both 2015 and 2016.

2.5.2. Host DNA amplification and sequencing

DNA was extracted from individual gnathiid blood meals following the methods developed by Hendrick et al. (2019). Briefly, DNA was purified using the PureLink® Genomic DNA extraction kit (Invitrogen) and concentrated from 50 to 15 µl using the Thermo-Savant ISS110 SpeedVac® System (Thermo Fisher Scientific). Host DNA was selectively amplified by

PCR using fish-specific primers of the mitochondrial gene cytochrome *c* oxidase subunit 1 (cox1, COI, or MT-CO1) (5′-TCA ACY AAT CAY AAA GAT ATY GGC AC-3′; 5′ACT TCY GGG TGR CCR AAR AAT CA-3′). PCR reactions (20 µl) included 10 µl of template DNA and 10 µl of a master mix solution containing both forward and reverse COI primers, 1.25 units GoTaq Hot Start Polymerase, 1× buffer with 1.5 mM $MgCl_2$ (Promega), and 0.2 mM dNTP Mix (Thermo Fisher Scientific). PCR was performed using a Veriti 96-well thermal cycler (Applied Biosystems) programmed for the following conditions: 2 min initial denaturation at 94°C; 30 cycles of 20 s at 96°C, 20 s at 55°C, and 45 s at 72°C; and a 7 min final extension at 72°C. Excess PCR reagents were digested using ExoSAP-IT (Applied Biosystems). For samples that resulted in failed sequencing reactions, PCR amplicons were reamplified using 10 µl of the original PCR product as template DNA. Samples were sent to the University of Chicago Comprehensive Cancer Center, DNA Sequencing & Genotyping Facility, for Sanger sequencing.

2.5.3. Host identification

DNA sequences were trimmed and visualized using Geneious R10 (Biomatters). Nucleotide sequences were entered into the Basic Local Alignment Search Tool (BLAST) on the National Center for Biotechnology Information (NCBI) website to search for homologous reference sequences. Query results indicating ≥98% identity were considered species-level identification. Sequences with <98% identity were identified to the highest taxonomic level (family) using neighbor-joining trees of the BLAST results using the methods described by Jones et al. (2007). Because DNA sequences were derived from partially digested blood meals, and not voucher specimens, all sequences were uploaded into the Biological and Chemical Oceanography Data Management Office (BCO-DMO) database.

2.5.4. Host assemblages from reef- and seagrass-collected gnathiids

Statistical analyses comparing the composition of host sequence identities across sites were conducted using R v4.1.3 (R Core Team 2022) and the package 'vegan' (Oksanen et al. 2022). To determine whether patterns of host use by gnathiids across sites are consistent, we assessed the variation among assemblages of identified hosts at each site using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances using the function 'metaMDS'. The significance of the NMDS ordination differences was tested by permutational multivariate analysis of variance (PERMANOVA) using the function 'adonis2'. To test whether beta-dispersion influenced the significance of the ordination results, an ANOVA was performed.

3. RESULTS

3.1. Field experiments

3.1.1. Transport of gnathiids between habitats during nocturnal migrations

Gnathiid abundance per fish was highly variable among the 4 treatments employed in Tamarindo Bay (Fig. 2). Overall, there was a significant difference in gnathiid abundance per fish among the 3 treatments where the fish had first been deployed in a reef habitat (χ^2 = 41.114, df = 2, p < 0.0001, Fig. 3), with loads from the Reef–Bucket treatment being highest

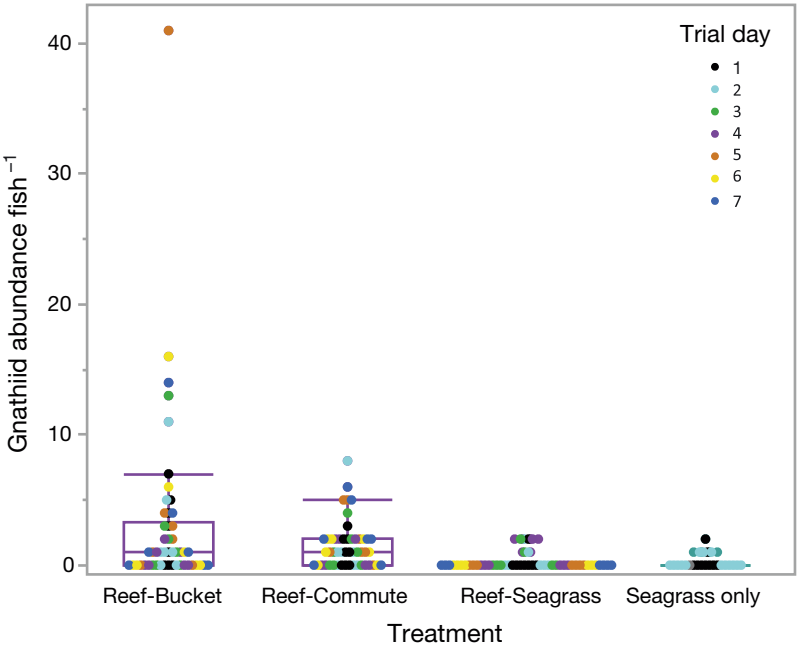

Fig. 2. Tamarindo Bay 4-treatment experiment. Boxplots of gnathiid abundance per fish according to cage treatment. Center line = median, box = interquartile range, error bars = 90th and 10th percentiles, and circles = outliers. Note: Seagrass only was sampled on Days 1 and 2 only

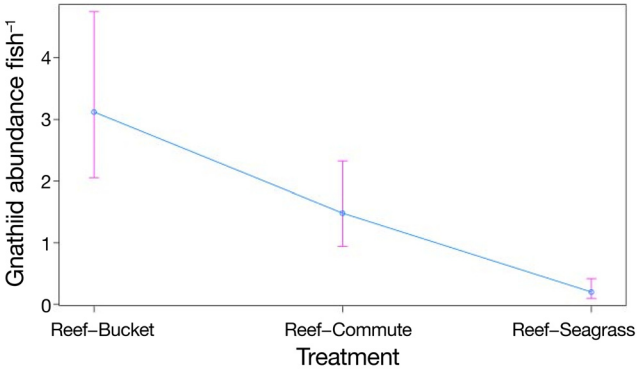

Fig. 3. Caribbean experiment. Results — visualized using an effect plot — of generalized linear mixed model showing the model-computed mean gnathiid abundance by cage treatment, accounting for the random factor 'trial day'. Error bars are 95% CI. Data were analyzed with a negative binomial error distribution; however, values were backtransformed here for ease of interpretation (and thus asymmetric)

(3.1 mean effect, 2.1–4.7 95% CI, n = 50), followed by the Reef–Commute treatment (1.5, 0.9–2.3, n = 50) and then the Reef–Seagrass treatment (0.2, 0.1–0.4, n = 50); both Reef–Commute ($p = 0.017$) and Reef–Seagrass ($p < 0.0001$) were significantly lower compared to the Reef–Bucket baseline treatment (Table S1). Using a smaller dataset for which FL was available, a model with FL included revealed similar patterns in median abundance among treatments (Fig. S1a); while the effect of treatment was also significant ($p = 0.0001$), only Reef–Seagrass differed from the baseline Reef–Bucket treatment ($p < 0.0001$); the effect of FL was not significant ($p = 0.062$, Fig. S1b, Table S1c,d). The Seagrass-only treatment was not included in the above analysis as it was treated differently (i.e. not placed on the reef like the rest were) and was used to assess the number of gnathiids that may have attached to fish in the Reef–Seagrass treatment; the values in both treatments were low with many zeros (Seagrass-only: 0 median, 0/0 25/75th quantile, 0–2 range, N = 24; Reef–Seagrass: 0, 0/0, 0–2). Therefore, the data were analyzed as presence/absence of gnathiids; the prevalence (Seagrass-only: 21%; Reef–Seagrass: 12%) was not significantly different between treatments ($\chi^2 = 0.9778$, df = 1, $p = 0.323$, Fig. 2, Table S1e,f). Model-computed mean fish FL among the 4 treatments ranged from 12.0 to 12.9 cm, with no significant difference among treatments ($F = 0.6175$, df = 3, $p = 0.606$, Fig. S1c, Table S2).

3.1.2. Gnathiid presence on diel-migratory hosts at the time of migration

At the other eastern Caribbean sites (Virgin Islands), gnathiids were present on grunts at the time of departure at all 3 sites (Fig. 4). There was no significant difference in gnathiid abundance per fish among sites ($\chi^2 = 4.236$, df = 2, $p = 0.120$, Figs. S2 & S4); mean effects (95% CI) per site were Brewers: 0.8 (0.3–1.7), West Lameshur: 0.8 (0.1–7.9), and White Bay 3.4 (1.0–11.1); abundance increased in a curvilinear relationship with fish size ($\chi^2 = 15.875$, df = 1, $p < 0.0001$, Figs. S3 & S4, Table S3), e.g. fish 4.6, 8.1, 12, 15, and 18 cm FL had an estimated mean 0.2, 0.5, 1.4, 2.9, and 6.0 gnathiids (for 95% CIs, see Fig. S3). At Brewers Bay, where fish from a broad size range that was skewed towards smaller sizes were used (fish 4.6–10 cm FL, a size range not sampled elsewhere), 76% had no gnathiids, the smallest fish with a gnathiid was 4.9 cm FL, and the remaining infected fish had 1 to 22 gnathiids (8–9.7 cm FL). Among larger fish from all sites (range: 10.1–18.5 cm, FL), there was much variation in gnathiids per fish, both among trial days and the sizes of fish sampled (range 0–31 per fish: Figs. S2 & S3). At sites where we quantified the size class of juvenile gnathiids (Tamarindo

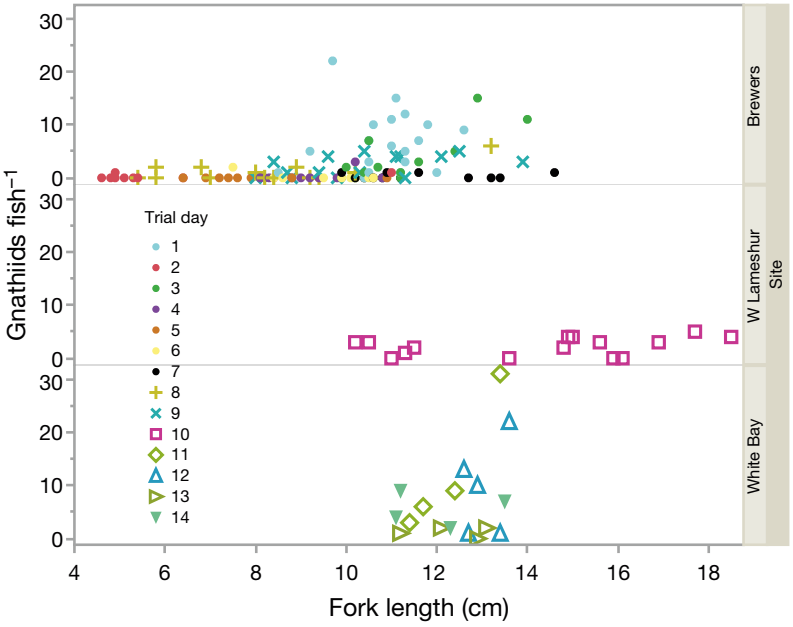

Fig. 4. Virgin Islands surveys. Gnathiid abundance per fish relative to fish fork length according to site (Brewers, West Lameshur, White Bay) and trial day (1–14) sampled

Bay, Culebra; Brewers Bay, St. Thomas; and Lameshur Bay, St. John), all stages were present on fish during the dusk emigration time (Table 2).

At the GBR site (Lizard Island), where up to 2 times, and up to 3 reef sites were sampled per species, both cardinalfish species and snapper species had gnathiids attached at the time of dusk departure in the Reef–Bucket treatment (Fig. 5). After pooling across times where applicable, of the cardinalfishes, *Cheilodipterus macrodon* had a mean (±SE) of 5 ± 2 gnathiids per fish at the single site sampled, and *C. quinquelineatus* had 2 ± 1 and 7 ± 3 at the 2 sites sampled. For the much larger snappers, *Lutjanus gibbus* had 4 ± 2 at the one site sampled, and *L. carponotatus* had the highest abundances, with 15 ± 2, 77 ± 9, and 92 ± 27 gnathiids per fish at the 3 sites sampled.

3.1.3. Gnathiid biomass transferred during grunt migrations

In White Bay, we counted 365 *Haemulon flavolineatum* (10–15 cm) and found an average of 7 ± 2 gnathiids per caged fish. Across the ~3000 m^2 reef area, we estimated that this population transferred ~21 g of gnathiid biomass per night. In Leinster and Round Bays, there were 400 and 450 grunts in aggregations surrounding our Reef–Bucket set, respectively. Caged fish at the Leinster aggregation had an average of 1.9 ± 2.1 gnathiids per fish for a total biomass (±SE) of 0.3 ± 0.1 g transported per aggregation. Gnathiid loads on caged fish placed at the Round Bay aggregation averaged 2.6 ± 4.4 gnathiids per fish, for a total of 0.4 ± 0.1 g of biomass transported per aggregation. At Cayo Enrique, we counted 337 *H. flavolineatum*, and caged fish had an average of 3 ± 3.8 gnathiids per fish. Over the total reef area (~3000 m^2), we estimated roughly 2 g of gnathiid biomass transported. Within Tamarindo Bay, 1671 French grunts were counted and the average load per caged fish was 3.1 ± 6.7 gnathiids. The gnathiid biomass transported in Tamarindo Bay was ~10 g across the entire bay (~3000 m^2 total area). Within Brewers Bay, we counted 2995 *H. flavolineatum* and an average of 2 ± 3.7 gnathiids per caged fish at migration. We estimated that 2.3 ± 0.4 g of biomass are transferred by grunt-transported gnathiids in Brewers Bay during each migration.

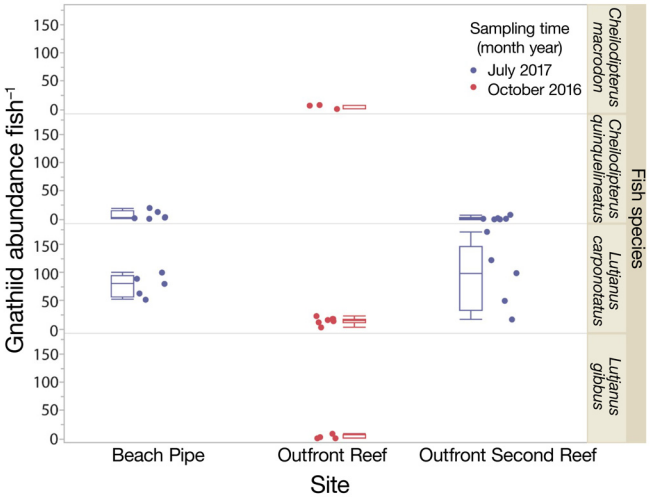

Fig. 5. Great Barrier Reef (Lizard Island). Gnathiid abundance per fish in the Reef–Bucket treatment according to fish species, sampling time, and site. Boxplot parameters as in Fig. 2. Raw data points are jittered and overlaid to one side of each plot so as not to obscure the boxplot

Table 2. Distribution of gnathiid isopod developmental stages among French grunt *Haemulon flavolineatum* at the time of departure from reef habitat at dusk

Site	Gnathiid developmental stage (%)			
	n	P1	P2	P3
Tamarindo Bay	246	16.2	21.2	62.6
Brewers Bay	238	24.3	47.1	28.6
Lameshur Bay	35	2.9	20.2	76.5

3.2. Host identification from gnathiid blood meals

A total of 128 sequences were obtained from gnathiids collected in seagrass beds from 4 Caribbean sites (Cayo Enrique, San Cristobal, Tamarindo Bay, and Brewers Bay). BLAST queries resulted in species-level identification for 87 sequences, with host identities matching 31 species from 15 fish families. Neighbor-joining trees constructed from BLAST results brought the total number of host families identified to 15 (Table 3). Sequence identification results from gnathiids collected in Brewers Bay and Lameshur Bay were not included in comparisons of assemblages of hosts from seagrass-collected gnathiids due to the low sample size (n = 9). A list of all hosts identified from reef- and seagrass-collected gnathiids is included in Table S4.

NMDS analysis in k = 2 dimensions indicated that the composition of host sequence identities did not vary across sites (stress = 0.048). This was further confirmed by a PERMANOVA analysis of the NMDS results (F = 0.827, p = 0.650) and a test of beta-dispersion (F = 0.997, p = 0.413). Because all

Table 3. Percentage of Caribbean host families identified by blood-meal sequencing of wild-caught gnathiids from both reef (R) and seagrass (SG) habitat for each site (San Cristobal: n = 153 R, 26 SG; Tamarindo Bay: n = 68 R, 23 SG; Cayo Enrique: n = 174 R, 70 SG). 'Night habitat' refers to the habitat exploited by each family at night

Night habitat and Family	Cristobal (%) R	Cristobal (%) SG	Tamarindo (%) R	Tamarindo (%) SG	Enrique (%) R	Enrique (%) SG
Reef						
Acanthuridae[a]	5.9	11.5	7.4	8.7	1.7	1.4
Gobiidae	0	0	2.9	0	0	0
Holocentridae[a]	5.2	0	1.5	0	4	5.7
Labrid parrotfishes	1.3	0	1.5	0	0	0
Labrisomidae	0.7	0	1.5	0	0.6	0
Muraenidae[a]	0	3.8	1.5	0	0.6	0
Pomacanthidae	0.7	0	0	0	0	0
Pomacentridae[a]	5.2	3.8	0	0	5.2	1.4
Serranidae	0	0	2.9	0	1.1	0
Reef/Sand						
Labrid wrasses[a]	2.6	3.8	1.5	0	1.7	0
Sand/Seagrass						
Haemulidae[a]	34	26.9	36.8	26.1	32.8	24.3
Lutjanidae[a]	15.7	15.4	7.4	8.7	16.1	30
Dactyloscopidae[a]	0	0	1.5	4.3	0.6	1.4
Microdesmidae[a]	0	0	0	4.3	0	0
Mullidae[a]	5.9	0	25	4.3	3.4	1.4
Gerreidae[a]	7.2	7.7	2.9	0	6.9	8.6
Kyphosidae[a]	3.3	0	0	4.3	0	0
Sparidae[a]	7.2	26.9	0	30.4	16.1	12.9
Transient						
Carangidae[a]	4.6	0	4.4	4.3	7.5	12.9
Clupeidae	0	0	1.5	0	0	0
Echeneidae	0	0	0	0	0.6	0
Ostraciidae[a]	0.7	0	0	4.3	1.1	0

[a]Host families identified by sequencing the blood meals of gnathiids collected in seagrass habitats

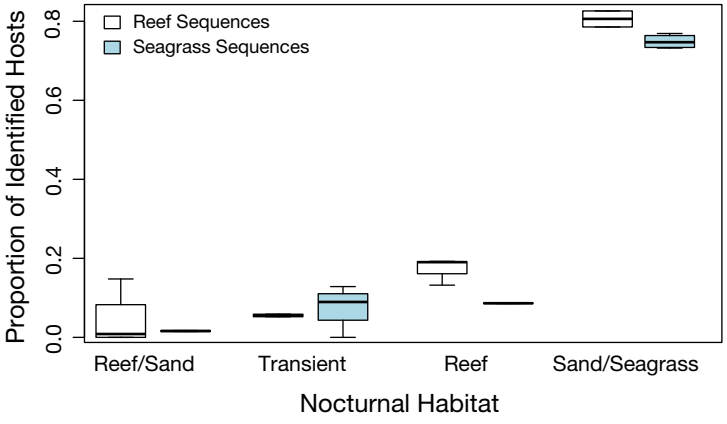

Fig. 6. Proportion of fish hosts identified by sequencing blood meals of light trap-collected gnathiid isopods (from reef plots and seagrass habitats) according to the habitat they exploit at night. Boxplots — center line: median; box: interquartile range (IQR); upper whisker: Q3 + 1.5 IQR; lower whisker: Q1 – 1.5 IQR. Host families across all sites were pooled and grouped according to the habitat type (Reef/Sand, Transient, Reef, Sand/Seagrass) where they reside or forage at night

sites had similar host assemblage compositions, results from Cayo Enrique, San Cristobal, and Tamarindo Bay were pooled for both seagrass and reef samples. Host species were grouped according to the habitat they exploit during peak activity periods of gnathiids (Table 3). The proportion of hosts belonging to each group ('Reef', 'Reef/Sand', 'Sand/Seagrass', or 'Transient') was visualized using a boxplot (Fig. 6). Most hosts identified from both reef-collected and seagrass-collected gnathiids consisted of species within the group 'Sand/Seagrass'. As shown in Table 3, most hosts identified within this group are species within Haemulidae and Lutjanidae (diel-migratory fishes).

4. DISCUSSION

Ecological communities are characterized and integrated by the transfer of energy among their constituents, and the import and export of energy is a significant component of their contribution to overall trophic structure (Dunne et al. 2023). One hypothesis for animal migration is reduction in parasite loads by avoiding habitats where parasite abundance is high (Shaw & Binning 2016, Shaw et al. 2018, Binning et al. 2022). While migrating animals may reduce parasitism overall, migrating animals may also transport parasites, contributing to the spread of parasites and trophic transfer via parasite biomass and through infection of other hosts (Barré & Uilenberg 2010, Douglas et al. 2015). Given the typically high biomass of migrating animals, even small numbers of parasites per animal can have a significant impact overall. However, these dynamics have not been examined for migrating fishes, including coral reef fishes. Our findings show that for sites in both the Caribbean and GBR, fish-parasitic gnathiid isopods are attached to diel-migratory fishes at the time they depart reef habitat for seagrass habitat. Field experiments in the Caribbean also showed that gnathiids from reef habitat dislodge in seagrass habitat. Sequencing of blood meals from free-living gnathiids collected in seagrass beds further showed that they feed on seagrass residents but feed most often on diel-migratory and other transient fishes.

Furthermore, we show that aggregations of French grunts, one of the most frequently infected host species in the Caribbean (Coile & Sikkel 2013, Sikkel et al. 2017, Hendrick et al. preprint doi:10.21203/rs.3.rs-2440357/v1), can transport over 20 g of gnathiid biomass per 3000 m^2 reef area per nightly migration.

In both the tropical Atlantic and Indo-Pacific, gnathiids are most active between dusk and dawn (Chambers & Sikkel 2002, Sikkel et al. 2006, 2009, Grutter et al. 2018, Santos & Sikkel 2019), and occur in higher densities in reef versus seagrass habitat (Sikkel et al. 2017, Artim et al. 2020). Thus, fishes that leave the reef at night experience reduced exposure to gnathiids. However, exposure is not eliminated entirely, and they can thus transfer gnathiids to seagrass beds when they commute. Similarly, while fish experience significantly reduced gnathiid infestation while feeding in seagrass, small numbers will attach (Sikkel et al. 2017) and can therefore be transferred to reef habitat. However, the majority of gnathiids that are attached to grunts upon their return to the reef in the early morning will be gnathiids that are living in reef habitat near daytime aggregation sites. Indeed, the average number of such gnathiids that attach to grunts upon their return (average of 5 per fish) is comparable to the number present on fish during dusk departure (Sikkel et al. 2017, this study).

The trophic connectivity provided by transported gnathiids depends on the fate of the gnathiids, direction of transport, and developmental stage. Gnathiids attached to French grunts during the dusk departure time represented all developmental stages. First- and second-stage gnathiids could molt and then be available to attach to new hosts, whereas third-stage gnathiids would metamorphose to adults, which have the potential to reproduce but would then die. In addition to infecting other hosts in the seagrass bed, gnathiids could be eaten by microcarnivorous fishes. Similarly, gnathiids transported to the reef can infect other fish species and be eaten by cleaners and other microcarnivores, as well as corals (Artim & Sikkel 2013, Artim et al. 2017, Paula et al. 2022).

Sequencing of blood meals from seagrass at some of our Caribbean sites indicated that diel-migratory fishes were the most exploited hosts. However, species that reside in the seagrass bed were also fed upon, as were species that reside in seagrass as juveniles but are associated with reef habitat as adults. Seagrass beds provide critical habitat for settlement-stage and juvenile fishes, which will eventually sustain the populations of surrounding habitat (Heck et al. 1997, Jackson et al. 2001, Nagelkerken et al. 2002, Dorenbosch et al. 2005). The seagrass provides a safe habitat with a low risk of predation, allowing the juveniles to allocate more energy towards growth as opposed to evasion of predators (Gilliam & Fraser 1987, Bax 1998). However, an influx of gnathiids can have negative consequences, as a single gnathiid can kill a settlement-stage fish (Artim et al. 2015, Grutter et al. 2017, Sellers et al. 2019) and can hinder the escape responses of juvenile individuals (Allan et al. 2020). There are also resident species that we have confirmed — through the results of sequencing of blood meals — are being fed on by gnathiids in the seagrass. This finding further supports the importance of diel-migratory fishes in the transport of gnathiids, and shows an important role of species that move between reef and seagrass.

Because diel-migratory and other highly mobile fish from different reefs interact with the same seagrass bed, seagrass beds can be hubs for 'exchange' of gnathiids. A series of reefs and seagrass beds can therefore become interconnected through the 'flow' of gnathiids (Fig. 7). Although smaller species, such as French grunt in the Caribbean and cardinalfishes in the Indo-Pacific, may travel less than 300 m, our sequencing of blood meals showed that much larger and more mobile species are fed on by gnathiids. These include Carangid jacks, such as permit *Trachinotus falcatus*, which have been shown to travel over 30 km (Boucek et al. 2022). This has important implications for the population-genetic structuring of gnathiids (Pagán et al. 2022) and even the spread of disease-causing microorganisms they may transmit (Cook et al. 2015, Sikkel et al. 2020).

At both our Caribbean and GBR sites, all diel-migratory fish tested were fed upon by gnathiids, and in many cases, fish had heavy loads of over 30 gnathiids. In the Caribbean, haemulid grunts and lutjanid snappers are also the most susceptible and the most frequently fed upon by gnathiids, relative to abundance, in reef habitat (Coile & Sikkel 2013, Hendrick et al. preprint doi:10.21203/rs.3.rs-2440357/v1). Because diel-migratory species typically aggregate, they have high local biomass, which can create a 'hotspot' for the accumulation of gnathiids, which are both carried back to the reef by fish in the early morning and await to feed on them shortly after their return (Sikkel et al. 2017). This further contributes to the ecological impacts of their 'transport' activity but also increases impacts on any other host species that live near aggregations. Because the migrating species would be absent during peak gnathiid activity, those gnathiids would then attack other hosts residing on the reef at night.

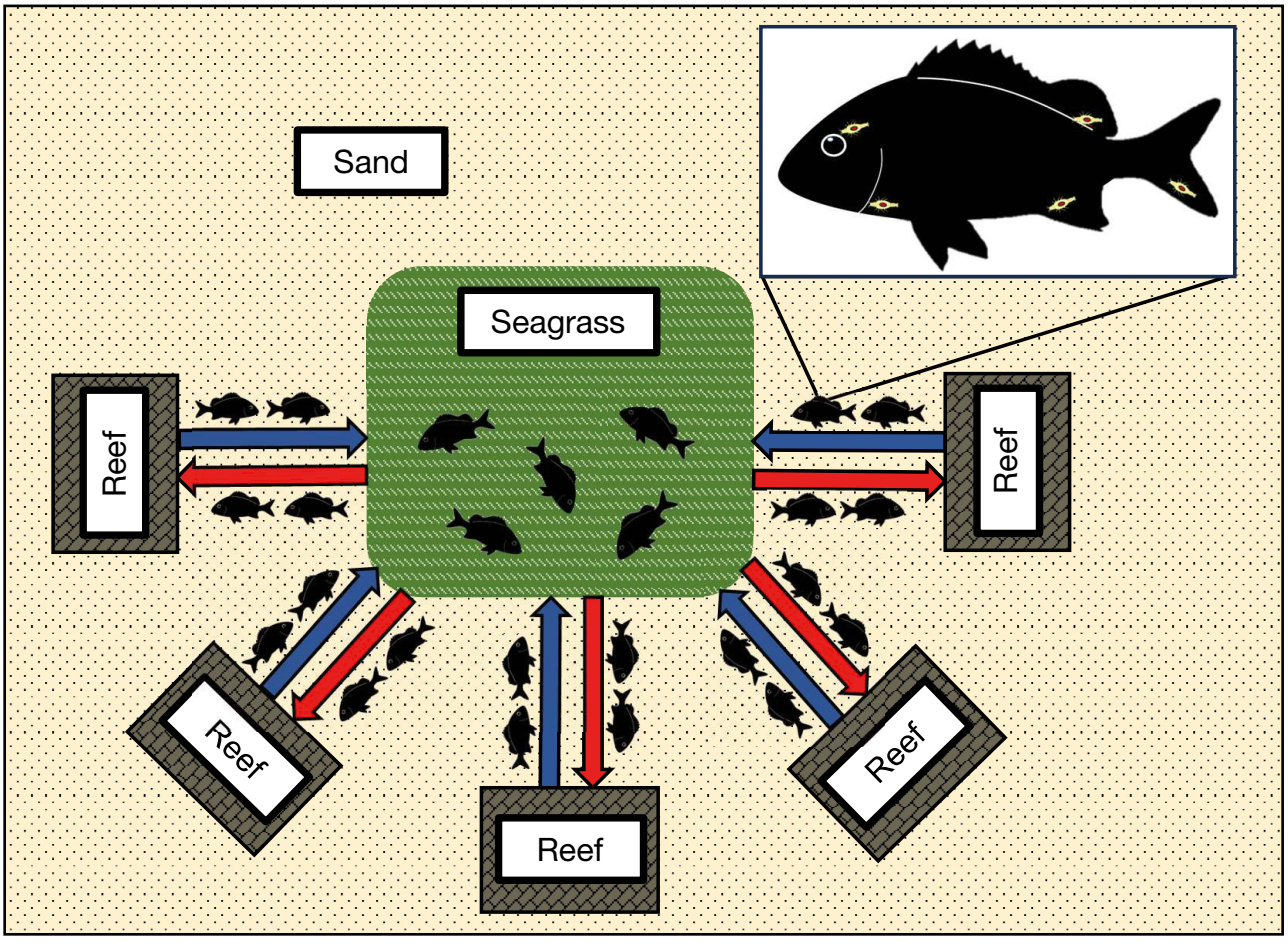

Fig. 7. Functional connectivity via transport of parasitic gnathiid isopods by diel-migratory fishes such as grunts (Haemulidae) that move daily between reef and seagrass habitat. Fish from different reefs enter the same seagrass bed at night. Gnathiids can be transported from reef to seagrass (blue arrows) and seagrass to reef (red arrows), and therefore between reefs and host fish populations. This connectivity has impacts on multiple processes, including the flow of energy between habitats, the level of infection that other fish such as juvenile fish are likely to experience, the spread of diseases transmitted by gnathiids, and the population genetic structure of gnathiids. Close-up of a fish (top, right) transporting attached gnathiid isopods

5. CONCLUSION

Migratory fishes contribute to the trophic connectivity across many habitats. Here we describe an additional mechanism of connectivity through the transfer of parasites. While we focused on one kind of ectoparasite (gnathiid isopods), most host species harbor a diverse suite of parasites, both internally and externally. Future studies should therefore include additional parasite species that may contribute to trophic transfer while also comparing parasite-mediated transfer to that of predation and waste production. While we have shown the mechanisms by which parasite transfer can occur among reef and seagrass habitats, mangroves are another critical habitat with resident, juvenile, and migratory fishes that harbor parasites, including gnathiids. However, the implications for parasite transport reach far beyond coastal communities. For example, some host fishes (i.e. lutjanid snappers and serranid groupers) make long migrations to offshore spawning locations and can transfer parasites between habitats. While we focused on coral reef systems, fishes in other marine habitats undergo migrations, such as the diel migrations of mesopelagic fishes. These fishes also harbor multiple parasites (Woodstock et al. 2020), but the influence of these migrations on the transfer of parasites is unknown. Thus, future studies should include a broader range of marine systems. Finally, given the increasing recognition of the importance of disease spread in marine systems (Panek 2005, Crane & Hyatt 2011, Sikkel et al. 2020), the direct and indirect effects of parasite transport on disease transmission cycles in marine habitats is clearly worth investigating.

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