

Are cleaner fishes replaceable on coral reefs as consumers of fish ectoparasites?

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Abstract

Specialist species have evolved to fill narrow niches but are especially susceptible to environmental change. With sufficient functional redundancy, ecosystem services can persist without specialists. Grooming behaviors are common in both terrestrial and aquatic organisms. However, in aquatic systems there is a heavy reliance on intraspecific mutualisms where specialist species groom or “clean” parasites off host fishes. Here, we sampled the gut contents of 709 fishes, representing 61 species and including both cleaner and non-cleaner fishes, to compare their consumption of gnathiid isopods, the most common fish ectoparasites. We found that cleaner fishes eat significantly more gnathiids, and eat them more frequently, compared to non-cleaner fishes. Our results highlight the importance of both dedicated and facultative cleaners as consumers of ectoparasites and show that their role cannot be supplanted by generalist consumers. Furthermore, we suggest that different cleaner species act as complementary rather than redundant specialists.

Introduction

Within an ecosystem, sympatric species can co-occur largely due to ecological adaptations that reduce competition for resources and habitat predation risk (Grether et al. 2017, Lankau 2011, Perri and Randall 1999, Siepielski and McPeck 2010, Zhao et al. 2020). The resulting community structure, where a collection of species fills a variety of ecological niches, is one that is fundamental to ecosystem functioning (Genung et al. 2020, Petchey et al. 1999, Spaak et al. 2017). However, shifts in environmental conditions can cause changes in these dynamics and disrupt the overall ecosystem structure, potentially altering key environmental functions or services. Generally, those niches with lower functional redundancy are less resilient to change (Bellwood et al. 2003, reviewed by Biggs et al. 2020, Micheli and Halpern 2005). For example, in African savannahs, the exclusion of even one of the primary consumers of invasive and problematic shrub (*Solanum campylacanthum*) led to increases in its abundance (Pringle et al. 2014). *S. campylacanthum* is toxic to livestock and has negative impacts on grazing species as well as vegetation (Pringle et al. 2014). Even though three herbivorous species are known to forage in the understory where the shrub grows, they function as complementary rather than redundant consumers.

Ecological specialists differ from generalists in their overall niche width (Clavel et al. 2010, Futuyma and Moreno 1988). That is, specialists occupy a narrower niche, typically with regard to some combination of habitat choice and food preference (Futuyma and Moreno 1988). Specialists have generally evolved to outcompete generalists, maximizing the exploitation of the selected resource. They thrive when environmental conditions are stable but can struggle to adapt in variable conditions (Scheiner 2002). Examples of the vulnerability of specialists to environmental perturbations exist throughout the fossil record (McKinney

1997) and modern-day specialists are similarly susceptible (Fourcade et al. 2021, Norden et al. 2013). The flexibility of generalists makes them more resilient to change, but the effectiveness of specialists makes them more difficult to replace. However, with enough functional redundancy, it is possible for multiple species of generalists to maintain an ecosystem service. For example, Memmott et al. (2007) showed that while specialist pollinators were more vulnerable to extinction, the network of resilient generalist pollinators is sufficient to sustain plant populations.

Grooming behaviors are common in terrestrial organisms, having been reported for mammals (Heine et al. 2017, Mooring et al. 2004), birds (Cox 2012, Goodman et al. 2020), and arthropods (El-Awami and Dent 1995, Invernizzi et al. 2015). These behaviors typically present in the form of autogrooming (grooming oneself), or social grooming (typically between conspecifics), and have two potential functions. First, the removal of parasites from the body of the client reduces the direct impacts of the parasites on the host and may also reduce the overall abundance of the parasites. Grooming can have a secondary effect of maintaining overall hygiene of external body surfaces, facilitating social interaction, and/or reducing stress (Soares et al. 2011).

Grooming of heterospecifics is rare in terrestrial systems and is limited primarily to generalists such as arthropod-feeding birds that will opportunistically eat insects and arachnids from the bodies of other animals (Samish and Rehacek 1999). The only apparent interspecific-grooming specialists in terrestrial systems are the two species in the family Buphagidae (oxpeckers, Bezuidenhout and Stutterheim 1980). In contrast to terrestrial species, intraspecific grooming is uncommon in marine organisms, having been reported for a small number of fish species (Clague et al. 2011, Sikkel 1986, Sikkel and Smit 2018). However, interspecific grooming, commonly referred to as “cleaning”, is well documented and is especially common in shallow reef systems.

In interspecific cleaning, certain fish or invertebrate species will obtain most of their dietary requirements by gleaning ectoparasites off other species of fishes. These interspecific mutualisms have evolved more than once in small, “picker-type”, fishes and in some shrimps (Vaughan et al. 2016). Cleaning interactions are of sufficient importance to individual “client” or “host” fishes that such fishes will interrupt other, biologically important activities (such as spawning) to get cleaned (Cheney and Côté 2003, Poulin and Grutter 1996, Sikkel et al. 2005). Within the many fish species that have evolved cleaning behaviors, most are “facultative” cleaners that clean occasionally or during specific life history stages but are overall not heavily dependent on consumption of external parasites. Examples of these include *Thalassoma bifasciatum* in the Caribbean (Dunkley et al. 2018, Feddern 1965, Itzkowitz 1979, Losey 1974), *Coris julis* in the Mediterranean (Zander and Sotje 2002), and *Johnrandallia nigrirostris*, in the Pacific (Quimbayo et al. 2017). Unique to coral reef systems, there are also obligate (or “dedicated”) cleaning specialists that rely primarily on the ectoparasites of client fishes as their main food source. (Vaughn et al. 2016). This group includes several species of *Elacatinus* gobies on coral reefs in the Caribbean region (Arnal and Côté 2000, Côté et al. 1998, Côté and Soares 2011) and *Labroides* wrasses on coral reefs in the Indo-Pacific (Côté and Brandl 2021, Grutter 1997a, Grutter 1997b, Losey 1972). Whereas wrasses tend to wander (even if associated with a “cleaning station”), cleaner gobies are often tightly associated with large boulder corals where they sit and await clients (Losey 1974, Whitley et al. 2021). While facultative cleaners tend to interact with a narrower diversity of client species compared to dedicated cleaners, they can at times eat a similar number of parasites (Grutter and Feeney 2016, Narvaez et al. 2015).

Cleaners provide numerous benefits to both individual clients and the overall community. Client-level effects of cleaners include facilitating wound healing (Foster 1985), reduced stress (Bshary et al. 2007, Soares et al. 2011), a decreased reliance on immune function (Ros et al. 2011), and increased client growth rates (Waldie et al. 2011). At the community level, the presence of cleaners impacts coral reef communities by locally increasing species richness and abundance (Bshary 2003, Grutter et al. 2003, Waldie et al. 2011). Among the myriad of services they provide, cleaners are best known for feeding on, and thus, removing the ectoparasites of client fishes. Although they consume several types of ectoparasites, the primary diet of cleaner fishes consists of gnathiid isopods (Arnal and Côté 2000, Grutter 1997a, Grutter and Feeney 2016, Losey 1974,

Sikkel et al. 2004, Vaughan et al. 2016) and cleaning activity can significantly reduce gnathiid populations (Grutter et al. 2018).

Gnathiid isopods (“gnathiids”) are hematophagous arthropods that spend the majority of their lives in the benthic substrate but emerge to feed on a fish host (Sikkel and Welicky 2019, Smit and Davies 2004). As the primary “broker” of cleaner-client interactions they can impact hosts in multiple ways. These include influencing host behaviors such as spawning (Sikkel et al. 2005), and migration (Sikkel et al. 2017), as well as interactions between clients and cleaners (Grutter 2001, Sikkel et al. 2004), reducing hematocrit (Jones and Grutter 2005), increasing stress hormones (Triki et al. 2016), reducing juvenile fitness (Allan et al. 2021, Sellers et al. 2019), and killing the host (Artim et al. 2015, Hayes et al. 2011, Penfold et al. 2008, Sellers et al. 2019). Consequently, gnathiids can negatively affect host populations (Hayes et al. 2011, Penfold et al. 2008) and thus impact community dynamics (Coile and Sikkel 2013, Grutter et al. 2018, Sikkel and Welicky 2019).

Gnathiids are most active during crepuscular and nocturnal periods (Grutter 1999, Santos and Sikkel 2017, Sikkel et al. 2006) and will parasitize a wide range of fish species (Coile and Sikkel 2013, Hendrick et al. 2019, Jones et al. 2007, Nagel and Grutter 2007, Santos and Sikkel 2017, reviewed by Sikkel and Welicky 2019). They attach to hosts only temporarily (up to several hours for most species) to feed, but once engorged with blood/body fluids, they return to the benthos to digest and molt. Thus, gnathiids spend most of their life free-living (Smit and Davies 2004, Tanaka 2007). Because of this unusual lifecycle, they have been referred to variously as temporary ectoparasites, protelean parasites, and micropredators.

There are several methods by which external parasites are consumed that do not involve grooming but still impact the parasite burden of hosts by reducing parasite population densities (reviewed by Johnson et al. 2010). This includes concomitant predation as well as predation of free-living stages (Artim et al. 2017, Kaplan et al. 2009, Thieltges et al. 2013). Because gnathiids spend most of their lives not associated with a host, they are susceptible to consumption by many fish species, including the up to 70% of species that consume invertebrates (Kramer et al. 2015). However, only one study, on a few nocturnal carnivores, has examined consumption by non-cleaners. (Artim et al. 2017).

Tropical western Atlantic coral reefs possess little functional redundancy of cleaners, and dedicated cleaner fish provide an apparently unique and critical ecosystem service that may not be compensated for were they to suffer declines in abundance. Even dedicated invertebrate cleaners are unlikely to provide sufficient compensation in the absence of dedicated cleaner fish. For example, *Ancylomenes pedersoni* (Pederson’s cleaner shrimp), are dependent on the short-lived, *Bartholomea annulata* (corkscrew anemone, Huebner and Chadwick 2012, O’Reilly et al. 2018, Titus et al. 2017) that are patchy in their distribution.

In contrast to the mostly nocturnal gnathiids, the dedicated cleaners that are considered their primary consumers are diurnal, consuming them only off the hosts’ body, and most active at dawn (Côté and Molloy 2003, Grutter 1999, Pierera et al. 2022, Sazima et al. 2000, Sikkel et al. 2004). When determining functional redundancy, we must therefore widen the scope beyond dedicated cleaners to consider the degree to which facultative cleaner species and non-cleaners might provide additional sources of gnathiid consumption. The main goal of this study was, therefore, to test predictions of the hypothesis that coral reefs possess a sufficiently high level of functional redundancy of gnathiid consumption through some combination of facultative cleaners and additional functional groups of non-cleaner fishes that consume free-living gnathiids. Specifically, we tested whether: 1) other fish functional groups consume significant numbers of free-living stages of gnathiids and 2) whether consumption by facultative cleaners is comparable to dedicated cleaners on Caribbean coral reefs. We accomplished this by sampling gut contents from 61 reef fish species from 16 families, representing multiple feeding guilds, collected across three sites in the northeastern Caribbean.

Materials and Methods

Collection Sites

Fish were collected from Lameshur Bay (18°19’0.2” N, 64°43’20.8” W), and Brewer’s Bay (18°20’25.3” N,

64°58'36.8" W) in the US Virgin Islands, and La Parguera, Puerto Rico (17°57'18.1" N, 67°03'08.1" W) (Fig. S1). All sites can be characterized as shallow reef habitat (<7m deep) with moderate to low coral cover, and a benthos largely dominated by macroalgal cover (Artim et al. 2020). Sampling occurred between May and September over a 5-year period (2017-2021).

Fish Collection Methods

A variety of methods and net types were used to collect fish while on snorkel or SCUBA. All fish were caught between sunrise and approximately 11:00 h. This time block was selected to maximize the interface between when diurnal fishes begin to feed and when gnathiids may still be active. Details on sampling for each site can be found in supplementary material (Table S1). We did not account for any effect of site because all sites are similar in composition regarding biodiversity and benthic composition, and all have been confirmed to have substantial gnathiid populations (Artim et al. 2020).

Sample Processing

Gut content samples were collected via lavage (stomach pump, Artim et al. 2017), dissection, or feces collection. Fish that were large enough to have surgical tubing (either 6mm or 3mm outer diameter) safely inserted were gut lavaged. They were then returned to the location on reef where they were caught after recovering in an aerated bin of fresh seawater. Fish that were too small to be lavaged were brought back to the lab and humanely euthanized prior to dissection. However, when possible, fish were placed in aerated tanks for ~24hrs and allowed to defecate. Fecal matter was collected, and the fishes were subsequently returned to the same area reef where they were caught. Samples were screened with a dissecting scope. Since their chitinous exoskeletons are not able to be digested, remnants of gnathiids (specifically the heads, Fig. 1), can be reliably identified by any of the sample collection methods detailed above.

Functional Groups

709 fishes across 61 species and 16 fish families were processed from our Caribbean field sites and were assigned to one of 12 functional groups (Table 1). Also included in Table 1 are results from Artim et al. (2017), where gnathiid isopods were positively identified in the stomach contents of Caribbean nocturnal microcarnivorous fishes. Two species from that study were also collected in this study but were grouped separately due to the different time of day they were caught. Fish species were separated by functional group rather than Family to cluster species with similar diets and, in some cases, habitat preference (Table 1). The only species in the “dedicated cleaner” group is *Elacatinus evelynae*, and the sole species in the “facultative cleaner” group is *Thalassoma bifasciatum*. We did not include any other species in this group (such as juvenile haemulids or pomacanthids) because they were rare at our sites. The “planktivore” group included species that primarily feed on invertebrates in the water column. “Roving herbivores” and “scrapers” include Acanthurid surgeonfishes and Labrid parrotfishes, respectively. Both groups are similar in that the species consume material off the substrate and often forage across an entire reef (if not multiple reefs) but differ in what they consume (Randall 1967). Site-attached Pomacentrid damselfishes and Blenneid blennies make up the “territorial herbivores”. Invertivorous species were separated based on habitat. Specifically, Mullid goatfishes, *Coryphopterus spp.* gobiids, and Gerreid mojarras comprised the “sand invertivores”, while small Labrisomid blennies and coral-associated gobiids and Chaenopsid blennies were grouped together as “benthic invertivores”. The mobile Labrid wrasses and Tetraodontid puffers were placed in the “invertivore” functional group. Carnivorous species were split into the “roving carnivores”, comprised of the Carangid jacks, and the “microcarnivores” which includes small Haemulid grunts, Lutjanid snappers, and Serranid hamlets that eat a variety of invertebrates but can also eat small fishes (Randall 1967). Finally, while many species exhibit omnivorous tendencies, such as benthophagous Pomacentrids that will occasionally consume invertebrates (Ceccarelli 2007), the Chaetodontid butterflyfishes and Pomacanthid angelfishes had the most even balance of algal and animal material and were thus the only fishes included as “omnivores”. Individuals from the Balistoid filefishes, Sciaenid croakers, and Scorpaenid scorpionfishes were not included because very few were encountered/collected. Additionally, 3 species were only identified to the Family level, but this did not impact the functional group they were assigned to.

Statistical Analysis

All statistical analyses were conducted in R programming language (R Core Development Team) and RStudio v.2022.02.1 (RStudio Team). In the first analysis, we fit a logistic regression with the presence/absence of gnathiids as a function of fish functional group to determine if any groups consumed gnathiids as often as dedicated cleaners. In the second analysis, a zero-inflated negative binomial (ZINB) regression was used to fit gnathiid count (per individual gut) against fish functional group to determine if any functional groups ate as many gnathiids as dedicated cleaners. We used ZINB due to overdispersion of other model fits as well as excess “0” counts which could not be predicted by model fits besides ZINB or Zero-Inflated Poisson (ZIP). This analysis utilized the `pscl` package (Zeileis et al. 2008)

Results

Likelihood of individuals to consume gnathiids

Gnathiids were identified in the gut contents of at least one individual from each functional group (Table 1) and, further, 13 out of the 16 fish Families. Functional group was a significant predictor of the presence of at least one gnathiid ($X^2=101.3$, $p > 0.005$). 100% of the dedicated cleaners consumed at least one gnathiid ($n=26$), while 64% of the facultative cleaners ($n=61$) and 33% of the planktivores ($n=36$) consumed gnathiids. All other functional groups had a gnathiid consumption rate of 13% or less.

Counts of gnathiid consumption

Fish functional group was a significant predictor of gnathiid counts ($Z=10.83$, $p < .005$). Gnathiid counts were statistically similar for dedicated and facultative cleaners, and both of those groups had significantly higher gnathiid counts than all other functional groups (Table 2, Fig. 2A). Dedicated cleaners had the highest average gnathiids per gut with 11.3 while facultative cleaners had 10.7 per gut (Table 1). Facultative cleaners were also found to consume gnathiids across all life history stages. The next highest gnathiid counts per gut were the planktivores with an average 0.6 (Table 1, Fig. 2A). Furthermore, when considering only those individuals that consumed at least one gnathiid, facultative cleaners consumed more gnathiids on average compared to dedicated cleaners. However, the magnitude of difference with respect to the other groups was largely unchanged (Fig. 2B). Based on our results, we determined the quantity of individuals from a given functional group that would be required to replace a single dedicated cleaner (Fig. 3). Facultative cleaners are a nearly one to one replacement, while planktivores would require 18 individuals, scrapers 44 individuals, and all other groups would need between 97 and 162 individuals to replace one dedicated cleaner (Fig. 3).

Discussion

The results of this study show that although upwards of 70% of fish species may consume invertebrate prey (Kramer et al. 2015), no other fish functional group has as high of a likelihood of consuming gnathiids as dedicated cleaners. Further, both dedicated and facultative cleaners consumed similar amounts of gnathiids, while all other functional groups rarely consumed them, and when they did, consumed very few.

Consumption of blood-feeding ectoparasites: A comparison with terrestrial systems

By comparison, Buphagid birds (oxpeckers) are the only terrestrial analog to dedicated cleaner fishes and the ticks they consume are the primary terrestrial analogs of gnathiids. Ticks are commonly removed from mammals by the Buphagid birds in mutualistic interactions (Bezuidenhout and Stutterheim 1980). However, like gnathiids, ticks spend a significant portion of their life cycle not associated with a host. In addition to the specialist oxpeckers, ticks are consumed by over forty species of birds across multiple orders of classification (Milne 1950, Mooring and Hart 1999, Samish and Rehacek 1999). Ticks are also susceptible to consumption by many arthropods, amphibians, reptiles, and mammals as well as infection by several pathogens (reviewed by Samish and Rehacek 1999). In fact, in some areas/habitats tick predation can be so high that populations become unsustainable (Krivolutsky 1963, Wilkinson 1970).

Culicid mosquitoes are biting flies that, like gnathiids, obtain blood meals by puncturing the external surfaces of their hosts. Due to negative impacts on human health via disease transmission, a significant amount of

effort has been dedicated to researching ways to control mosquito populations (Eba et al. 2021). To our knowledge, there are no mosquito “cleaners”, which may be one reason why many hosts have developed fly-repelling behaviors (Hart 1994). *Elephus maximus* (Asian elephants) even use branches as a tool to keep biting flies away (Hart and Hart 1994). While consumption of adults seems insufficient to control mosquito populations, it is the larvae which are aquatic, that are highly susceptible to pathogens and predation. In fact, entire mosquito populations can be biologically controlled by consumption of larval stages (Reddya Naik 2018). Predators of mosquitoes found to be useful in biocontrol include macroinvertebrates such as Odonates (Mandal et al. 2008), Dysticids (Aditya and Saha 2006), and Nonectids (Eba et al. 2021), as well as many larvivoracious fishes (Brahman and Chandra 2016, Ghosh et al. 2005) and amphibians (Lee 1967). Thus, for both ticks and mosquitoes there exists a robust functional redundancy of consumers that can lessen the ectoparasite burden of terrestrial organisms.

Can non-cleaners replace dedicated cleaners?

Dedicated cleaner fishes are considered amongst the most functionally critical and most vulnerable organism groups on coral reefs (Wolfe et al. 2020). However, this assessment is based solely on studies on Indo-Pacific cleaners. The reputation of cleaners as the major consumers of gnathiids is based on extensive gut content studies aimed at determining what cleaners are removing from clients (Losey 1974, Soares et al. 2010, Whiteman and Côté 2002). However, such studies have almost completely ignored the myriad of other fishes that could potentially consume as many or more gnathiids during their free-living stages, and that could therefore have greater impacts on gnathiid populations. While many feeding studies have been conducted on coral reef fishes (Choat et al. 2004, Hobson 1975, Randall 1967, Russell 1983) gnathiids appear to be overlooked and characterized as “unidentified crustaceans”. This is because very few individuals are trained to detect and identify them and genetic barcodes which would allow for DNA metabarcoding approaches to gut content analysis (Matley et al. 2018) have been almost completely lacking. Within each of the 10 non-cleaner functional groups was at least one individual fish that consumed at least a single gnathiid. Although some herbivores will on occasion supplement their diet with invertebrates (Ceccarelli 2007), this result was surprising because the species within the scraper and herbivore groups are not considered to be major consumers of invertebrates, let alone parasitic species. Given the infrequent occurrence of gnathiids in the gut contents of herbivores and scrapers, it seems likely that these were cases of incidental consumption where the gnathiid was consumed along with the targeted benthic algal matter. The various invertivores sampled here also consumed gnathiids quite infrequently, regardless of the microhabitat they occupied. In fact, dedicated cleaners, which comprise less than 1% of fish biomass, consumed 18 times more gnathiids per gut relative to the highest invertivore group (the planktivores) and 100 times more than the next highest group (the benthic invertivores, Table 1). This suggests that gnathiids are not a key prey item for non-cleaner invertivores. This is likely due to low habitat mediated availability (such as in the case of sand invertivores) or no preference relative to the many other available invertebrates.

Nicholson et al. (2020) showed that gnathiids sometimes travel above the benthos (upwards of 3.5m) into the water column to attach to a fish host. Planktivorous fishes in this study were the non-cleaner group most likely to consume a gnathiid (33%, Table 1) and ate gnathiids more often than the nocturnal consumers examined from one of the same study sites from Artim et al. (2017). This suggests that either gnathiids are spending time swimming above the reef during post-dawn morning times, or, more likely that they are being eaten by planktivores feeding closer to the reef substrate during dawn emergence from, or dusk entrance to, nocturnal refuges. The low-level of consumption by demersal feeding invertivores further suggests that when gnathiids are on the benthos, they are most often hiding in crevices and rubble (Artim and Sikkell 2013, Santos and Sikkell 2017).

Our data included many instances where no gnathiids were detected in fish gut samples. In cases where at least one gnathiid was consumed, non-cleaner gut contents still typically only contained the remnants of one or two gnathiids, and never more than 5 (Fig. 2B). This eliminates the possibility that there may be some intraspecific variation among non-cleaners, where some individuals have an increased likelihood to consume gnathiids. Furthermore, the consistently low levels of gnathiid consumption by non-cleaners means it would

take, for nearly all non-cleaner functional groups, nearly 100 or more individuals to compensate for the loss of a single cleaner goby (Fig. 3). These results are in line with previous studies on gnathiid consumption by nocturnal microcarnivores (Artim et al. 2017) and show that while many species and functional groups are capable of consuming gnathiids, there is not sufficient functional redundancy of gnathiid consumption by non-cleaner fishes to replace dedicated cleaners.

Can facultative cleaners replace dedicated cleaners?

Although they are the most prominent species of facultative cleaner fish on Caribbean reefs (Feddern 1965, Losey 1974), previous studies of *Thalassoma bifasciatum* cleaning behavior have reported contrasting results. However, sampling methods across studies have not been consistent. Losey (1974) specifically observed and collected *T. bifasciatum* paired with *Elacatinus spp.* at prominent cleaning stations. Dunkley et al. (2018) used focal surveys and video analyses, and our study collected individuals haphazardly from local populations. Losey (1974) found that *T. bifasciatum* associated with goby cleaning stations spent the majority of their time cleaning while also cleaning a greater diversity of hosts and consuming more gnathiids than *Elacatinus spp.* Conversely, Dunkley et al. (2018) found that *T. bifasciatum* spent most of their time foraging on the benthos and interacted with a narrower range of client species compared to dedicated cleaners. However, they did observe a single cleaning station where *T. bifasciatum* cleaned more often than any other cleaners but only cleaned Acanthurid surgeonfishes. Both studies found that the majority of *T. bifasciatum* clients were comprised of mobile species such as Acanthurids and Labrid parrotfishes. This means most resident reef species such as Pomacentrids, Holocentrids, Haemulids, and the predatory Serranids, all of which solicit cleaners, would be reliant on alternative cleaning sources (Walsh et al. 2017). Our results show that, although they were less likely to clean than *E. evelynae* (100% vs. 64%), *T. bifasciatum* can consume as many gnathiids as the dedicated cleaners. This is similar to findings from Pacific cleaners (Grutter and Feeney 2016). Further, the maximum gnathiid count for *T. bifasciatum* was nearly five times higher than that of *E. evelynae* (138 vs. 29), suggesting that *T. bifasciatum* has a higher maximum potential for gnathiid consumption. While previous studies have found that only juveniles engage in cleaning behaviors (Feddern 1965, Itzkowitz 1979, Losey 1974), we found evidence of cleaning in the gut contents of all life history stages (juvenile, sub-adult, adult, and terminal male). Thus, dedicated cleaners seem to consume gnathiids more consistently and with less variance compared to the facultative wrasse individuals, but perhaps with a lower ceiling in terms of potential consumption due to their smaller size.

Based solely on the amount of gnathiids consumed, facultative cleaners appear capable of replacing dedicated cleaners (Fig. 3). Indeed, they may be able to impact gnathiid populations solely based on predation pressure. This is supported by the fact that reefs with low coral cover but high *T. bifasciatum* abundance had lower than expected gnathiid densities (Artim et al. 2020). However, given the apparent differences in client diversity, it seems that in the absence of dedicated cleaners there would be a notable gap where certain species may suffer an increased parasite burden while also lacking the additional benefits cleaning services provide. It seems more likely that facultative cleaners such as *T. bifasciatum* and dedicated cleaners such as *E. evelynae* occupy complementary cleaner roles as opposed to redundant cleaner roles.

Can cleaning services persist without corals?

Scleractinian corals are the main architect of coral reefs and have experienced massive die-offs, leading to fundamental changes in reef substrates (Box and Mumby 2007, Cramer et al. 2020, Hughes 1994, Hughes et al. 2007, Jackson et al. 2014). These corals are known, and likely underestimated, nocturnal consumers of gnathiids (Artim and Sikkell 2013, Paula et al. 2021). Not only has high coral cover been associated with lower gnathiid abundance (Artim et al. 2020, Paula et al. 2021, Santos and Sikkell 2017), but dead coral “rubble” is the preferred refuge for gnathiids (Artim and Sikkell 2013). Moreover, corals serve as critical habitat for goby cleaning stations (Whiteman and Côté 2002) as well as a visual beacon for client fishes locating cleaning stations (Losey 1974). Thus, live coral facilitates the cleaner-client mutualism of the primary diurnal cleaner fish on Caribbean coral reefs and likely acts as the primary nocturnal consumer of gnathiids. *Elacatinus* gobies can reside in alternative sponge-based microhabitats but tend to clean significantly less compared to individuals on coral (Whiteman and Côté 2002). *T. bifasciatum* are not reliant on any specific reef

characteristics (Dunkley et al. 2018), making it unlikely for them to be directly impacted by coral loss (Artim et al. 2020). Thus, the loss of live coral will likely increase the parasite burden of those fish functional groups that rely on goby cleaning services, potentially impacting species populations and disrupting community dynamics.

Conclusions

While it has been well documented that only select species engage in cleaning behaviors, any additional functional redundancy of gnathiid consumption provided by the many fish species that consume invertebrates either primarily or nominally was unknown. Here we show that although many species consume gnathiids, the totality of their consumption is insignificant compared to both dedicated and facultative cleaners. Additionally, while dedicated and facultative cleaners consumed similar amounts of gnathiids, the differences in client diversity suggests that facultative cleaners occupy a complementary cleaner role to that of dedicated cleaners. Thus, we feel that both cleaner functional groups are high priority for conservation and that, in fact, they cannot be replaced. However, the preservation of complete cleaning services for all species requiring it will be dependent on the conservation of reef-building Scleractinian corals that serve as the base for goby cleaning stations. The results presented here show that cleaning may be a more significant component of the ecology of *T. bifasciatum* than previously thought. Indeed, they may have the capability to suppress gnathiid populations on the Caribbean coral reefs. However, the factors determining how often *T. bifasciatum* engages in cleaning, as well as the degree to which intraspecific differences in cleaning behavior exist, will be important to determine going forward. Cleaning services are unique and critical for the maintenance of coral reef health. Although we find both facultative and dedicated cleaners to be important, dedicated cleaners occupy a niche that is in jeopardy and seems to be irreplaceable by any other fish functional group.

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Tables and figures:

Figure 1: Images of gnathiids positively identified from gut contents retrieved via dissection of *Malacoctenus macropus* (Rosy blenny, left) and fecal matter from *Elacatinus evelynae* (Sharknose ‘Cleaner’ goby, right). Images were captured through a dissection microscope at approximately x40 magnification.

Table 1: Fish families and number of species in each functional group. Average gnathiids per fish (with associated confidence intervals) and percentage of fishes in each group that consumed at least one gnathiid are also included. *does not include unidentified juvenile Labrid wrasse as a separate species, +includes unidentified Serranid hamlet as a separate species, ++does not include unidentified parrotfish as a separate species, ^{SS}data are from Artim *et al.* (2017).

Table 2: Model results for the zero-inflated negative binomial regression model showing the significant influence of the functional group (categorical independent variable) on gnathiid count (discrete dependent variable). *denotes a significant difference ($p < 0.05$) from the reference level, which was the “dedicated cleaner” functional group.

Figure 2: Boxplots depicting gnathiid consumption of all functional groups (A) and the gnathiid consumption of all functional groups excluding those that did not consume a gnathiid (B). The two highest facultative cleaner values are not shown due to the truncated X-axis.

Figure 3: Estimated number of individuals required for a given functional group to replace a single dedicated cleaner. Calculated based on the average gnathiids per gut for each group.

Figure S1: A map of study sites

Table S1: Site level gnathiid consumption for all functional groups.



