

## Abundance of a cryptic generalist parasite reflects degradation of an ecosystem

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**Abstract.** Ecosystem degradation due to anthropogenic activities is the primary issue of our times. Theoretical analyses as well as efforts to restore and manage ecosystems depend on comprehensive metrics of ecosystem function. In the case of complex ecosystems such as tropical coral reefs—especially where monitoring, management, and restoration are important—multiple metrics reflecting key functional groups are required to accurately reflect ecosystem function and when necessary, diagnose degree and kind of ecosystem degradation. We propose inclusion of the generalist ectoparasite functional group as a measure of ecosystem function of coral reefs. This functional group is adaptable to loss of other community members and may experience an increase in abundance as ecosystem function declines. Fish-parasitic gnathiid isopods are a member of this group, resident though inconspicuous in coral-reef communities. On Caribbean coral reefs, based on 938 light-trap samples, we observed a negative correlation between abundance of smaller-sized gnathiids and abundance of live coral, a natural predator of gnathiids. Plots grouped by coral cover—a measure of success of the ecosystem engineer—and ectoparasite abundance varied significantly in community composition including abundance of macroalgae, turf algae, and farming *Stegastes* spp. damselfish reflecting shifts in community structure. Changes in gnathiid abundance with respect to the abundance of organisms participating in each of the core functional processes driving coral-reef ecosystems reflect broad connectivity of gnathiid parasites across the ecosystem. We conclude that the hyperabundance of a small, cryptic, generalist parasite, when used in combination with a metric of abundance of the primary ecosystem engineer, can provide one nuanced measure of the ecosystem vulnerability to collapse.

**Key words:** climate change; coral reef; ecosystem alternate states; ecosystem functional measures; ecosystem vulnerability; functional group; Gnathiidae.

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### INTRODUCTION

The latter part of the twentieth century was a period when environmental degradation became an obvious and compelling focus of ecological study (Union 1992) and the pace of this degradation has steadily accelerated since then (Crutzen

and Steffen 2003, Ripple et al. 2017). These changes have driven extinction and range restriction or migration (Mortiz and Agudo 2013, Urban 2015), reduced ecosystem function and increased potential for collapse (Valiente-Banuet et al. 2015, Ceballos et al. 2017).

The use of multiple metrics in assessing ecosystem function is increasingly common. Multiple metrics including measures of the abundance or redundancy of key functional groups have been used to assess ecosystem function in, for example, prairie wetlands (Wilson and Bayley 2012), managed forests (Rempel et al. 2016), and undisturbed and recovering riparian forest (Vasconcellos et al. 2013). Multiple metrics are especially relevant and useful in studies of complex ecosystems such as tropical forests (Chazdon et al. 2010) and tropical coral reefs (Heenan and Williams 2013), but also where ecosystem monitoring, management, and restoration is important, such as in designing and monitoring a system of marine protected areas (Hamilton et al. 2010). What's more, measures of overall diversity are only weakly predictive of measures of diversity of individual functional groups (D'agata et al. 2016).

Some ecosystems are known to degrade to an alternate stable state (Scheffer et al. 2001, Beisner et al. 2003). Coral reefs—habitat dominated by stony coral, an ecosystem engineer—can be replaced by macroalgal dominance (Knowlton 1992, Aronson and Precht 2000, Bruno et al. 2014) or at the very least, a coral-dominant state can be replaced by one characterized by a lack of coral (Mumby 2009). Recent work suggests there may be multiple alternate stable states for degraded coral-reef ecosystems (Pawlik et al. 2013, Baker et al. 2015, Edmunds 2018). As a practical matter, much of the coral-reef ecology literature focuses on functional groups that minimize macroalgal cover, thus increasing ecosystem resilience to a transition to an alternate stable state (Bellwood et al. 2006b, Hughes et al. 2010) though rare species can have a disproportionate influence on resilience (Mouillot et al. 2013).

Focusing exclusively on positive indicators—abundance of ecosystem engineers or resilience-enhancing functional groups—is problematic when tracking ecosystem function. Mumby (2017) argued that the current coral-reef ecology literature is primarily reporting on the most-pristine remaining habitat and that we have little data on moderate-function reef sites, and no theoretical or empirical basis for differentiating degrees of ecosystem function across a range of low-, medium-, and high-functioning reef sites.

He further emphasized the need to study a greater range of degradation in coral-reef ecosystems and the ecological function of a range of degraded reefs. Following degradation of Caribbean reefs in the end of the twentieth century, plankton abundance and composition—and in particular, increases in phytoplankton reflecting nutrient enrichment—has been used as an indicator of function on degraded reefs in the Caribbean (Webber et al. 2005).

When ecosystems are degraded, one key predictor of which species benefit is whether a species is a generalist or specialist. As habitat degrades, species tend to be lost from that system. Specialists are less adaptable to the resulting change than are generalists (Clavel et al. 2011) including on coral reefs (Munday 2004). Generalists that promote ecosystem collapse to an alternate stable state may provide a nuanced indication of distance from a critical transition.

Parasite abundance has long been suggested as an indicator of ecosystem stress (for example, Odum 1985, Mackenzie 1999, Sures 2004). However, the impact of ecosystem stress on parasites appears variable and dependent on parasite life history—for example, mode of host-infestation and whether they are host specialists or generalists (Lafferty et al. 2008, Wood et al. 2014, Sures et al. 2017). While parasites as a broad group can have variable responses to environmental impacts, the functional group generalist ectoparasites—including micropredators (Lafferty and Kuris 2002, Rafael et al. 2008)—appear adaptable to ecosystem decline due to their mobility and broad host range, and thus may be a candidate metric of ecosystem function for degraded habitat.

Well-known generalist ectoparasites and micropredators on land include ticks and mosquitoes. Their ecological equivalents in the ocean, so-called “ticks (or mosquitoes) of the sea,” are isopods in the family Gnathiidae. Gnathiid isopods are found world wide, from estuaries to the abyss where they are known to feed on the blood of fishes (Smit and Davies 2004, Tanaka 2007, Sikkell and Welicky 2019). They are particularly common on coral reefs where, while feeding on host fish, they are the main prey of cleanerfishes (Grutter 1996, Soares et al. 2010). Gnathiids associate only temporarily with host fish, feeding on a single host during each of three juvenile stages,

and residing in the benthos between feedings and as non-feeding adults. Adults and non-feeding juveniles are subject to predation as free-living organisms (Artim et al. 2017). In the laboratory, live coral polyps consume some gnathiid life stages and entangle others in mucous (Artim and Sikkel 2013) which makes gnathiids vulnerable to predation by living coral—the ecosystem engineer that creates much of the habitat gnathiid fish hosts depend on. Gnathiids also tend to have broad host ranges covering multiple fish feeding guilds. For example, *Gnathia marleyi* in the eastern Caribbean feeds on at least 42 host species from 17 families (Farquharson et al. 2012, Coile and Sikkel 2013, Hendrick et al. 2019; G. Hendrick, *unpublished data*). In field surveys, gnathiid parasites have been previously associated with the reef periphery (Jones and Grutter 2007) and with dead coral or coral rubble (Jones and Grutter 2007, Artim and Sikkel 2013, Santos and Sikkel 2019).

Gnathiid isopods have substantial impact on reef fishes (reviewed in Sikkel and Welicky 2019). Infestation on adult fish hosts leads to tissue damage (Honma and Chiba 1991, Hayes et al. 2007) elevated stress hormones and decreased hematocrit levels (Jones and Grutter 2005, Triki et al. 2016), impaired cognitive function (Binning et al. 2018) and in extreme cases, increased host fish mortality (Mugridge and Stallybrass 1983, Hayes et al. 2011). Gnathiids may also transmit blood-borne parasites (Smit and Davies 2004, Curtis et al. 2013). Settlement-stage fish are also parasitized by gnathiids (Penfold et al. 2008, Artim et al. 2015) with survivorship a function of fish size at time of settlement (Grutter et al. 2017) but even sublethal levels of infestation have significant negative impacts on performance (Sellers et al. 2019). Taken together, these results suggest that impacts to host fish range from mild to severe and are dependent on gnathiid parasite abundance, especially relative to local fish abundance.

Given the relationship between gnathiids and the benthos, and their impacts on hosts, assessment of the impacts of habitat changes in coral reefs associated with human activities requires an understanding of how benthic habitat, interacting with host availability, influences gnathiid abundance. Because coral reefs are interdependent with adjacent habitat such as mangroves and seagrass beds (for example, Negelkerken

et al. 2002, Dorenbosch et al. 2004, Mumby et al. 2004, Unsworth et al. 2008), studies incorporating gnathiids and other external parasites also need to include these adjacent habitats (Sikkel et al. 2017).

Abundance of live coral cover is the primary measure used to assess coral-reef state. In this study, we examine fine-scale and larger reef-scale predictors of gnathiid abundance—especially live coral cover; host abundance, including abundance of various functional groups; and putative predators of gnathiids—to determine the utility of this ectoparasite functional group as an indicator of coral-reef ecosystem function. We hypothesize that (1) gnathiid abundance, especially first-stage abundance, will increase with decreasing cover of living coral, (2) gnathiid abundance will increase with host availability, and (3) differences in abundance of other functional groups can offset some increases in gnathiid abundance due to the loss of live-coral predation.

## METHODS

### *Study sites and sampling plots*

Study sites were located in the north-eastern-Caribbean basin, including Guana Island (British Virgin Islands), Culebra, Puerto Rico, and St. John and St. Thomas (U.S. Virgin Islands). At each site, one to five plots were established for a total of seventeen plots (Fig. 1; Appendix S1: Table S1). Study plots were 10 × 20 m in size and were chosen to reflect local coral-reef conditions and included coral colonies, cleaning stations, and large resting fish aggregations. Sampling of gnathiids was conducted within plots and, for a subset of plots with adjacent seagrass beds, along transects projecting from the reef edge into the seagrass bed. There were no plots with adjacent mangroves. Gnathiids were collected and densities compared with habitat variables as described below.

### *Gnathiid abundance and potential impact on fish hosts*

Gnathiids were sampled using light traps (Artim and Sikkel 2016). These are highly effective for capture of *G. marleyi*, which is primarily nocturnal (Sikkel et al. 2006, 2009b). To compare gnathiid abundance in reef versus seagrass habitat, reef-to-seagrass transects were laid



Fig. 1. A map of the Eastern Caribbean showing the study sites: (A) Guana Island, BVI, (B) St. John, USVI, (C) St. Thomas, USVI, (D) Culebra, Puerto Rico, and (E) La Parguera, Puerto Rico.

perpendicular to and away from seven plots, extending anywhere from 30 to 85 m into the seagrass bed, and traps were set every 4 m (Saint John) or 5 m (all other islands) for a total  $n = 96$  traps. For sampling of reef-plots (total  $n = 842$  traps), traps were placed using a stratified-random sampling approach for a total of 30–98 samples per plot. Random traps were spaced at 2 m intervals along both  $x$  and  $y$  axes. For plots on St. John in the U.S. Virgin Islands (STJ), all random points were sampled. On all other islands, these gridded points were sampled randomly without replacement so that half of all sample points were taken from this set of gridded points. Stratified sampled locations within or immediately adjacent to plots included patches of high-coral abundance, fish aggregations, and cleaning stations. Stratified sampling was of habitat extremes both rare—representing <3% of habitat at these locations—but also thought to have significant impact (positive or negative) on gnathiid abundance and represented no more than half of all points on any one plot.

All traps were set in late afternoon and retrieved after sunrise the next day. One design (Artim and Sikkell 2016) was used for all sample points on St. John. In addition to this design, two trap entrance modifications based on local parts availability were used on subsequently sampled locations. Trap sensitivity was compared using a Kruskal–Wallis non-parametric test of differences in counts of each gnathiid stage by trap design. Counts from the three trap designs significantly differed from each other, and gnathiid abundance by juvenile stage was adjusted prior to calibrating to comparative emergence data (Artim and Sikkell 2016: Table 6). These corrections were separately applied for counts of each of the three gnathiid juvenile stages.

Trap contents, approximately 1 L in volume, were filtered through plankton mesh, then rinsed into ~250 mL of seawater. Sample contents were sorted under a dissecting microscope and gnathiids removed from the sample.

To determine juvenile stage, gnathiids were either measured against 2-mm graph paper using



a dissecting microscope or were photographed against graph paper using a mounted DSLR camera and macro lens. For gnathiids that were photographed, ImageJ (Schneider et al. 2012) was used to estimate size. Size was used to assign gnathiids to the appropriate juvenile stage (Artim and Sikkel 2016: Figure 3). Total fish-host-fluid extracted per sample point was calculated using average blood-volumes by juvenile stage (Artim and Sikkel 2016: Figure 4) multiplied by adjusted gnathiid counts for each juvenile stage.

#### **Substrate cover assessment**

Because seagrass beds have uniform substrate composition, substrate cover was not assessed. Substrate cover was assessed for all reef-based samples using photo quadrat methods. GoPro Hero cameras were used to photograph substrate surrounding each trap placement during the day using natural lighting. A numbered sample marker of known size was included in each image and used to crop photographs to  $1 \times 1$  m. Cropped image size was chosen based on prior work estimating a 1–2 m average maximum travel distance of gnathiids seeking a fish host (Artim and Sikkel 2016). Photoshop was used to white-balance photographs. For very shallow sample points (less than about 1 m), photographs were less than  $1 \times 1$  m in extent. Proportions of substrate cover for each sample point were determined using Coralnet (Beijbom et al. 2012) configured to place 200 random points per photograph. All sample points were verified by human raters. Cover types included sand, living stony coral (hereafter simply “living coral”), dead bare stony coral (dead coral; coral devoid of living polyps and without other epibionts such as turf algae), rock, octocoral, sponge, and *Dictyota* spp. (the dominant macroalgae on these plots, often found on dead coral or rock surfaces). A complete list of substrates is shown in Appendix S1: Table S2.

#### **Fish abundance**

Fish density in seagrass habitat was very low, and thus, fish density was not assessed near seagrass traps. For reef-plots, fish abundance was determined day and night for each sample point. On all plots, nighttime counts of fish were determined by divers surveying on SCUBA. On St. John, fish counts were done on each  $5 \times 5$  m

subsections of each plot. At all other locations, counts were done separately for a 3 m diameter area surrounding each sample point.

For daytime fish counts on St. John only, a belt-photo survey was conducted. A pair of points projected from camera to substrate and spaced 4 cm apart was used to calibrate sizes on each photograph and approximate length of each fish was recorded. The substrate photographs were matched to a point in the photograph mosaic and counts from the surrounding images were combined producing a count for an area of approximately  $9 \text{ m}^2$  centered on the sample point. For all other locations, daytime fish counts were conducted in an area of  $\sim 7 \text{ m}^2$  centered on each sample point. Fish were identified to the lowest taxa possible. The presence of Caribbean cleaning goby (*Elacatinus* sp.) cleaning stations within a meter of each sample point was noted and the number of gobies at each station recorded. Cleaner shrimp were seen on fewer than 3% of plot sample points.

Fish biomass was estimated using published length-to-mass regression parameters by species (Froese and Pauly 2019). For fish counts derived from belt-photo survey (St. John), length was estimated from these images. For all other plots, fish counts by juvenile, sub-adult, and adult individuals were used to estimate biomass based on typical fish standard lengths for each species and life stage. Mean fish biomass estimates per sample varied considerably between the belt-surveyed plots (St. John) and all other plots. The three St. John plots were thus omitted from subsequent biomass analyses only.

#### **Analysis**

All analyses were performed in R using R packages when specified. Gnathiid abundance was fit against various distributions using the R package *fittest* (Delignette-Muller and Dutang 2015). The best-fit distribution, as determined by minimum AIC value, was used for subsequent generalized linear modeling using the R package *glmmTMB* (Brooks et al. 2017). Estimates of abundance for each gnathiid juvenile stage best fit a negative binomial distribution.

Factors were broken into three groups. The first group included substrate factors such as cover of sand and cover of sponges. The second grouping of factors included possible gnathiid

fish hosts: counts of all fish, highly susceptible fish (Coile and Sikkell 2013), major herbivores (parrotfish and surgeonfish), territorial damselfish which could be further broken down into farming damselfish and grazing damselfish (Ceccarelli et al. 2001), and non-*Stegastes* damselfish. The third grouping of factors was known or suspected predators of gnathiids (Artim and Sikkell 2013, Artim et al. 2017) and included cover of living coral; daytime counts of dedicated cleanerfish (*Elacatinus* spp., Gobiidae); daytime counts of Blueheaded wrasse (*Thalassoma bifasciatum*), a facultative cleaner and invertivore; daytime counts of benthic invertivores including grunts (Haemulidae), Blackbar soldierfish and squirrelfish (Holocentridae); and of counts of epibenthic planktivores including Cardinalfish (Apogonidae) and other planktivores (Priacanthidae and Pempheridae).

Sample plot was treated as a random variable in the mixed modeling analysis in order to account for plot-to-plot variability in gnathiid abundance. Percent zero samples were calculated for abundance data by gnathiid stage and, where justified, models with and without a single zero-inflation intercept were compared.

All single-factor models within each of the three groups of predictive factors were evaluated via model selection using Akaike information criteria corrected for sample size (AIC<sub>c</sub>). Differences of AIC<sub>c</sub> of two or less are considered equivalent while differences in AIC<sub>c</sub> of 4–7 may represent significant explanatory content and should be more closely examined (Anderson and Burnham 2004).

Parasite hyperabundance—the values of extreme density of parasites found on each plot—was estimated for each reef-plot using the 90th percentile abundance for that plot. The plot-level factors of third-quartile cover of living coral and first-stage gnathiid hyperabundance were used to determine a threshold value of third-quartile coral cover above which large 90th percentile counts of gnathiids did not occur. A third-quartile coral-cover threshold was chosen to reflect coral abundance in potential fish refugia within the plot. Plots falling below this third-quartile live coral-cover threshold were referred to as low-coral plots, those above the threshold as high-coral. The low-coral plots were further subdivided into high-function plots—those whose

90th percentile gnathiid counts were similar to high-coral plots—and low-function plots—those with excessive 90th percentile gnathiid counts. This yields three subgroups of plots: (1) high-coral, high function; (2) low-coral, high-function; and (3) low-coral, low-function. These post hoc plot groups were equally sampled across the lunar calendar ( $\chi^2_2 = 3.3487$ ,  $P = 0.1874$ ).

A Kruskal–Wallis test across reef-plot subgroups was performed for estimates of abundance for each gnathiid stage, blood-and-plasma volume extracted per fish biomass, substrate cover, and community composition. If significant, a Dunn corrected test of differences was performed.

Differences in hyperabundance across reef-plot subgroups were assessed using a Kruskal–Wallis test and, when significant, a Dunn corrected test.

## RESULTS

### Seagrass transects

Counts of gnathiids fell off with distance from the reef (coefficient =  $-0.0303 \pm 0.0048$ ,  $n = 96$ ). This model performed significantly better than a null model ( $\chi^2_1 = 30.984$ ,  $P \ll 0.0001$ ), indicating that gnathiid density is higher in reef versus seagrass habitat.

### Sample-level factors and gnathiid abundance in reef-plots

Single-factor models grouped by substrate, fish-host groups, and gnathiid predators and sorted by AIC<sub>c</sub> are reported for models of first-stage through third-stage gnathiid abundance. For first-stage gnathiid counts, the best model using substrate cover predictors was sand which was positively correlated with count. Though the single-factor models using live coral or dead coral as predictors exceeded the a priori  $\Delta AIC_c$  value of 7, they were the next-best models, performed equivalently to each other, and each featured a statistically significant negative coefficient. A number of the fish abundance models predicting first-stage gnathiid counts had equivalent explanatory power (as measured by  $\Delta AIC_c$ )—counts of non-*Stegastes* pomacentrids (*Chromis* spp.) were negatively correlated with first-stage counts while nighttime counts of all fish, nighttime biomass of all fish, daytime counts of grazing *Stegastes* spp., and daytime counts of all fish

were positively correlated with first-stage counts. Three models using factors assessing abundance of a predator were equivalently predictive—live coral was negatively correlated with first-stage count while nighttime counts of epibenthic invertivores and nighttime counts of all fish were positively correlated with first-stage counts. These first-stage gnathiid count models are compared in Table 1. The relative impact of live and dead coral on first-stage gnathiid counts is compared in Fig. 2.

The best substrate predictor of second-stage gnathiid counts was sand which was positively correlated—though live coral, dead coral, coral rubble, and *Dictyota* macroalgae provide an inferior model fit when compared to sand, they performed equivalently to each other and all featured negative coefficients. The best predator predictor of second-stage gnathiid count was live coral, which was negatively correlated with

second-stage count. These second-stage gnathiid count models are compared in Table 2.

Sand was the best substrate predictor of third-stage gnathiid count. The next-best substrate models were *Dictyota* spp., dead coral, and coral rubble—all with equivalently effective model fits and all with negative coefficients. No models with fish abundance predictors and none with predator predictors featured statistically significant coefficients. These third-stage gnathiid count models are compared in Table 3.

### Plot grouping by coral cover and gnathiid abundance

*Gnathiid abundance and fish biomass across plot types.*—Tests of differences in abundance across plot types for first-stage, first-stage hyperabundance, second-stage, third-stage, and total gnathiid abundance, and for fish-blood extracted were all significant. Using a Kruskal-Wallis test of differences, all subgroup to subgroup differences were significant except for the comparison of the first-stage abundance of the high-coral, high-function subgroup to the low-coral, high-function subgroup. Differences in the distribution by plot subgroups are depicted for first-stage gnathiid abundance (Fig. 3A), first-stage hyperabundance (Fig. 3B), total gnathiid abundance (Fig. 3C), and blood volume extracted per fish biomass (Fig. 3D). Mean fish biomass was 591 g/m<sup>2</sup> on high-coral, high-function plots, 930 g/m<sup>2</sup> on low-coral, high-function plots, and 1716 g/m<sup>2</sup> on low-coral, low-function plots.

*Differences in community composition across plot types.*—Cover of living coral, macroalgae, and turf algae and daytime counts of farming *Stegastes* spp. damselfish all varied significantly across plot subgroups (Appendix S1: Table S3). Distributions of the counts of first-stage gnathiids for each plot type (see Fig. 3a) and of all gnathiid stages by plot type (Fig. 3b) are relatively similar across plot type, though with the suggestion that there may be more extreme counts of first-stage gnathiids. Distributions of extreme first-stage counts—that is, counts exceeding the 90th percentile for each plot type—do show a pattern of a greater extreme values on low-coral, low-function plots compared with high-coral plots, with the low-coral, high-function plots intermediate in the extreme values seen (Fig. 3c). The relationship between plot type

Table 1. Results of single-factor models of first-stage juvenile gnathiid abundance.

Factor	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model coefficient ± SE
<b>Substrate</b>			
Sand	1761.7	0.0	0.0078 ± 0.0019
Living coral	1770.7	9.0	-0.0166 ± 0.0057
Rock	1774.2	12.5	-0.0281 ± 0.0126
Dead coral	1752.0	13.8	-0.0070 ± 0.0035
<b>Fish hosts</b>			
Nighttime counts of non- <i>Stegastes</i> pomacentrids	1773.6	0.0	-0.7061 ± 0.2771
Nighttime fish counts	1773.8	0.2	0.0433 ± 0.0213
Nighttime fish biomass	1774.1	0.5	0.0003 ± 0.0001
Daytime counts of grazing <i>Stegastes</i> spp.	1774.2	0.6	0.0918 ± 0.0425
Daytime counts of all fish	1775.1	1.5	0.0024 ± 0.0012
<b>Gnathiid predators</b>			
Living coral	1770.7	0.0	-0.0166 ± 0.0057
Nighttime counts of epibenthic fish invertivores	1772.1	1.4	0.1984 ± 0.0835
Nighttime counts of fish gnathiid predators	1772.1	1.4	0.0532 ± 0.0231
Nighttime counts of benthic fish invertivores	1774.0	3.3	0.0544 ± 0.0286

Note: Only factors performing significantly better than the null model (AIC<sub>c</sub> = 1777.0, n = 576) are shown.

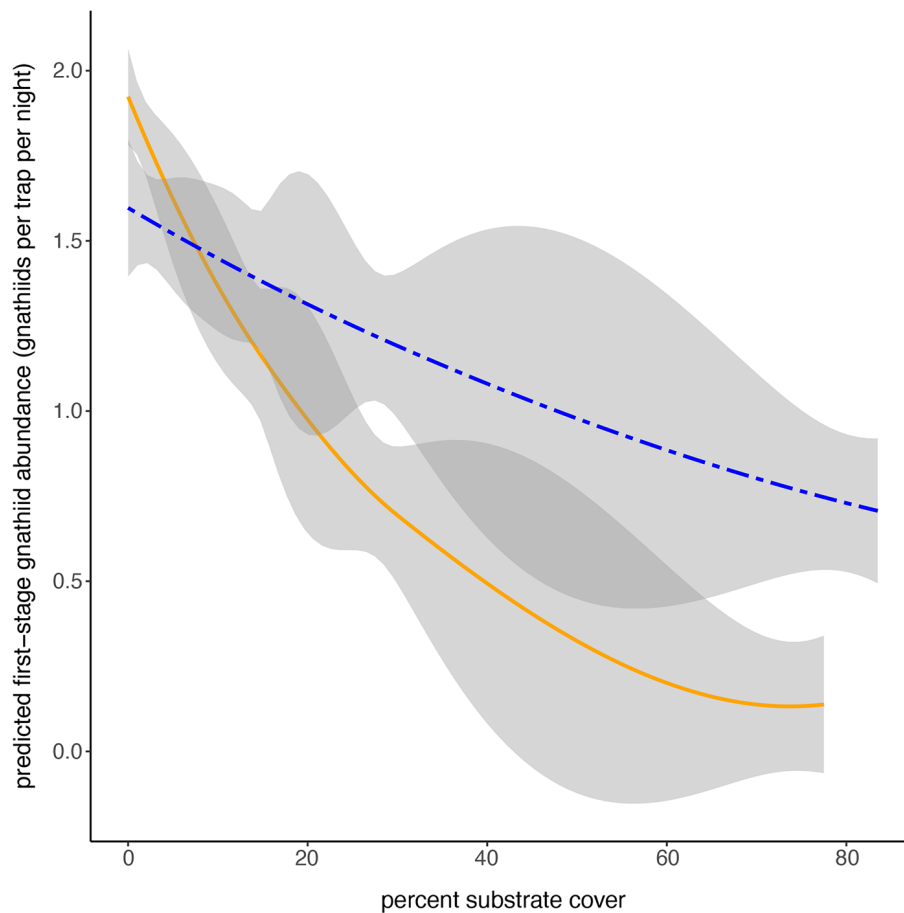


Fig. 2. Predicted first-stage gnathiid abundance across the range of live and dead coral cover seen in this study. The solid line depicts predictions for live coral cover while the dashed line depicts predictions for dead coral cover.

Table 2. Results for single-factor models of second-stage juvenile abundance.

Factor	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model coefficient ± SE
Substrate			
Sand	3297.0	0.0	0.0068 ± 0.0012
Living coral	3322.1	25.2	-0.0099 ± 0.0031
Dead coral	3325.8	28.8	-0.0060 ± 0.0023
<i>Dictyota</i> macroalgae	3325.8	28.9	-0.0050 ± 0.0020
Coral rubble	3325.9	28.9	-0.0059 ± 0.0023
Fish hosts			
None			
Gnathiid predators			
Living coral	3322.1	0.0	-0.0099 ± 0.0031

Note: Only factors performing significantly better than the null model (AIC<sub>c</sub> = 3329.9, *n* = 576) are shown.

Table 3. Results for single-factor models of third-stage juvenile abundance.

Factor	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model coefficient ± SE
Substrate			
Sand	3949.0	0.0	0.0061 ± 0.0011
<i>Dictyota</i> macroalgae	3972.7	23.7	-0.0059 ± 0.0018
Dead coral	3975.2	26.2	-0.0062 ± 0.0021
Coral rubble	3975.2	27.5	-0.0056 ± 0.0021
Fish hosts			
None			
Gnathiid predators			
None			

Note: Only factors performing significantly better than the null model (AIC<sub>c</sub> = 3980.9, *n* = 572) are shown.



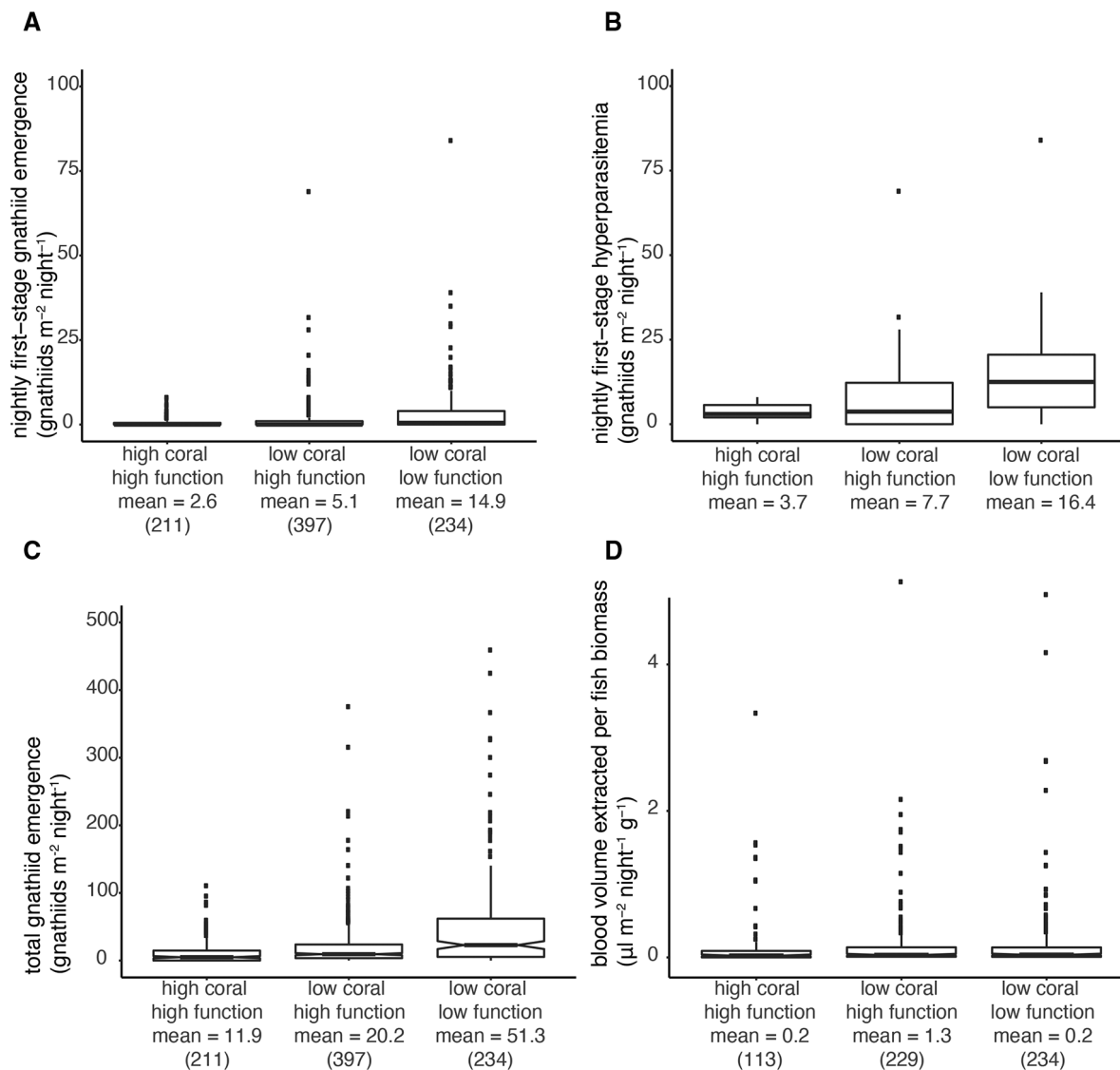


Fig. 3. Boxplots showing differences in distribution of first-stage abundance (A), first-stage hyperabundance (B), total abundance (C), and blood volume extracted per fish biomass (D). Sample size for each subgroup is shown in parentheses under each subgroup mean. Boxes display first- and third-quartile edges while whiskers show the third quartile plus 1.5 times the interquartile range. For (C), hinges are an approximation of the 95% confidence interval. Differences seen at (A), (B), and (C) are significant—see Appendix S1: Table S7.

and distribution of extreme values of first-stage counts can also be seen in the violin plots of Fig. 4 which depict the overall distribution of first-stage counts for each plot with plots grouped by plot type and the third-quartile values shown for each plot. Patterns of influence of facultative cleaning wrasses, grazing *Stegastes* spp. damselfish, and cover of soft coral,

macroalgae, and living and dead stony coral varied by plot subgroup (Appendix S1: Tables S4–S6).

## DISCUSSION

Our data show that fish-parasitic gnathiid isopods in shallow coral-reef systems, which often

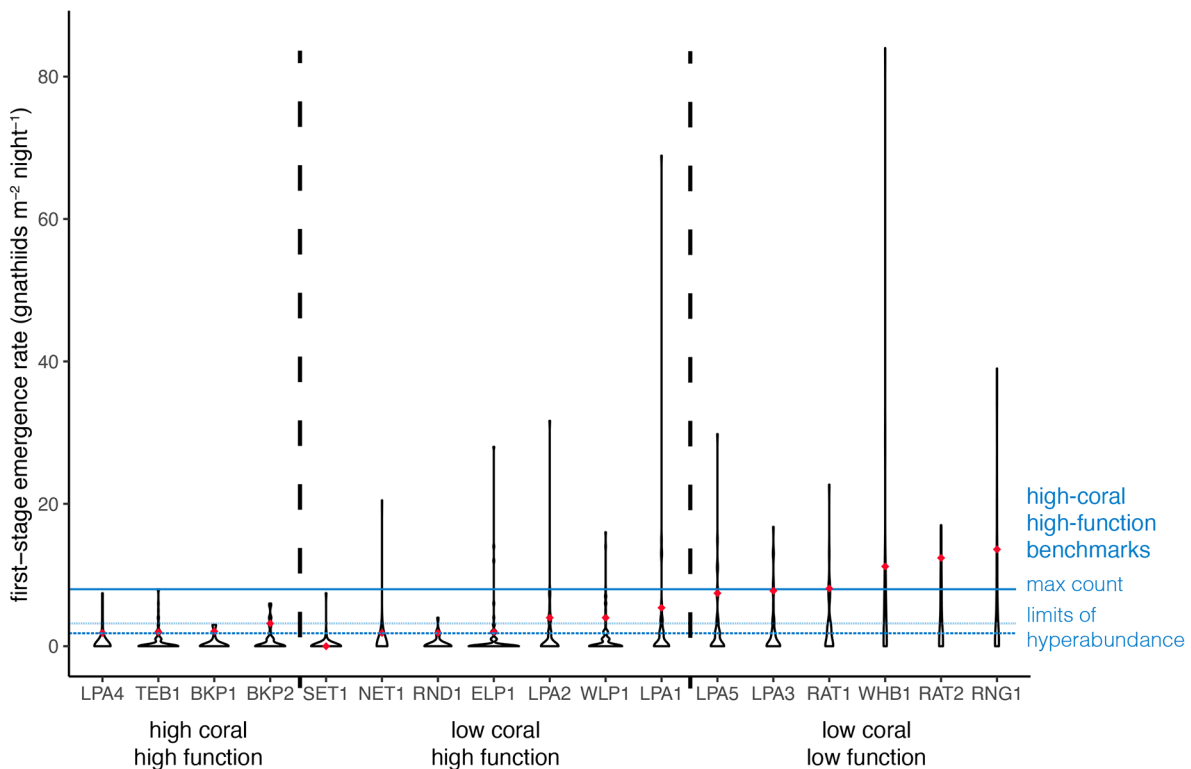


Fig. 4. Distribution of first-stage gnathiid abundance for study plots grouped by subgroup then sorted by 90th percentile first-stage gnathiid abundance. The 90th percentile cutoff for each plot is shown as a filled diamond. High-coral plot metrics are summarized as reference lines.

include adjacent seagrass beds, are concentrated around the reef itself primarily in sand substrate. They further show that cover of living coral—a functional metric reflecting activity of the system's ecosystem engineer—is the primary limit of gnathiid ectoparasite abundance on coral reefs through predation of particularly smaller-sized gnathiid juveniles. Abundance of the smallest-sized gnathiids only was positively correlated with the nighttime abundance of fish.

In addition to hosts and mobile predators, aquatic parasites with free-living, benthic, life history stages should be impacted by attributes of the substrate. In two previous studies, Caribbean reef fish occupying habitat with higher coral cover had fewer overall ectoparasites (Sikkel et al. 2000) or fewer monogeneans (Sikkel et al. 2009a). However, because of the methods used, gnathiids were largely or completely neglected, and only one to three host-fish species were considered. Moreover, these studies did not

include other habitat variables. In monogeneans, the only free-living stages are the eggs and the recently hatched larvae (Dinh Hoai and Hutson 2014) and the vast majority of the life cycle is spent on the host, but they too appear less abundant in high-coral habitat (Sikkel et al. 2009a). In contrast, gnathiids spend the majority of their life in the benthos and, as shown by these data, are strongly affected by substrate composition with live coral cover providing intense predation of smaller—especially first-stage—gnathiid juveniles. The two previous studies that have shown a link between live coral and gnathiid abundance (Artim and Sikkell 2013, Santos and Sikkell 2019) were limited in both the range of sites and in the number of other variables considered. The only study to compare multiple substrate types was conducted in the laboratory, where *Gnathia marleyi* avoided live stony coral, which was shown to consume them, preferred dead coral but also associated with sand, macroalgae, and sponge

(Artim and Sikkell 2013). Thus, this field study is unprecedented in demonstrating that this one cryptobenthic organism interacts with all of the key substrate types in this complex ecosystem.

We found that, on plots with more than ~12% coral cover, gnathiid hyperabundance is relatively low, while on plots with <10–12% live coral cover gnathiid hyperabundance varies considerably. This transition region is in agreement with functional transitions seen for reef accretion (Kennedy et al. 2013), the breakpoint in predicting change in fish biomass (Komyakova et al. 2013) and just above the breakpoint defining a shift to a stable algal-dominated state (Mumby et al. 2014).

Below the critical threshold of coral cover, first-stage gnathiid abundance, especially hyperabundance, generally increases. Stony coral is unusual in the sheer number of mouths on a healthy reef. For example, the coraltraits database (Hoogenboom 2016) yielded a figure of around 50,000 coral polyps (mouths) per square meter for *Orbicella annularis*, the primary reef-building coral on our plots. No other known or suspected gnathiid predator approaches this potential intensity of predation. The typical brood size of *G. marleyi* is about 30 first-stage juveniles (Coile et al. 2014) which in situ are released over a short period of time (see Artim and Sikkell 2016: Figure 5). This correlation of very low hyperabundance of first-stage gnathiid counts on high-coral plots and earlier laboratory work (Artim and Sikkell 2013) suggests that live coral may be an extremely efficient predator of the smallest gnathiid juveniles. This would further suggest that sedentary stony coral provides reef fish reliable refugia from gnathiid predation.

On low-coral plots, cover of living coral did not significantly differ between low-function and high-function plot subgroups, but first-stage gnathiid hyperabundance did vary across these low-coral plots. On these low-coral plots, abundance of gnathiids appears to be dependent on additional community factors with different combinations of factors dominating individual reefs. Analysis of our dataset provides some insights into the interplay of these secondary factors that may be responsible for the control of gnathiid abundance.

Dead coral is a prominent component of coral reefs in all stable but degraded system states

primarily serving as cryptobenthic habitat, although this relationship is likely multifactorial (Harborne et al. 2012). As dead coral habitat was utilized and preferred by gnathiids in the laboratory (Artim and Sikkell 2013), it is unlikely dead coral was inherently aversive and likely that some cryptobenthic occupant of dead coral either outcompetes gnathiids for space or directly preys on gnathiid parasites. The negative impact of live coral cover was much greater, leading to relatively greater gnathiid abundance on dead compared with live coral (see Fig. 2).

At sample scale and across all plots, macroalgal abundance had a negative impact on second- and third-stage gnathiid abundance. The relationship of macroalgae and gnathiid abundance was visible in the low-coral subgroups only. While macroalgae does not consume gnathiids, the surface of some algae may be difficult to attach to (Walters et al. 2003, Othmani et al. 2014) or even toxic (Walters et al. 2003, Hutson et al. 2012, Othmani et al. 2014) or there may also be a risk of inadvertent consumption by herbivores. As macroalgae provides habitat for a variety of fish and invertebrates (Mumby et al. 2008), gnathiids may also be preyed upon by other associated cryptobenthic fauna.

Cleanerfishes are the best-known predators of gnathiids in coral-reef systems (for example, Grutter 1996, Soares et al. 2010). However, the impact to gnathiid populations is unclear (Grutter et al. 2019). In our data, sample-scale models of gnathiid abundance by counts of cleaning gobies did not perform better than a null model. Bluehead wrasse, a facultative cleaner (Losey 1974), also had no significant impact. However, both dedicated goby cleaners and facultative wrasses did appear as factors in model averaging for plot subsets (Appendix S1). Facultative cleaning wrasses can eat gnathiids both on substrate and off of host fishes and may thus consume as many or more gnathiids overall than dedicated cleaners (Grutter and Feeney 2016).

Given that gnathiids depend on hosts, host biomass would be expected to influence gnathiid abundance on some scale. Consistent with findings from the Philippines (Santos and Sikkell 2019), we saw no effect of fish biomass at sample scale. However, fish biomass does correlate with gnathiid abundance at the plot scale and we did see evidence of an effect of counts of fish on first-

stage gnathiid abundance at the sample scale, likely reflecting trophic dependency of gnathiids on a reliable presence of fish hosts.

Because increased dead coral creates additional living space for gnathiids that is not provided by live coral, if fish biomass remains similar or even slightly higher on degraded reefs, the per capita infestation rates of fishes on degraded reefs would also be higher. However, we found that fish biomass actually increased on degraded reefs—our low-coral low-function plots—resulting in no increase in estimates of fluid removed per unit fish biomass on degraded versus high-coral reefs. None of our sites experience heavy fishing pressure, which is expected to have differing effects on abundance, burden, and diversity of fish parasites that are dependent on parasite life history strategy (Wood et al. 2014). Our results suggest that coral cover could interact with fishing pressure to influence gnathiid burden, such that in heavily fished areas that have low coral cover, per capita infestation by gnathiids and similar ectoparasites would indeed be high compared with unfished areas or areas with higher coral cover.

Our finding that gnathiid abundance was lower in seagrass compared to reef is consistent with previous studies using caged fish (Sikkel et al. 2017). Seagrass serves as fish nursery for coral reefs (de la Morinière et al. 2002, Nagelkerken et al. 2002) though there are predation-pressure and food-availability trade-offs (Nagelkerken 2009). The interconnectivity of reef, seagrass, and mangrove habitat is significant (Unsworth et al. 2008) and has the potential to bolster fish populations on low-coral-abundance reefs and act as temporal or ontological refugia from gnathiid micropredation. Given the lack of a planktonic dispersal phase and limited swimming ability, the primary transport mechanism of gnathiids to seagrass beds is likely nocturnal migratory fishes (Sikkel et al. 2017) and thus the density of gnathiids in seagrass beds should be a function of both gnathiid abundance on reefs and the biomass of nocturnal migratory fishes. However, our sample sizes did not allow us to assess this correlation.

Among the factors we did not consider during study design are abiotic factors such as current velocity. However, this likely explains the low gnathiid counts on the Culebra plots despite low

coral cover. This site was noticeably more turbulent than others. Because high water velocity reduces the ability of gnathiids to swim, it reduces the likelihood that gnathiid juveniles successfully find and attach to fish hosts (Samsing et al. 2015), and swim toward traps.

Shifts in coral-reef cryptobenthic assemblage may also play a role in altering gnathiid population density. A longitudinal study of Great Barrier Reef coral bommies observed long-term shifts in cryptobenthic fish assemblage after a coral bleaching episode (Bellwood et al. 2006a), though cryptobenthic invertebrates were not a focus of this Bellwood study. Farming *Stegastes* damselfish living in degraded coral-reef habitat are known to alter the community composition of cryptobenthic invertebrates (Ceccarelli et al. 2001). Our high and low function, low-coral plots differed in abundance of farming and grazing *Stegastes* spp. damselfish. As farming *Stegastes* spp. inhabit both coral and rocky reefs, the impact of these damselfish on gnathiid abundance should be further investigated.

Coral polyps, polyp oral opening, and preferred prey size all vary tremendously across coral species, and this likely creates selection pressure on gnathiid body size. Gnathiid body size, which in *G. marleyi* varies over a seven-fold range from first to third-stage juveniles (the feeding stages), will affect the likelihood of each gnathiid juvenile stage being preyed upon by each coral species. Gnathiid body size also affects brood size in gnathiids (Tanaka 2007: Figure 6; Coile et al. 2014: Fig. 1). Larger gnathiids require larger blood meals to successfully metamorphose and reproduce which may mean selectivity for larger fish hosts. In the Pacific, there is a much greater diversity of coral species (Veron et al. 2015: Fig. 4). There also appears to be much greater diversity of gnathiids in the tropical Indo-Pacific (Svavarsson and Bruce 2012, Svavarsson and Bruce 2019) compared with the Caribbean (Farquharson et al. 2012). This interplay of selection forces on diverse Pacific coral reefs deserves future study including the effect of gnathiid-species specialization and diversity on the overall transport of energy and nutrients by the ectoparasite functional group among fish species comprising Brandl et al.'s eight core processes (Brandl et al. 2019).



Brandl et al. (2019) took the view that ecological function corresponds to the flow of nutrients or energy within an ecosystem (Bellwood et al. 2019). The four compartments defined by Brandl's core processes include fish taxa susceptible to gnathiid parasite micropredation and, as a host- and habitat-generalist, gnathiids have the potential to impact the balance among these compartments by altering the flow of energy and nutrients, and therefore affecting the likelihood of transition to alternate ecosystem stable states. While our data do demonstrate that on low-coral plots, there is a higher likelihood of fish encountering a hyperabundance of gnathiid parasites, we have no evidence of an increase in average impact to fish on low-coral reefs—the volume of blood extracted per fish biomass appears to remain constant across low- and high-coral plots. Regardless, smaller fish and especially recently settled juveniles are more likely to suffer increased mortality due to gnathiid hyperabundance (Grutter et al. 2017, Sellers et al. 2019). Current molecular techniques (Hendrick et al. 2019) provide tools to begin to characterize which fish species are being most impacted by gnathiid micropredation, which may clarify whether or not there may be a change in the flow of energy and nutrients that is due to gnathiid interaction with the fish within Brandl et al.'s four functional compartments.

Our data strongly suggest that measures of cover of living coral and hyperabundance of a common coral-reef fish ectoparasite correspond to a transition point in the function of coral-reef communities. Below this inflection point in cover of live coral, gnathiid abundance, especially for the smallest juveniles, shifts with community composition. To our knowledge, this is the first study demonstrating the utility of the generalist ectoparasite functional group as an inverse metric of ecosystem function. These community interactions featuring dramatically understudied cryptic organisms (Plaisance et al. 2009, Brandl et al. 2019) highlight the need to pay far more attention both to cryptic community members, to their interaction with large conspicuous organisms, and to their ecosystem functional role. This focus on cryptic diversity is especially important in communities such as coral reefs that are both highly biodiverse and in steep decline (Hughes et al. 2018). Our window of opportunity to

identify and study cryptic diversity and to understand its functional significance is rapidly closing.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3268/full>