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REPORT

Changes in abundance of fish-parasitic gnathiid isopods associated with warm-water bleaching events on the northern Great Barrier Reef

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Abstract Mass coral bleaching events due to rising seawater temperatures are occurring with increasing frequency and are among the most conspicuous consequences of human-induced climate change. While bleaching events have clear impacts on the corals themselves, the impacts on other organisms and on the overall reef community are more difficult to assess. This is particularly true for parasitic organisms, which in spite of their high diversity and biomass are typically ignored in ecological monitoring studies. Here, we take advantage of long-term monitoring of host–parasite–cleaner interactions on experimental patch reefs to assess the effects of mass bleaching events on gnathiid isopod populations around Lizard Island, Great Barrier Reef. Compared with non-bleaching years, gnathiid abundance was consistently low during the warm-water period in bleaching years, but rebounded during the cooler months. This pattern is likely due to the interaction between the short-term negative impacts of thermal stress and declines in hosts on gnathiids, combined with the longer-term positive impacts of declines in cleaner wrasses and of increased dead coral on gnathiid abundance.

Keywords Coral reefs · Climate change · Cleaning mutualism · Fish parasites · Predator–prey interaction · Long-term monitoring

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Introduction

Mass coral bleaching events due to rising seawater temperatures are becoming increasingly frequent throughout the tropical Indo-Pacific and Western Atlantic (Glynn 1996; Hoegh-Guldberg 1999; Loya et al. 2001; Hughes et al. 2017). While bleaching events clearly impact corals, the impacts on other reef-associated organisms are more difficult to assess. This is attributable to two main factors. First, the location of bleaching events or even the probability of a bleaching event cannot be predicted with sufficient accuracy and sufficiently far in advance to plan pre-bleaching characterization of a site. Thus, proper BACI-type studies, and especially properly replicated studies (e.g., Underwood 1994), are generally not possible, leaving only comparisons of bleached and separate unbleached sites, after an event. This is particularly problematic if bleaching is widespread, as increasing distances between bleached and non-bleached sites decreases their comparability. Second, in cases where bleaching occurs at a site where pre-monitoring has occurred, the variables monitored may vary with, and depend on, the particular research teams.

While pre-bleaching monitoring efforts needed to assess post-bleaching consequences differ in the variables measured, there is some consistency in what is not measured. Parasitic organisms make up about 40% of the earth's biodiversity (Hatcher and Dunn 2011), likely more in coral reef systems (e.g., Rohde 1976; Justine 2010; Justine et al. 2012), and can have high local biomass (Kuris et al. 2008). However, they are typically ignored in marine ecological monitoring studies and are represented in only about 5% of publications in marine journals (Poulin et al. 2014). Parasites can influence populations (e.g., Hatcher and Dunn 2011), food webs (e.g., Huxham et al. 1995; Thompson et al. 2005; Lafferty et al. 2006; Hatcher and Dunn 2011; Amundsen et al. 2009; Johnson et al. 2010), and thus community dynamics (e.g., Thomas et al. 1998; Mouritsen and Poulin 2002; Hatcher et al. 2006; Wood et al. 2007; Lafferty et al. 2008; Raffel et al. 2010; Hatcher and Dunn 2011). Neglect of this major component of biodiversity likely stems from their small size ("out of sight, out of mind"), and inconspicuous position on or within their hosts (Hatcher and Dunn 2011; Poulin et al. 2014), as well as lack of appropriate cross-training by marine ecologists.

Given the high diversity of parasites and their hosts, and their wide range of life history strategies, it is difficult to predict how any given environmental perturbation will impact them (Brooks and Hoberg 2007; Marcogliese 2001, 2008; Adlard et al. 2015). In the short term, bleaching events are characterized by unusually high water temperatures and changes in benthic substrate, associated with coral bleaching. In the long term, if warming events are protracted, more permanent changes in benthic community structure, associated with the death of corals, may occur. Parasites and hosts may be impacted in similar or different ways during the initial heating event, and impacts may change during the subsequent period. Understanding the effects of bleaching events on host–parasite interactions therefore requires pre- and post-bleaching monitoring of multiple parasite–host systems.

Juvenile gnathiid isopods are one of the most common ectoparasites of coral reef fishes and are perhaps best known for their role in cleaning symbioses, where they influence visitation in host fishes to cleaning stations (Grutter 2001; Côté and Molloy 2003; Sikkel et al. 2004) and are the main prey of cleanerfishes (Losey 1974; Grutter 1996; Arnal and Côté 2000). Gnathiids are born as small (approx. 1 mm) stage-1 juveniles. After feeding on a fish host, they become engorged with blood or fluid. They then molt into the second juvenile stage, feed again, and repeat the process a third time before metamorphosing into non-feeding adults. Adult females die within days after reproducing while males may persist for over a month after their last feeding (Smit and Davies 2004; Tanaka 2007). As generalists, gnathiids feed on a variety of host fishes (Jones et al. 2007; Coile and Sikkel 2013; Ota et al. 2012; Grutter et al. 2017). Unlike internal parasites such as nematodes and cestodes, and some ectoparasites such as copepods and monogeneans, gnathiids associate temporarily with their hosts, feeding on a different fish during each of their three juvenile stages. Because of this feeding strategy, which is similar to blood-feeding arthropods on land, gnathiids have been referred to as "ticks" or "mosquitoes" of the sea (e.g., Grutter et al. 2011) and may more appropriately be considered "micropredators" (Lafferty and Kuris 2002; Raffel et al. 2008).

In addition to their influence on host interactions with cleaners, gnathiids can have impacts on host physiology through reduced hematocrit (Jones and Grutter 2005), increased levels of corticosteroid stress hormones (Triki et al. 2016), and the creation of wounds that can lead to secondary infection (Honma and Chiba 1991). Gnathiids may also transmit blood-borne parasites (Smit and Davies 2004; Curtis et al. 2013). In cases of extreme infestation, they can cause death in adult hosts (Mugridge and Stallybras 1983; Hayes et al. 2011). However, for juvenile fishes, even a single gnathiid can prove fatal (Grutter et al. 2008; Artim et al. 2015; Grutter et al. 2017; Sellers et al. 2019), and even sublethal infestation can impact performance (Sellers et al. 2019).

Given that gnathiids spend most of their lives in the benthos, must swim to attach to hosts, and must successfully feed and metamorphose three times in order to reproduce, warming per se, changes in benthic structure, and changes in fish communities that are associated with bleaching events may each impact their abundance in different ways. For example, increased temperature may impact rates of metamorphosis and swimming performance, but may can also impact the susceptibility of hosts to infestation. Changes in fish communities may impact host availability or abundance of gnathiid predators, and changes in substrate may impact the availability of suitable habitat (Artim and Sikkel 2013; Santos and Sikkel 2017).

In 2016, and again in 2017, the northern portion of the Great Barrier Reef (GBR) was impacted by a large-scale bleaching event that included the area around Lizard Island Research Station (Hughes et al. 2017). The presence of multiple long-term monitoring efforts provided the opportunity to assess the effects on multiple members of the coral reef community (e.g., Madin et al. 2018; Richardson et al. 2018). In this study, we take advantage of the only long-term monitoring of any marine parasite or micropredator in a coral reef system (Grutter et al. in press) to assess the impacts of the 2016–2017 Great Barrier Reef mass bleaching events on gnathiid isopod populations.

Materials and methods

Study location

This study was conducted on 12 patch reefs off Lizard Island Research Station, GBR (14°40′S, 145°28′E; Fig. S1), from July 2000 to October 2018; sampling after the first year was done opportunistically, with increased sampling done after the 2016 bleaching event and involving sampling over different seasons. These reefs were part of a cleaner wrasse (*Labroides dimidiatus*) removal study (Waldie et al. 2011) initiated in September 2000. For the present study, only the Lagoon site was used, and *L. dimidiatus* were removed from six reefs (removals), approximately every three months, and left undisturbed on six (control) reefs. Gnathiids were sampled during 21 trips. Removal Reef 4 at Lagoon (Fig. S1) was dropped after March 2008, due to a lone wandering male from neighboring Reef 5 (observed on three occasions in 2007 making short visits), but the samples were retained in analyses for the periods prior to this.

Field sampling

Gnathiid abundance was estimated using 1-m^2 emergence traps (Jacoby and Greenwood 1988; Grutter et al. 2000; Chambers and Sikkel 2002). During all years, traps were set for three consecutive days at the Lagoon site, except for March 2008 and October 15 (2 d) and August 2017 (1 d). Traps were moved every 24 h. Sampling was conducted around the full moon (see Table S1 for dates) because gnathiid emergence at this site is highest at times of full and new moon (Grutter et al. 2000). When an additional site (Casuarina Beach) was sampled as part of another study (Grutter et al., in press), sampling order of each site was determined randomly (4 d before or after full moon, Table S1); when only the Lagoon reefs were sampled, this occurred after the full moon. In this study, only the Lagoon site was analyzed, with a maximum 180 samples per sampling trip.

We obtained both a day sample and a night sample from each trap within a 24-h period. Traps were positioned such that they would not cause damage to or be damaged by the reef. Thirty traps were positioned haphazardly across all reefs beginning at sunrise, with 2–3 reef^{-1} and the number depending on reef size. Sampling bottles were replaced with new ones at sunset each day to obtain daytime and nighttime samples. Samples from traps that were damaged or dislodged were excluded. Processing of samples followed Grutter et al. (2000).

The present study began in July 2000 and involved sampling initially at several month, then several year intervals until 2012, and then after the first recent (2016) GBR mass bleaching event, at approximately 3-month intervals. Exceptions to this protocol were a subset of samples in November 2017, one sample per reef for each day and each night (total $n = 34$) which were used for another study to identify the juvenile stage and species identity of gnathiids using host-feeding experiments; no counts were made of these samples. The sampling trips included the 2002 warm-water bleaching year, but not the 2006 year, and the 2016 and 2017 warm-water bleaching years (https://www.aims.gov.au/docs/research/climate-change/coral-bleaching/bleaching-events.html, Hughes et al. 2017).

Statistical analysis

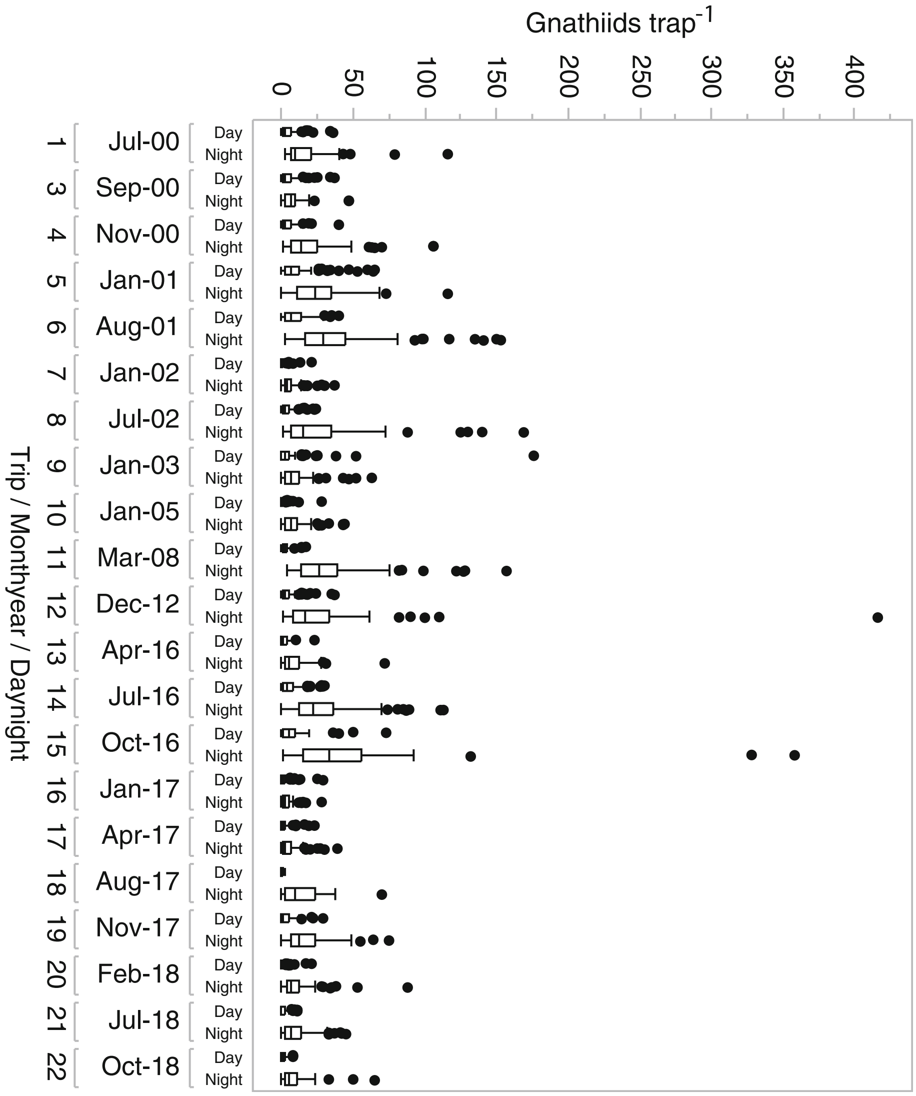
Since July 2000 was the earliest sampling trip and cleanerfish had not yet been removed from removal reefs, this dataset was used as the baseline for the analysis of gnathiid abundance per trap. We tested for differences in gnathiid abundance (counts) using a generalized linear mixed effect model (GLMM), with cleaner presence, day/night, and sampling trip as categorical fixed effects; soak time (amount of time trap was deployed) to adjust for trap sampling duration as a covariate; and reef identity, area sampled, and sampling date as random factors. Since the data were very non-normal (Fig. 1), we used a negative binomial error distribution (with a log link function). To further explore the role of time and the potential effect of deviations from the norm in temperature, we conducted two additional analyses: one using time and the second using temperature difference (the difference between the ambient and long-term average, °C; for source and values, see Table S1) as a covariate instead of the fixed factor sampling trip in the above model. The GLMMs were done using the function “glmmadmb” in the package “glmmADMB” (Fournier et al. 2012; Skaug et al. 2016) and function “Anova” in the package “car” (Fox and Weisberg 2011), in R, version 3.2.3 (R Development Core Team 2016). We looked for data points with high influence (large residual and large Cook’s D statistic) by fitting multiple regression models to the data. Plots of residuals showed assumptions of analyses were met. Significant interactions were interpreted using plots of predicted values.

Results

Emergence trapping

A high percentage (83%) of samples contained gnathiids, with 35,720 gnathiids collected from 3338 samples.

Fig. 1 Abundance of gnathiids. Boxplots of raw counts per trap among sampling trips (trip = sampling trip number), for day and night. Boxplots: center line = median, box = inner interquartiles, error bars = 90th and 10th percentiles, and circles = outliers



Gnathiid abundance trap^{-1} was highly variable (range 0–416, Fig. 1).

Gnathiid abundance patterns differed according to an interaction between day/night and sampling trip (GLMM: $P < 0.0001$, Table 1). This was due to numerous (nine) sampling trips differing from the day and night pattern of July 2000 ($P < 0.05$), with all significant coefficient estimates being positive indicating a greater abundance at night than day (Fig. 2a, Table S2). The higher night values ranged from 85 to 97% more gnathiids at night than the day per sampling trip (percentages calculated using backtransformed log values). Overall, ignoring sampling trip, pooled mean predicted log abundances for daytime and nighttime when backtransformed were 2 and 12 gnathiids trap^{-1}, respectively, as shown in Fig. 2a. Ignoring day and night, the backtransformed predicted abundance ranged from 0.5 to 34 gnathiids trap^{-1} across sampling trips (Fig. 2b).

Table 1 Analysis of deviance table (Type II tests) showing model results for gnathiid abundance

Coefficient	*df*	χ^2	*P*
Cleaner	1	0.1042	0.7468
Daynight	1	10.2725	0.0013
Trip	20	134.5078	< 0.001
Soak time	1	2.5530	0.1100
Cleaner:daynight	1	0.6220	0.4303
Cleaner:trip	20	31.6778	**0.0468**
Daynight:tip	20	142.8137	**< 0.001**
Cleaner:daynight:trip	20	27.9527	0.1105

Probability values in bold are those mentioned in the text

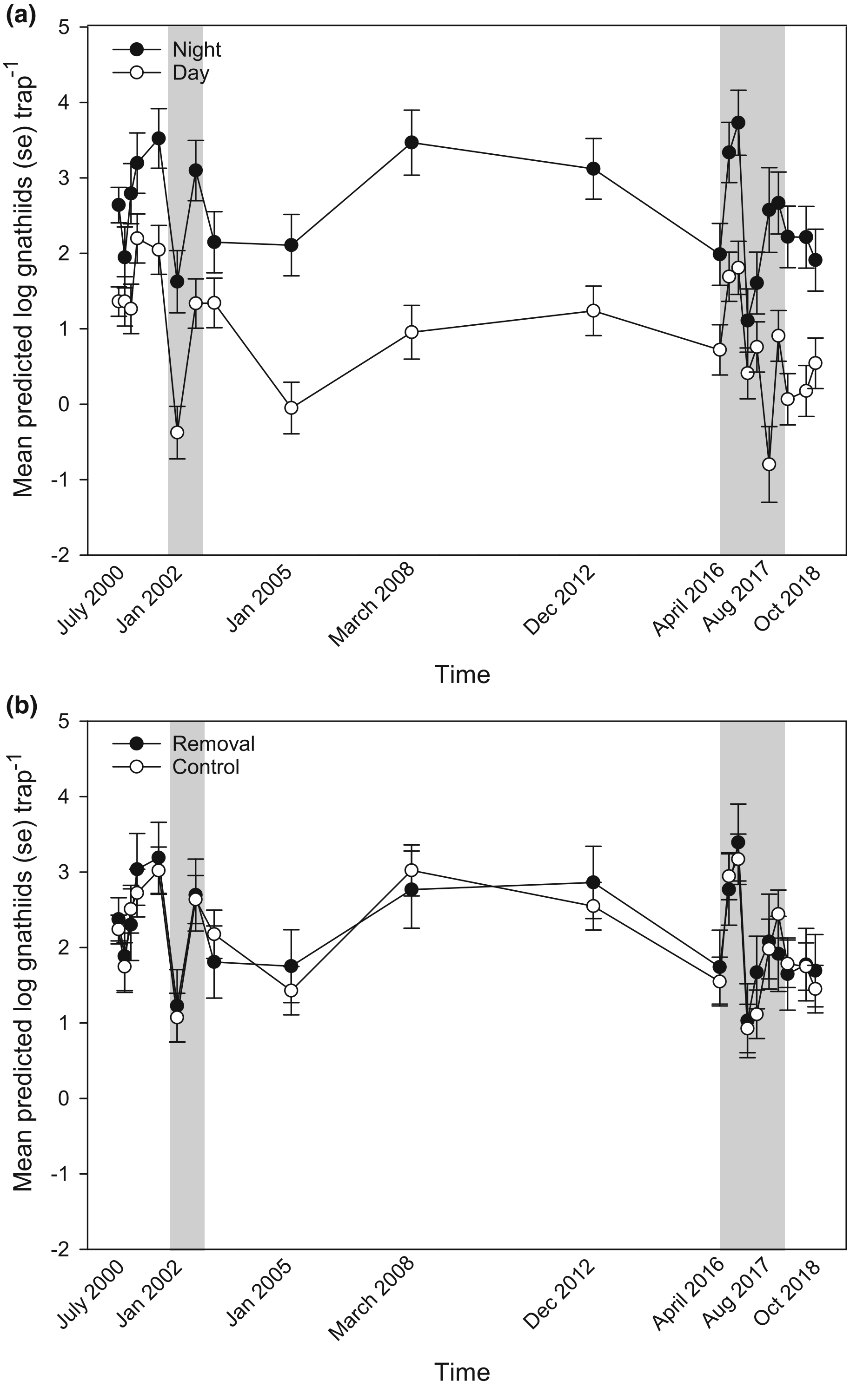


Fig. 2 Abundance of gnathiids. Interaction plots with predicted mean log gnathiids trap^{-1} for **a** day (open symbol) and night (solid symbol) over time (i.e., trips or sampling trips) and **b** control (open symbol) and removal (solid symbol) cleaner presence treatments over time. Error bars are standard errors. Gray backgrounds represent bleaching years

Gnathiid abundance differed according to an interaction between cleaner presence treatment and sampling trip (GLMM: $P = 0.04686$, Table 1, Fig. 2b). The four significant differences, relative to pre-removal values in July 2000, involved more gnathiids present on removal reefs compared with controls in January 2001 (27%), December 2012 (27%), October 2016 (20%), and April 2017 (43%) (percentages calculated using backtransformed values, Fig. 2b, Table S2).

When sampling trip was converted to time and used as a covariate instead of as a fixed effect, the interaction between day/night and time was significant (GLMM:

$P = 0.0010$ Table S3a). This was due to a decrease in gnathiids over time in the day, whereas in the night there was no such decrease (Fig. 2a, Table S3b). In contrast, when the temperature difference between daily ambient and long-term average was used as a covariate instead of time, it was not significant (GLMM: $P = 0.3425$, Table S4).

When examining patterns by month and year separately for day and night, to account for any potential seasonality, in the day samples there were no obvious patterns with bleaching, even without the possible outlier August 2017 which had very low gnathiid abundance values (Fig. 3a). By contrast, for night samples, when mean gnathiid abundance was always higher, there were fewer gnathiids collected from sampling trips during or just before (January 2002, 2017) and just after (April 2016, 2017), bleaching months (Fig. 3b). During bleaching years, gnathiid abundance from night samples rebounded during cooler months to levels that were comparable to, or higher than, those of non-bleaching years (Fig. 3b). Indeed, the highest levels ever recorded were during the October sampling trip during the 2016 bleaching year (Fig. 3b). However, in the non-bleaching year of 2018, after the two previous bleaching years, this “rebound” in the cooler months did not appear to occur, with levels appearing to decline slightly instead by October 2018 (Fig. 3b).

There was no consistent effect of cleaners over time. However, it is important to note that some reefs began to lose all cleaners in April 2016 (April 2016: one out of six reefs; July 2016: 4 out of 6 reefs). Despite this sudden decline in cleaners on these control reefs, no increase in gnathiids occurred there at this time. Eventually two reefs regained their cleaners (Jan 2017 Reef 5, February 2018 Reef 1, Fig. S1) and the remaining two regained their cleaners in October 2018 (Reefs 10 and Reef 13, Fig. S1). Thus, “cleaner” effects should be interpreted with caution.

Discussion

Because environmental factors can impact hosts, parasites, and the interaction between them (Lafferty and Kuris 1999; Mackenzie 1999; Sures et al. 1999; Williams and Mackenzie 2003; Sasal et al. 2007), understanding the impacts of extreme environmental changes on ecological communities requires an understanding of the impacts on parasites. We took advantage of our long-term monitoring of gnathiid isopods on experimental patch reefs to examine changes in gnathiid abundance associated with mass warm-water bleaching events around Lizard Island, GBR. To our knowledge, ours is the only research team to examine long-term population trends for any parasite or micropredator in coral reef systems and thus the first study to examine potential impacts of bleaching events. Given the widespread occurrence of these events, we were unable to compare bleached and unbleached reefs pre- and post-bleaching and were thus limited to a longitudinal comparison of our 12 patch reefs. Compared with non-bleaching years, the number of gnathiids collected in emergence traps was much lower during January and April sampling, which was the warm-water period during or shortly after the bleaching event. However, in subsequent samples during cooler months of these years, populations recovered to levels similar to those of non-bleaching years. This pattern occurred only during “night” samples that also include dawn and dusk periods—when more gnathiids are typically active (Grutter and Hendrikz 1999; Sikkel et al. 2006). Compared with bleaching years, population levels during non-bleaching years remained similar across seasons.

Decreases in abundance associated with above-normal water temperatures have been reported in other studies on small aquatic arthropods (e.g., Hogg and Williams 1996; reviewed by Przeslawski et al. 2008), and there are several non-mutually exclusive hypotheses that might explain the low levels of gnathiids observed in our study during summer in bleaching years. First, the high temperatures associated with bleaching may impair physiological performance. Tropical marine invertebrates have generally low tolerance for temperature fluctuations (Compton et al. 2007) and may suffer high mortality during warming events due to heat stress (Blidberg et al. 2000; Chan et al. 2006). In addition, high temperatures may impact rates of development (e.g., Reitzel et al. 2004; O’Connor et al. 2007). For gnathiids, this may mean that molting could begin before the blood meal is digested or that both digestion of the blood meal and metamorphosis are similarly expedited, meaning that gnathiid juveniles would need to find hosts sooner during their next feeding stage and have less time to do it before dying, due to increased metabolic demands and depleted energy reserves. Similarly, adults may utilize their final blood meal more quickly, leaving less time and energy for reproduction.

Bleaching events also appear to have significant impacts on host fishes (Booth and Beretta 2002; Wilson et al. 2006), attributable both to heat-induced mortality and to habitat degradation. Indeed, during the 2016 bleaching event, fish populations near our study reefs declined significantly (Triki et al. 2018), and fish assemblage structure was significantly altered (Richardson et al. 2018) through some combination of mortality and emigration. Given that gnathiids depend on host fishes for food, a significant decline in host fish populations and/or a change in the types of available host species could have significant negative impacts on gnathiid populations. The return of at least some fish species may contribute to the increase in gnathiid

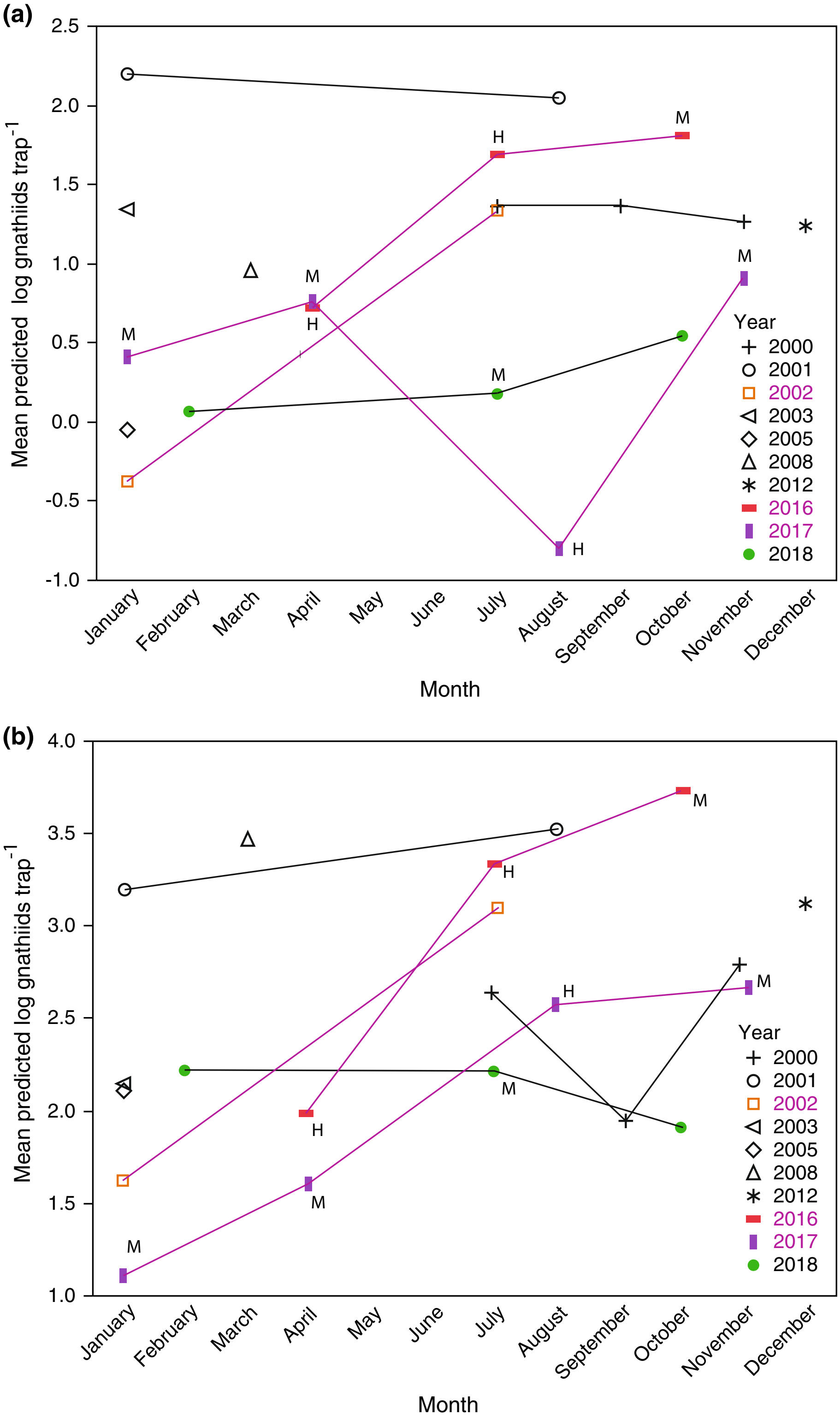


Fig. 3 Mean predicted log gnathiids per trap rearranged by month for each year separately for **a** day and **b** night. For standard errors, see Fig. 2. *M* = moderate temperature (0.44–0.92 °C) and *H* = high (1.1–1.44 °C) temperature increase between absolute and long-term average temperatures. Lines connect times sampled in same year. Lines and years in the legend that represent bleaching years are colored pink (i.e., 2002, 2016, 2017)

populations when waters cool, even when there is high coral mortality. The degree of "recovery" of gnathiid populations may further depend on the abundance of high quality host species versus smaller microcarnivores that may eat gnathiids (Artim et al. 2017).

Another factor that likely contributes to the recovery of gnathiid populations following bleaching events is the loss of live scleractinian corals. Corals can eat gnathiids, even when bleached, and even if gnathiids survive corals' attempts to feed on them, they become covered in mucus from the coral (Artim and Sikkel 2013). Moreover, when given a choice, gnathiids actively avoid live corals, and fish hosts placed (in cages) on live coral are less likely to be infested with gnathiids than when they are placed on dead coral (Santos and Sikkel 2017). Given the strong negative impact of live corals on gnathiids, we expected that gnathiid abundance during the cooler months following high coral mortality would be consistently high, similar to the high October 2016 abundances observed. The lower number of fish hosts and/or the return of extreme warm water may have limited this. In addition and/or alternatively, coral cover prior to bleaching events may have been below the threshold necessary to effectively limit gnathiid populations.

Finally, the primary purpose of our monitoring efforts was a long-term experimental study on the effects of cleaner wrasses on gnathiid isopod populations and coral reef communities. Cleanerfish can consume hundreds of gnathiids daily (Grutter 1996), and they have been shown to reduce per capita infestation levels on host fish (Grutter et al. 2018). However, their impacts on gnathiid populations are less clear. This appears to be due to the dual effects of cleaner wrasse on clients. Cleaner wrasse depend on clients to provide food (mostly parasites) and remove parasites from them, and the presence of cleaner wrasse has been shown to locally enhance the abundance of fish, especially larger, highly mobile species (Bshary 2003; Waldie et al. 2011). Thus, mobile client fishes can both serve as local hosts for gnathiids (positive impact on gnathiids) that bring gnathiids to cleaners (negative impact on gnathiids), but also bring gnathiids to and from reefs through their diel movements (Sikkel et al. 2017). This could have positive (importing gnathiids) or negative (exporting gnathiids) impacts on local gnathiid abundance.

While half of our reefs had cleanerfish continually removed over years, during at least the most recent bleaching months, cleaner wrasse on most control reefs also disappeared. This disappearance corresponded with an overall decrease in fish abundance in the region (see above). It is therefore unclear whether cleanerfish drove changes in fish abundance, vice versa, or whether both were similarly impacted by thermal stress and either died or relocated. Triki et al. (2018) reported a 50% decrease in the abundance of “large” (> 10 cm) client species, but an 80% decrease in cleaner wrasse abundance near our study sites, resulting in an increase in the ratio of clients to cleaners. However, because the abundance of ectoparasites on clients is proportional to surface area, there was likely a decrease in available client surface area per cleanerfish biomass. Client removal experiments would be required to determine if a decrease in client biomass/surface area drives the departure of cleaner wrasses.

In summary, by including multiple bleaching and non-bleaching years during our monitoring, our data suggest a significant impact of bleaching events on the abundance of gnathiid isopods in shallow coral reef environments. While our data include multiple years pre and post for the earlier bleaching event, the occurrence of consecutive bleaching years in 2016–2017 resulted in only one (2018) post-bleaching year for these most recent events, which showed weak intra-annual variation similar to other non-bleaching periods. Given that the 2016 and 2017 bleaching events were particularly severe and widespread, “if recovery” of the broader coral reef community does occur, the expected recovery trajectory is long. This makes assessment of post-bleaching population trends for cryptic species like gnathiids more difficult. Given the expected increase but unpredictability of mass bleaching events, we therefore encourage more research teams to incorporate sampling of gnathiids, and other parasites and cryptic organisms in their monitoring efforts to increase our capacity for assessment of bleaching events on these organisms, which dominate coral reef biodiversity and have major impacts on coral reef community dynamics.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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