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RESEARCH ARTICLE

Variation in emergence of parasitic and predatory isopods among habitats at Lizard Island, Great Barrier Reef

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Abstract Gnathiid isopods are one of the most abundant groups of ectoparasites on coral reef fishes. They, and other isopods, have been shown to significantly affect the health and behaviour of many reef fish. Whether isopod emergence differs among habitats on coral reefs is not known. In this study, we measured emergence rates of parasitic isopods (Gnathiidea and Flabellifera) in six habitats at two sites at Lizard Island during new moon periods in March and December 2004. Isopods were collected from the periphery and centres of micro-reefs, patch reefs, continuous reefs, and from inter-reefal habitats (sand or rubble) with 1 m^2 emergence traps. Sites (Casuarina and Coconut Beach) were located on opposite sides of Lizard Island. Live gnathiids were collected with light traps in November 2005 to investigate species differences between sites. At both sites, the most abundant gnathiid species was exclusive to that site. More gnathiid larvae emerged at night, and emergence of fed gnathiids (pranizae) and flabelliferan isopods was almost exclusively nocturnal. Diurnal emergence was greater at Coconut Beach than Casuarina Beach. Although emergence counts were not consistently affected by parameters such as habitat, site, or sampling period, gnathiid size and feeding state were. Where significant differences existed, gnathiids were larger and more often fed over reef borders than centrally. We suggest first stage larvae (Z1) have the largest influence on total abundance and are patchily distributed in accordance with adults from which they have recently hatched. As later stage larvae depend on fish, more successful (fed) and older larvae are found on the edges of reefs where appropriate hosts may be more abundant, or predation is lower. Gnathiids were overdispersed in all habitats investigated, including apparently homogeneous beds of coral rubble and sand. This indicates that their distributions may be better predicted by very fine scale differences in substrate or that aggregations are the result of gregariousness and may be difficult to predict on the basis of substrate. Emergence traps collected comparatively few parasitic flabelliferan isopods. This community differed greatly from the previously described community of scavenging isopods at Lizard Island. These differences are probably the result of differences in trapping methodology.

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Introduction

Gnathiid isopods are one of the most prevalent and abundant groups of ectoparasites of coral reef fishes (Grutter 1994; Grutter and Poulin 1998). They are mobile parasites during their three larval stages, eventually moulting into free-living benthic adults (Mouchet 1928), upon which their taxonomy is based. Once unfed larvae (zupheae) feed on blood and/or plasma from their hosts, they are termed pranizae and return to the benthos to moult (Cohen and Poore 1994). The cumulative effect that gnathiids have on the health and behaviour of reef fishes is becoming increasingly evident. Several studies have shown infections are short-lived and have a rapid turnover (Monod 1926; Grutter 1999, 2003), can reduce blood cell volume (Jones and Grutter

2005) and cause mortality (Mugridge and Stallybrass 1983) at high densities. They also cause some infected fish to seek out cleaners (Grutter 2001; Sikkel et al. 2004). At Lizard Island, Great Barrier Reef (GBR), each adult individual of the cleaner wrasse *Labroides dimidiatus* consumes an average of 1,218 ± 118 gnathiids from 2,297 ± 83 fish inspected each day (Grutter 1996). When cleaner fish are removed from habitats, fish species diversity is reduced (Grutter et al. 2003). Therefore, it is possible that gnathiids have a significant indirect impact on the composition of coral reef fish species and provide the stimulus for much of the cleaning behaviour that is widespread on coral reefs.

The effects of chronic low-level blood feeding and secondary infections on hosts after parasitism by gnathiids remain unstudied. Although there is little evidence to suggest that natural densities of gnathiids directly affect the mortality of adult fishes on the GBR via tissue damage or haemophagy, gnathiids may affect fish in other ways. For example, gnathiids have been implicated as vectors in the transmission of haemogregarine blood parasites on South African temperate reefs (see Smit and Davies 2004 for a review).

In addition to gnathiid isopods, four other isopod families, the Aegidae, Cirolanidae, Corallanidae, and Cymothoidae have many representatives which are parasites, predators, or micropredators (taking a small meal from many sources, see Lafferty and Kuris 2002) of fish. These and other taxa collectively form the Flabelliferan isopods that, like gnathiids, have potential to serve as disease vectors and to negatively affect fishes. For example, cirolanid isopods can kill confined fishes (Stepien and Brusca 1985) and corallanid isopod infections intensify rapidly on confined wrasses deprived of cleaning by *L. dimidiatus* (Grutter and Lester 2002). Cymothoid isopods are mostly permanent parasites as adults, but have micropredatory or predatory juvenile and male stages (Brusca 1981). Little is known of the patterns of activity for these mobile fish pathogens, except that they may be more active at night (Stepien and Brusca 1985).

Several studies have demonstrated seasonal, lunar, and diel abundance patterns of larval gnathiids on coral reefs. More gnathiid isopods emerge (enter the water column) diurnally on Caribbean reefs (Chambers and Sikkel 2002); however, this pattern is reversed on the GBR (Jacoby and Greenwood 1988) except during some full and new moons (Grutter et al. 2000a). Finer-scale temporal differences show gnathiid emergence is usually greatest at crepuscular periods in the Caribbean and GBR (Jacoby and Greenwood 1988; Grutter et al. 2000a; Chambers and Sikkel 2002). Furthermore, Jacoby and Greenwood (1988) found a number of differences in gnathiid emergence between coral and sand substrates at Heron Island lagoon, southern GBR. They found that during the last quarter and new moon phases in winter, more gnathiids emerged from coral than sandy substrates. Hence, it is clear that investigations of differential emergence among habitats must control for the effects of season and lunar cycle.

Distribution patterns of gnathiid species on coral reefs are completely unstudied because many adults have not been described and larvae are difficult to identify. Thus, emergence patterns have not been considered for individual species. Even for gnathiid larvae collectively, little is known of how emergence varies among large-scale habitats. What is known is that larger patch reefs generally accommodate more abundant and diverse fish communities than small patch reefs (Sale and Douglas 1984; Clarke 1988; McLain and Pratt 1999) and that planktivorous and piscivorous fish are frequently observed aggregating near reef margins that face into the current. As gnathiids and other isopods feed on such fish (Grutter 1994; Grutter and Poulin 1998), it is possible that these differences in the spatial distribution of reef fish influence the abundance of gnathiid larvae emerging from the underlying benthos. Therefore, to investigate variation in the emergence of larval gnathiids and other isopod micropredators among reef habitats, three types of reef (subdivided into peripheral or central areas) and the benthos between these reefs were sampled at two sites at Lizard Island. Trapping was done during new moon phases in March and December 2004 to control for season and lunar period. To examine differences in species composition between these two sites, live third stage pranizae (P3) were collected and typed in November 2005 using small light traps.

Materials and methods

Study sites

Two sites at Lizard Island, GBR (14°40′S, 145°28′E), were emergence trapped during the weeks following the new moon from March 22–29 to December 10–17, 2004 (see Pratchett 2005 for map). Coconut Beach (0–10 m deep) is exposed to the predominant Southeast trade wind and has high living coral cover. Casuarina Beach (0–6 m deep) is a lagoonal habitat protected from most winds with large areas of dead and soft corals. The inter-reefal substrate differs between sites: at Coconut Beach, it is mostly coral rubble, and at Casuarina Beach it is sand. Sites were sampled every other day and traps were moved between sites on the days between sampling. A site was chosen randomly and sampled, followed by the site not chosen, so that each site was sampled twice for 24 h in each period.

Emergence trapping procedure

At each site, five to six 1 m^2 emergence traps (Jacoby and Greenwood 1988) were placed on three different-sized reefs, peripherally on the edge of each reef or centrally, and on the inter-reefal substrate (Fig. 1b). These areas are termed habitats. Reefs were categorised based on their approximate two-dimensional area: micro-reefs were ~1 m^2, patch reefs and continuous reefs were 3–12 and > 50 m in diameter, respectively. Micro-reefs were sampled entirely with one emergence trap and were too scarce to be sampled at Coconut Beach. Reefs were considered discrete when separated by more than 2 m of inter-reefal substrate. Traps were randomly positioned on reef edges by SCUBA divers swimming along the edge for the number of seconds displayed on the diver's watch at the time of selecting the trap. Traps were placed 'centrally' on continuous reefs in a similar manner; they were carried perpendicularly to the reef edge for a randomised duration and placed more than 2 m inside the reef edge. Traps were placed haphazardly on inter-reefal substrate and on the estimated centres of patch reefs. The aim of this procedure was to randomise trap placement on habitats (fixed factors). However, placement of the traps was subject to the following criteria: they needed to remain relatively upright for 24 h and in a position where they would not damage the coral or be damaged.

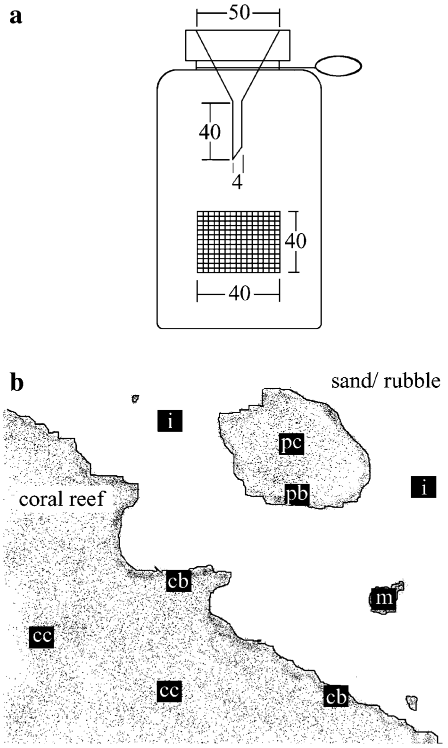

Fig. 1 Schematic diagrams showing light trap construction with measurements in mm (**a**) and emergence trap layout in aerial perspective (**b**). *Black squares* represent emergence traps, habitat codes are: continuous reef central (*cc*), continuous reef border (*cb*), inter-reefal (*i*), micro-reefal (*m*), patch reef central (*pc*), and patch reef border (*pb*)

Emergence traps were placed on habitats at dawn (between 0600 and 0730 hours). A bottle was affixed to the trap and the time, habitat, and bottle number was recorded. The order of start times was randomised across the habitats to reduce temporal confounding. Bottles were then exchanged at dusk and collected again at dawn, both times in the same order they were affixed, to reduce variation caused by differences in trapping time. Dusk collection periods began between 1630 and 1730 hours (~10 h later).

The contents of each bottle were filtered through a 62-µm sieve and preserved in 10% formalin in seawater. Isopods were sorted from contents, then counted and measured using a dissecting microscope (125×). The feeding state of the gnathiids (praniza or zuphea) was recorded. Flabelliferan isopods were cleared by immersion in chlorolactophenol for 10–20 min, which allowed observation of fine structures with a compound microscope (400×). Adult flabelliferans were identified to genus or species where possible and undescribed species were assigned to types.

Light trapping procedure

Light traps were made of 1 l, clear, wide-mouthed bottles (http://www.nalgenelabware.com) with a funnel entry through a hole in the screw-top lid and a breathing window (Fig. 1a). Each trap was illuminated with a 6-in. dive cyalume stick (http://www.glowproductions.com.au). The breathing window was covered with 1.2 mm fly-screen mesh. This mesh was large enough to enable some gnathiids to escape, but finer mesh collected so much zooplankton that samples would spoil by morning. Each trap was tethered 20 cm above a brick on a float line to the surface. Five traps were placed on sand or rubble adjacent to reefs each evening and collected at dawn the next day. The contents of the five traps were emptied into a 20-l bucket and aerated while live P3s were sorted from smaller volumes of the catch using pipettes. Pranizae were digitally photographed and typed. Selections of abundant types were moulted into adults in an attempt to confirm their identity. From the 1st to the 26th of November, Casuarina and Coconut Beaches were trapped ten and three times, respectively.

Statistical analyses

Because of unequal sampling effort and limited catches, only qualitative taxonomic comparisons were made for P3 larvae collected from light traps. For emergence trap, data quantitative comparisons were made with the appropriate statistical tests.

A *t*-test was used to investigate the difference in overall emergence counts between day and night. Means of emergence from each habitat/site combination were used as data points in this comparison to satisfy the assumptions of normality and equal variances.

Emergence data (counts) were highly aggregated for both flabelliferan and gnathiid isopods. Differences in gnathiid emergence with respect to habitat, site, and sampling period were analysed with a quasi-Poisson generalised linear model using the *R* statistics package (http://www.r-project.org). Quasi-Poisson regression was used because residual deviance (1,614) was more than six times greater than the critical value of the χ^2 distribution ($\chi^2_{\text{crit}} = 266$, $df = 230$, $\alpha = 0.05$), indicating data were too over-dispersed to use Poisson regression (Dobson 1991). Day and night data were analysed separately because nocturnal and diurnal communities appear distinct and it is not possible to perform repeated measures with quasi-Poisson regression. Models were constructed following Crawley (2005) by entering factors in order of likely significance, based on the literature (Jacoby and Greenwood 1988; Grutter et al. 2000a; Chambers and Sikkel 2002) (i.e. site, habitat then sampling period). Non-significant interaction terms were then sequentially removed from the model. Interaction plots were used to determine the nature of the interactions between parameters (Fig. 2).

Flabelliferan isopod emergence was also analysed with quasi-Poisson regression using *R* in the same manner described above. Only night data was used because all but 2 of the 68 (97%) flabelliferans were collected at night. We attempted to investigate specifically which habitats differed in flabelliferan isopod abundance with Tukey-type Non-parametric multiple comparisons for ranked data (with corrections for tied data and unequal sample sizes) (Dunn 1964). Test statistics were compared to critical values of *Q* (Zar 1999), but due to small number of isopods collected, none of these comparisons were significant.

The gnathiid size frequency distribution was heavily skewed and multi-modal. It could not be normalised using any of the transformations in Zar (1999). Thus, for both day and night data sets, comparisons between sites and period were done using Wilcoxon rank-signed tests, and comparisons among habitats for a particular site were done using Kruskal–Wallis tests.

Differences in the feeding state of gnathiids with respect to habitat, site, and period were analysed with logistic regression using *R*. Because 98.8% of pranizae were collected at night, only these data were used. To explore the significant interaction that existed between habitat and period, we used an interaction plot (Fig. 4). Fewer pranizae were collected in period 2 in all habitats except micro-reefs where there were slightly more pranizae in period 2. Thus, the period/habitat interaction for habitats (except micro-reefs) is a product of the degree of change, but not the direction. Therefore, differences in the proportion of pranizae emerging between central and border areas of continuous and patch reefs within each site were examined for data pooled from both periods using Fisher exact tests.

Results

Taxa captured

Emergence traps yielded a total of 1,785 (7.66 $\mathrm{m}^{-2}\,\mathrm{day}^{-1}$) juvenile gnathiid and 68 (0.28 $\mathrm{m}^{-2}\,\mathrm{day}^{-1}$) parasitic or predatory flabelliferan isopods. Collections from Coconut Beach accounted for 65 and 79% of the total gnathiid and flabelliferan abundance, respectively. Isopods resembling *Cirolana improceros* were the most

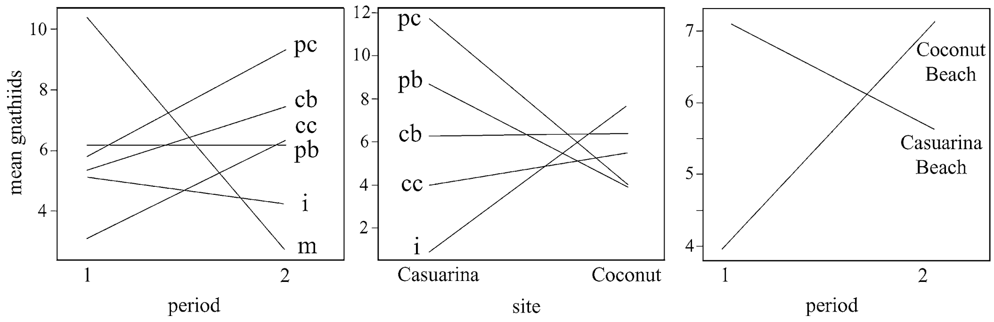

Fig. 2 Plots describing the interaction between habitat and period (**a**), habitat and site (**b**), and site and period (**c**) for the response variable, gnathiid abundance, collected at night

abundant flabelliferans ($n = 19$), followed by *Eurydice* spp. ($n = 17$) and juvenile cirolanids ($n = 10$) (Table 1). Isopods resembling *C. improceros* were morphologically similar to the description by Bruce (1986), except for their uropodal spination, and are regarded as a Lizard Island variant. Four of the specimens of *Eurydice* were *E. orientalis* and the remainder were identifiable only to genus. *Argathona macronema* was the most common corallanid isopod captured ($n = 6$), and corallanid sp. 3 is probably a juvenile of a species of *Argathona*. Each of the five most common taxa was collected at both sites except for *C. improceros*, which was only collected from emergence traps at Coconut Beach.

Gnathia sp. C and *G. falcipines* were the two most abundant P3 larvae collected in light traps and were only collected at Coconut Beach and Casuarina Beach, respectively (Table 1). *Gnathia* sp. B and *G. calmani* were found in both sites, and *Gnathia* sp. N and F were found only at Casuarina Beach.

Spatial and temporal differences in emergence

Using habitat means, overall gnathiid emergence was greater during night (5.05 ± 0.58) than day (1.6 ± 0.58) ($df = 10$, $t = 4.16$, $P = 0.002$). Quasi-Poisson regression of diurnal gnathiid emergence counts showed habitat and period were not significant parameters, and there were no significant interactions. However, sites differed significantly ($df = 1$, residual $df = 232$, $P < 0.001$), with greater diurnal emergence at Coconut Beach than Casuarina Beach.

For night data, there were significant second order interactions between period, site, and habitat, but each parameter alone was non-significant (Table 2). An interaction plot between habitat and period showed emergence increased in some habitats and decreased in others between sampling periods (Fig. 2a), indicating that pooling data from the two periods was not appropriate. Emergence was also greater in some habitats at Coconut Beach compared to Casuarina Beach, but not others (Fig. 2b). Furthermore, emergence at sites also changed between sampling periods. At Coconut Beach, there were more gnathiids collected in period 2 and vice versa for Casuarina Beach (Fig. 2c).

In the regression of flabelliferan isopod counts, both site ($df = 1$, residual $df = 224$, $P = 0.01$) and habitat ($df = 5$, residual $df = 225$, $P = 0.001$) were significant parameters. More flabelliferan isopods were collected from Coconut Beach than Casuarina Beach.

Gnathiids collected from emergence traps at Coconut Beach were larger than those from Casuarina Beach during the day ($df = 1$, $\chi^2 = 6.14$, $P = 0.013$) and night ($df = 1$, $\chi^2 = 89.78$, $P < 0.001$). Median gnathiid lengths from Coconut and Casuarina Beach, respectively, were 0.8 and 0.72 mm in the day and 1.2 and 0.98 mm at night. Gnathiids collected in the night were smaller in period 2 ($df = 1$, $\chi^2 = 69.01$, $P < 0.001$) while gnathiids collected during the day did not differ in length between periods. There were significant differences in gnathiid length among habitats within each site. At Casuarina Beach, habitats differed in the day ($df = 4$, $\chi^2 = 21.11$, $P < 0.001$) and night ($df = 5$,

Table 1 Summary of all parasitic and predatory isopods collected in emergence traps and third stage pranizae (only) collected in light traps

Trap type	Taxa	Casuarina Beach		Coconut Beach		Total
		Abundance	% catch	Abundance	% catch	Abundance
Emergence	Gnathiid larvae	617	35	1,168	65	1,785
	Zupheae	416	29	1,031	71	1,447
	Pranizae	201	59	137	41	338
	C. improceros	0	0	19	100	19
	Euridice spp.	9	53	8	47	17
	Juvenile cirolanids	1	10	9	90	10
	A. macronema	1	17	5	83	6
	Cirolana brocha	1	20	4	80	5
	C. erodiae	0	0	2	100	2
	Juvenile corallanids	0	0	2	100	2
	Anilocra nemipteri	1	50	1	50	2
	Corallanid sp. 1	1	50	1	50	2
	Corallanid sp. 2	0	0	1	100	1
	Corallanid sp. 3	0	0	1	100	1
	Aega sp.	0	0	1	100	1
Light	*G. falcipines*	35	100	0	0	35
	Gnathia sp. C	0	0	31	100	31
	G. calmani	12	80	3	20	15
	Gnathia sp. B	7	78	2	22	9
	Gnathia sp. N	4	100	0	0	4
	Gnathia sp. F	2	100	0	0	2

Table 2 Quasi-Poisson regression analysis of nocturnal gnathiid emergence counts between sites, sampling periods, and among habitats

Source	*df*	Deviance	Residual *df*	Residual deviance	*P* > chi
NULL			230	1,614.92	
Habitat	5	41.67	225	1,573.25	0.24
Site	1	6.23	224	1,567.02	0.31
Period	1	5.93	223	1,561.09	0.33
Habitat × site	4	244.06	219	1,317.02	**<0.001**
Habitat × period	5	96.53	214	1,220.49	**0.01**
Site × period	1	58.68	213	1,161.81	**0.002**

Significant probablilities ($\alpha = 0.05$) are shown in bold

$\chi^2 = 58.17$, $P < 0.001$), but at Coconut Beach, sizes varied among habitats only at night ($df = 4$, $\chi^2 = 29.08$, $P < 0.001$). Where significant differences among habitats existed (i.e. at both sites at night and at Casuarina Beach during the day), the same pattern of gnathiid size with respect to habitat was present (Fig. 3); inter-reefal and micro-reefal habitats (m, i) had the largest gnathiids, with smaller gnathiids in border areas (cb, pb), and the smallest gnathiids in central areas (cc, pc). No gnathiids emerged from inter-reefal habitats at Casuarina Beach (sand) (Fig. 3).

Pranizae emerged almost exclusively at night ($df = 1$, $\chi^2 = 103.73$, $P < 0.001$) with nocturnal emergence accounting for 98.8% of total abundance. Logistic regression of the proportion of pranizae showed habitat, site, and period were significant parameters, as was the interaction between habitat and period (Table 3). In period 1, 37.4% of gnathiids were fed compared to only 12.9% in period 2. The interaction between habitat and period is the result of variable declines in the proportion of pranizae in habitats between sampling periods, with the exception of micro-reefs, where there was a slight increase (Fig. 4). At Coconut Beach, there was a greater proportion of pranizae in continuous border (cb) areas than central (cc) areas ($df = 1$, $\chi^2 = 18.3$, $P < 0.001$; Fig. 5); however, there was no such difference between border and central areas of patch reefs. At Casuarina Beach, border areas of both continuous ($df = 1$, $\chi^2 = 18.67$, $P < 0.001$) and patch reefs ($df = 1$, $\chi^2 = 15.84$, $P < 0.001$) had a greater proportion of pranizae than central areas (Fig. 5).

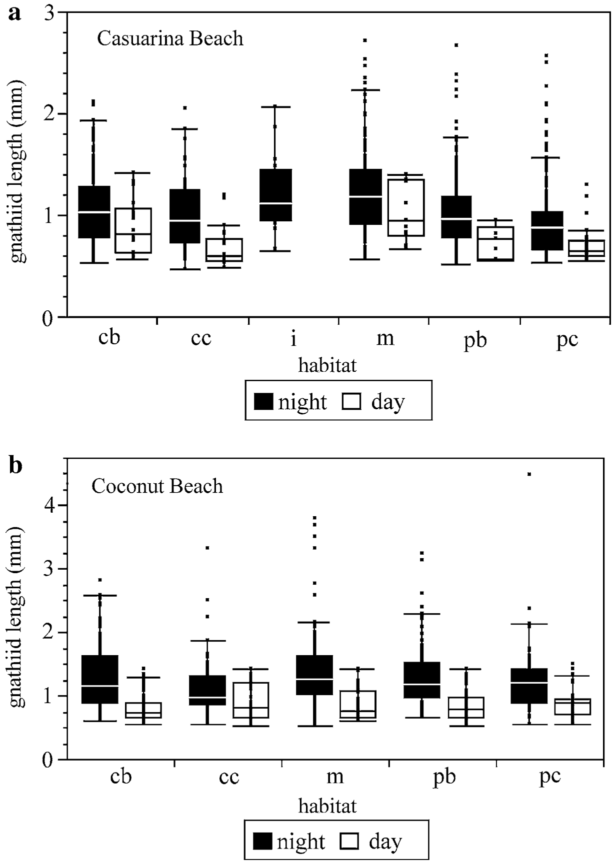

Fig. 3 *Box and whisker plots* of median gnathiid length in habitats during the day and night from Casuarina Beach and Coconut Beach. Twenty-five and 75% quartiles are represented as *boxes* around the median with 10 and 90% quartiles displayed as *whiskers*. *Dots* are outliers

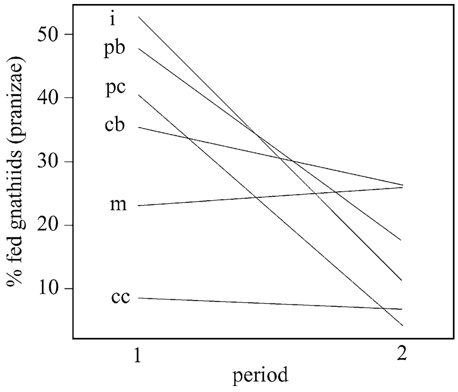

Fig. 4 Interactions between habitat and period for the response variable, percentage of fed gnathiids (pranizae), collected at night

Discussion

There is reasonable evidence that the distribution of *Gnathia facilpines* does not include Coconut Beach, and that *Gnathia* sp. C is not present at Casuarina Beach. Coconut Beach was only sampled three times so it is possible that *G. falcipines* may have been collected with greater sampling effort, but it appears that *Gnathia* sp. C was not present at Casuarina Beach during November 2005. Localised site specificity has been demonstrated in several parasite taxa (Adlard and Lester 1994; Rigby et al. 1997; Grutter 1998; Cribb et al. 2000) and may be

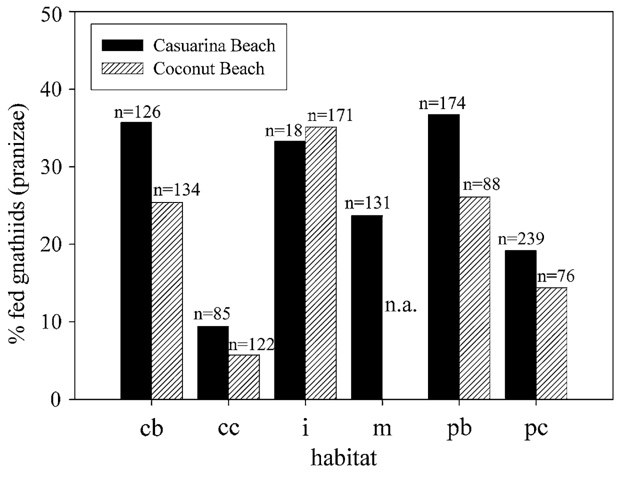

Fig. 5 Variation in the percentage of pranizae emerging from habitats at Casuarina Beach and Coconut Beach during the night. Sample sizes are displayed above *bars*

Table 3 Logistic regression analysis of the proportion of fed gnathiids (pranizae) between sites, sampling periods, and among habitats

Source	*df*	Deviance	Residual *df*	Residual deviance	$P >$ chi
NULL			1,363	1,520.73	
Habitat	5	74.91	1,358	1,445.82	**<0.001**
Site	1	7.11	1,357	1,438.71	**0.01**
Period	1	87.95	1,356	1,350.75	**<0.001**
Habitat × site	4	1.18	1,352	1,349.57	0.88
Habitat × period	5	45.99	1,347	1,303.58	**<0.001**
Site × period	1	2.81	1,346	1,300.78	0.09

Significant probabilities ($\alpha = 0.05$) are shown in bold

related to the often extreme site attachment of host fishes on coral reefs. Unfortunately, host-specificity data for gnathiids on the GBR are almost non-existent; thus, host distributions cannot yet be related to parasite distributions.

Gnathia sp. A was not collected at all using light traps, despite it and *Gnathia* sp. B being the two most common species on fish collected during the day from Lizard Island (Smit et al. 2006). *Gnathia* sp. B was collected at both sites; hence, *Gnathia* sp. A is probably diurnal or not attracted to light traps. Differences in species composition between the two sites may account for greater diurnal emergence from Coconut Beach. Alternatively, more diurnal emergence may result from early afternoon shading (Chambers and Sikkel 2002) by the hills of Lizard Island.

Nocturnal gnathiid abundance did not vary consistently according to site, habitat, or sampling period. Numerous interactions between these factors (Fig. 2) suggest abundance is highly variable temporally and over both spatial scales used in this study (i.e. site and habitat). These variables did, however, explain variation in gnathiid size and feeding state.

At both sites during the night and at Casuarina Beach during the day, the pattern of size with respect to habitat was similar (Fig. 3). Central areas of reefs had smaller gnathiids than border areas, while the biggest gnathiids were found emerging from micro-reefs and inter-reefal areas. Central areas of reefs also had lower proportions of fed larvae (pranizae) than border areas (Fig. 5). Because fed larvae are longer than zupheae, it may appear that this size trend is simply the result of differential proportions of pranizae. However, the same trend is evident at Casuarina Beach during the day when pranizae are virtually absent. This suggests differences in size among habitats are not purely the result of feeding state, but may also be caused by an ontogenetic shift in habitat use. Gnathiid size differences among habitats are probably not the result of inter-specific variation considering the same trend is present at both sites where different species occur.

Gnathiid abundance was not significantly different among habitats, yet gnathiids were larger and more often fed over reef borders than in central areas. We propose these findings are the combined result of gnathiid behaviour and host distributions. Factors affecting adult gnathiid distributions will differ from those affecting larvae because adults are non-feeding, hence, decoupled from host distributions (Tanaka and Aoki 1999). Thus, the parameter 'habitat' in this study, chosen because it reflected differences in host abundance, probably had little explanatory power for adult gnathiids. Adult gnathiids give rise to first stage larvae (Z1) which are the smallest and most abundant stage; therefore, adult distributions determine where the first emergence of Z1 larvae will occur. If adult gnathiids have an over-dispersed and stochastic distribution (with regard to the variables used in this study), then the majority of larvae (Z1) will too. This would explain the non-significant differences in gnathiid abundance among habitats. Larvae then find hosts, engorge, and return to the benthos. Grutter et al. (2000a) suggest pranizae emerge nocturnally because there is more risk of predation in daylight. Pranizae presumably have lower vagility than zupheae; so it seems likely that they leave their hosts, return to the benthos directly underneath them, and re-emerge at night when there is less chance of being eaten. The presence of more pranizae at reef margins implies greater feeding success there than at central sites. This may relate to host availability or levels of predation. The presence of larger gnathiids in these areas also supports the idea of greater feeding success, in that it can be inferred that older stages remained or returned to those habitats after moulting. Gnathiids are readily consumed by juvenile damselfish in captivity (R. Penfold unpublished data) indicating that planktivores as well as cleaner fish feed on gnathiids. It seems unlikely that the borders of reefs would be safer habitats for gnathiids given the abundance of planktivores in these areas. Instead, we suggest that greater gnathiid feeding success in border areas may be the result of host abundance there. However, it is interesting that a relatively large percent of gnathiids were fed in inter-reefal areas where hosts are typically less abundant. In these areas, greater feeding success could be the result of less predation by planktivores or invertebrate predators.

Gnathiids were by far the most abundant micropredatory isopod collected in emergence traps and were present in all habitats except for sandy patches between reefs during the day at Casuarina Beach (i). We found more gnathiids, flabelliferans, and pranizae emerged at night than day. This agrees with some studies (Hobson and Chess 1976; Stepien and Brusca 1985), but diurnally biased gnathiid emergence has been reported at some lunar phases by Grutter et al. (2000a) and by Chambers and Sikkel (2002). Some of this discrepancy may be explained by different trapping times of about 4 h favouring night in this study. Considering that gnathiid emergence has been reported as greatest during crepuscular periods (Chambers and Sikkel 2002), differences between what are considered ‘day and night’ may in fact be the result of minor temporal differences either side of dawn and sunset.

Emergence of gnathiids from inter-reefal areas (rubble at Coconut Beach and sand at Casuarina Beach) was not significantly different from emergence from any of the other habitats containing living coral and other large live sessile animals. *Gnathia* sp. A has been cultured on Lizard Island for many years using dead coral rubble (Grutter 2001), but the extent to which gnathiid juveniles naturally inhabit coral rubble was not known. Our results suggest that gnathiids at Lizard Island emerge from sandy substrates and hard structures, and that they do not specifically require living coral or other large sessile fauna. Several studies have found non-coral reef dwelling adults and larvae in sponges (Monod 1926; Klitgaard 1991; Tanaka and Aoki 1999) and adults of Australian species have been found in a wide variety of habitats such as mud, sand, coral rubble, coralline algae, wood, and barnacles (Holdich and Harrison 1980; Cohen and Poore 1994). Interestingly, inter-reefal habitats appeared relatively homogeneous; yet, gnathiid emergence data was still highly over-dispersed. This suggests juveniles seek common places to shelter and moult in an apparently featureless environment. Juveniles may aggregate to other gnathiids or to microhabitats. If aggregations contained only first stage juveniles, then over-dispersion could be explained entirely by the simultaneous hatching of siblings from a gravid female. However, observed aggregations included juveniles of a range of different sizes, indicating that more developmentally advanced gnathiids or gnathiids of different species were sharing the same m^2 of habitat. Upon completing their parasitic life phase, gnathiids must find mates, after possibly being substantially relocated during their final attachment to a moving fish. Larvae may aggregate in the same way that adults do, although clearly they lack the imperative to find a mate.

While it is convenient to make generalisations about the behaviour of juvenile gnathiids as a whole, we suggest that, as other studies have done, these must be qualified at several temporal levels, geographically, and for the species involved. Had we been able to identify species differences among larvae from emergence traps, more distinct differences in behaviour may have been apparent. Unfortunately, the study of juvenile gnathiid behaviour is perhaps most limited by poor taxonomic understanding. Although molecular identification techniques exist for larval gnathiids (Grutter et al. 2000b), these, and differences in morphology, are not yet practical for identifying thousands of preserved juveniles (Smit and Davies 2004) that vary according to preservation, life history stage, and species.

The species of flabelliferan isopods we collected with emergence traps differ markedly from previous baited trap collections at Lizard Island. Keable (1995) targeted scavengers and found, in descending order, *Cirolana erodiae*, *Cirolana Kendi*, and *Cirolana capricornica* to be the most abundant isopods, followed by juvenile cirolanids. The only species collected by both the present study and Keable’s was *C. erodiae*. This difference may exist because we used different trapping methods, but *C. improceros* were also very abundant in baited 2 l bottle traps (similar to Keable’s) deployed in December 2005 (C. Jones, unpublished data). *C. improceros* is found surrounding continental islands and *C. erodiae* inhabits coral reefs (Bruce 1986). Because Lizard Island represents both of these habitats, temporal variation in the abundance of *C. improceros* and *C. erodiae* between samples may reflect changes in the scavenging community.

Emergence traps at Casuarina Beach completely failed to capture *C. improceros*, despite plentiful catches in baited traps (C. Jones, unpublished data). This indicates that *C. improceros* can either avoid emergence traps, or can move to baited traps from long distances (i.e. other sites). Future study of the detection capabilities of emergence traps would facilitate more accurate estimates of total emergence for both gnathiids and flabelliferans.

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