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Interactions between juvenile marine fish and gnathiid isopods: predation versus micropredation

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ABSTRACT: Theory suggests that micropredators can be virulent and that they will impact smaller hosts more than larger ones. We examined the interactions between micropredatory gnathiid isopods and juvenile damselfish *Acanthochromis polyacanthus*, the only fish on the Great Barrier Reef without a pelagic larval stage. Compared to most other fishes, *A. polyacanthus* can potentially interact with reef-based micropredators much earlier in life. To determine whether gnathiid isopods feed on juvenile *A. polyacanthus*, 150 juvenile fish sub-sampled from 20 fish broods were surveyed for ectoparasites and micropredators. Gnathiids were associated with 5 *A. polyacanthus* broods with mean standard lengths (SL) between 4.2 and 21.1 mm. Gnathiids were also found attached to 5 individual *A. polyacanthus* juveniles <10 mm SL. To determine if infection is detrimental, and/or if juveniles eat gnathiids, we exposed juveniles from a range of sizes (7.2 to 23.5 mm SL) to an individual third stage gnathiid *Gnathia falcipenis* for 6 h. Gnathiids fed on 29% of fish and gnathiid feeding success was significantly reduced by time in captivity. In 99% of these infections, gnathiids were not eaten afterwards, indicating that micropredation and predation were mutually exclusive. In 40% of trials the fish ate the gnathiid before the gnathiid could feed on the fish, and the probability of gnathiids being eaten was significantly greater for larger fish. Gnathiids only caused mortality in fish <10 mm SL. These data indicate that larger juvenile *A. polyacanthus* were more likely to eat gnathiids, which preempted micropredation, and less likely to die after gnathiid infection than were smaller juveniles.

KEY WORDS: Micropredator · Host–parasite interactions · Coral reef fish · *Acanthochromis polyacanthus* · *Gnathia falcipenis* · Gnathiid isopod · Mortality

INTRODUCTION

Parasitism can have serious implications for individual fish, regulate reef fish populations, and contribute to fish community structure (Lester 1984, Adlard & Lester 1994, Barber et al. 2000, Finley & Forrester 2003). However, we still know very little about the interactions between parasites and juvenile or larval fish. Because fish community structure is determined in part by the number and types of juveniles that survive the larval phase and successfully enter the community (Shulman 1985, Caley et al. 1996), understanding the repercussions of parasitism on the growth, condition, and survival of juveniles may be crucial for understanding variation between and within communities.

Mobile temporary parasites fall under a distinct trophic strategy termed micropredation (Kuris & Lafferty 2000, Lafferty & Kuris 2002). Like predators, micropredators attack multiple prey (hosts), but the impact of an individual micropredator on the victim is usually small, like that of a typical parasite (i.e. macro-

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parasite). However, typical parasites often only parasitise one definitive host. Most micropredators of vertebrate hosts are blood feeders and the feeding bouts are generally brief: mosquitos and ticks are classic examples. Unlike typical parasites, micropredators have a sophisticated behavioural attack strategy and frequently serve as vectors for pathogenic microbial diseases. Although micropredation is often brief and not very host-specific, it can still greatly impact host populations (Edman & Scott 1987). In the present study we focussed on interactions between a micropredator and a juvenile host and on the potential outcomes for both species.

Since micropredators use more than one individual host during their life cycle, they obtain no evolutionary benefit by minimising damage to hosts (Barber et al. 2000), particularly if they can rapidly dissociate should the host become impaired or die (Murray 1990, Lehmann 1993). The chance of a micropredator achieving feeding 'success' should theoretically increase as host mass increases and decrease as micropredator mass increases (Kuris & Lafferty 2000). This is because feeding success is dependent on the micropredator not being detected by the host and a greater relative size difference between micropredators and hosts makes the former harder to detect. However, micropredators also elicit behavioural responses from hosts, such as grooming or cleaning, that reduce their chances of successful feeding (Grutter 1995a, Hart 1990, 1997). In light of these theories, our first aim was to investigate whether micropredators feed on small juveniles of the damselfish *Acanthochromis polyacanthus* (spiny chromis) in the laboratory or field, and whether micropredator success (engorging without being eaten by the host) varied with host size.

Gnathiid isopods are the most common micropredators of fishes on the Great Barrier Reef (GBR) (Grutter 1994, Grutter & Poulin 1998) and are abundant on hard and soft substrates within the reef system (Jacoby & Greenwood 1988). The 3 larval stages of gnathiids are micropredatory and on the GBR they range in size from 0.5 to 8.7 mm (C. M. Jones unpubl. data). Larvae must feed on host blood 3 times, returning to the benthos to moult after each feeding bout, finally moulting into non-feeding adults (Kabata 1984). Moulting can take days to weeks under laboratory conditions. Gnathiids feed on adult teleosts for minutes to hours (Grutter 2003) and those that feed on elasmobranchs can attach for days to weeks (McKiernan et al. 2005). Hence, gnathiids can readily detach from teleosts, escaping detection in parasite surveys unless hosts are placed in plastic bags immediately after capture (Grutter 1995b). The ubiquitous distribution of gnathiids means most fishes are at risk of attack. Because gnathiids are harmful to adult fish at high densities (Paperna & Por 1977, Honma & Chiba 1991, Jones & Grutter 2005), we hypothesised that juvenile fish attacked by a single gnathiid would be similarly affected due to the low host to micropredator size ratio. Thus, our second aim was to investigate the lethal effects of gnathiid isopods on juvenile *Acanthochromis polyacanthus* in the laboratory. We tested the hypothesis that the impact of micropredation on the host decreases with increasing host size (Adlard & Lester 1994) by examining the impact of gnathiid feeding on the mortality of juvenile fish over a range of sizes.

Acanthochromis polyacanthus was chosen because it is one of the few coral reef fishes in the world, and the only one on the GBR, that can potentially interact with gnathiid isopods over its entire life cycle because it does not have a pelagic larval phase (Robertson 1973). *A. polyacanthus* feeds on small invertebrates (Kavanagh 2000), a diet which could include gnathiid isopods. Therefore, our third aim was to investigate whether *A. polyacanthus* ate gnathiids and the extent to which this varied with ontogeny.

MATERIALS AND METHODS

Study species. *Acanthochromis polyacanthus* were collected from the reefs surrounding Lizard Island, GBR, Australia (14° 40′ S, 145° 28′ E) between October and December 2005. Collections were carried out during daylight hours between 09:30 and 16:00 h at Casuarina Beach, Coconut Beach, Horseshoe Reef, The Lagoon, and Mermaid Beach. Juvenile *A. polyacanthus* (4.0 to 23.5 mm standard length, SL, n = 578, from 48 broods) were captured by SCUBA divers using hand-nets (mouth size 15 × 20 cm, 1 mm mesh). To minimize ectoparasite loss, anaesthetics were not used to collect fish. Groups of fish from the same brood were transferred from the net into quick-sealing plastic bags (25 × 30 cm) for live transport back to the laboratory.

Gnathia falcipenis were collected from the shallow reefs (2 to 6 m deep) surrounding Lizard Island using small illuminated bottle traps (see Jones & Grutter 2007). Each bottle was weighted with a brick and suspended 20 cm above the benthos. Traps were set at 17:00 h and collected at 21:00 h. Gnathiids were removed from the catch by pipette and transferred to individual 5 ml vials containing seawater. They were kept in vials for 1 to 11 d before use in our experiments. Fed (i.e. with an engorged gut) third stage *G. falcipenis* at Lizard Island are on average 2.7 (2.4–3.0) mm long, while fed second stages average 1.7 (1.5–2.1) mm in length. Although identifying first stage gnathiids is notoriously difficult (Smit & Davies 2004), we estimated that fed first stage *G. falcipenis* are 1.0 to

1.3 mm long based on 5 individuals that showed strong morphological similarities (unusually large eyes and apparently species-specific colour patterns) to older stages.

Only unfed third stage *Gnathia falcipenis* were used in the experiments for logistical and identification purposes. Using a species which was indeed a natural micropredator of damselfishes was very important. Although gnathiids are exceptionally rare on adult damselfish collected during the day (Grutter & Poulin 1998), recent blood-meal sequencing data suggests that damselfishes make up a reasonable component (14%) of the diet of *G. falcipenis* (Jones et al. 2007). *G. falcipenis* are abundant at night and a pilot study showed that they did not attach to host fishes in daylight; therefore, interaction experiments were carried out at night.

Gnathiid and ectoparasite intensity on wild juvenile *Acanthochromis polyacanthus*. Divers sub-sampled fish from 20 broods. Each sub-sampled brood was held separately in a plastic bag and euthanized by submersion in an ice-slurry. Fish (n = 150, 4.0 to 23.0 mm SL) were then preserved individually in 80% ethanol. Seawater from the collection bags was filtered through a 62 µm sieve to collect any gnathiids that detached during transportation or euthanasia. Fish and the contents of collection bags were examined with a stereomicroscope. The external body surface of the fish was inspected and the pelvic fins, pectoral fins, and gills were removed and examined. Micropredators and ectoparasites were recovered at magnifications of between 50 and 90×. Fish were weighed and measured before dissection.

Host–micropredator interactions in the laboratory. *Acanthochromis polyacanthus* (7.2 to 24.0 mm SL) were acclimated with brood members in 20 l aquaria with running filtered seawater for 24 to 48 h after capture. This allowed any existing gnathiids to detach from the fish, as a pilot study revealed that *Gnathia falcipenis* larvae remained attached on fish for several hours (R. Penfold unpubl. data). Fish were not fed during this period. Each fish was then transferred into a black plastic container (16 × 11 × 4 cm) with 350 ml of filtered seawater (62 µm) and acclimated for 60 min. Half of the fish were randomly allocated to the exposure treatment, the other half were unexposed controls. Trials were conducted over 15 evenings from 9 to 30 November 2005. A single gnathiid was pipetted into exposure treatment containers (n = 214). Seawater only was pipetted into unexposed treatment containers (n = 214). The room was dark at all times and a small hand-light was used to make observations. Containers were surveyed every 2 h for 6 h to determine if the gnathiid had fed (gut was engorged). If the gnathiid was missing we presumed it had been eaten by the fish, as predation was witnessed on 8 occasions. If the gnathiid was still present in the container after 6 h and had not attached to the host fish, it was removed by pipette. Host mortality was recorded for a further 12 h. All fish were then euthanized, measured, and weighed.

Statistics. For wild-caught fish, it was not possible to examine the effect of fish SL on gnathiid presence using individual fish because of non-independence with respect to brood. Instead, we investigated the effect of mean brood SL on whether gnathiids were found in association with the brood using logistic regression. This allowed inclusion of gnathiid presence data retrieved from collection water that could only be assigned to broods and not to individual hosts. Thus, associations consisted of gnathiids either still attached to a fish when the brood was separated into individuals and those found in the collection water after removing fish.

For laboratory trials, logistic regression was used to determine if gnathiid time in captivity, the date of the experiment, fish SL, and interactions among these parameters could predict: (1) gnathiid feeding success (engorgement), (2) survival of *Acanthochromis polyacanthus*, and (3) gnathiid survival. Due to the non-orthogonal nature of the data, parameters were added to models in order of likely significance (Crawley 2005) as follows: (1) fish SL, (2) gnathiid captivity time, and (3) date of experiment. Models were fitted and simplified according to Crawley (2005) whereby the maximal model was fitted and non-significant terms ($p > 0.20$) were sequentially removed, starting with high-order interactions, then by removing terms with the lowest significance, until only significant terms remained. Simplified models were accepted if Akaike's information criterion (AIC) was reduced by simplification.

The regression examining gnathiid survival revealed a significant second-order interaction between fish SL and gnathiid captivity time ($p = 0.02$). We explored this interaction visually and statistically by fitting the probability of gnathiid survival with respect to fish SL for each time in captivity. Gnathiids were held captive for 1, 3, and 5 to 11 d inclusive. This interaction occurred because SL had variable effects on the probability of gnathiid survival over different durations of gnathiid captivity. The overall effect of SL on gnathiid survival probability was negative (i.e. all captivity times combined). However, in 4 instances (1, 7, 8, and 11 d) SL had a positive effect on gnathiid survival probability, but SL was not a significant parameter ($\alpha = 0.05$) in any of these analyses, which were composed of fewer observations (1 d: $p = 0.56$, $n = 15$; 7 d: $p = 0.48$, $n = 19$; 8 d: $p = 0.49$, $n = 12$; 11 d: $p = 0.34$, $n = 8$) than regressions that agreed with the overall effect (3 d: $p = 0.35$, $n = 8$; 5 d: $p = 0.17$, 6 d: $n = 32$; $p = 0.2$, $n = 45$;

9 d: p = 0.6, n = 33; 10 d: p = 0.04, n = 42). Importantly, fish SL was not evenly distributed over the various captivity times, thus, comparisons among times in captivity involved non-overlapping SL data. Further, positive associations were spread over the entire time series, rather than at the beginning or the end, as would be expected if the interaction had a meaningful biological explanation related to gnathiid captivity time. For these reasons we considered the interaction between SL and gnathiid captivity to be a product of non-overlapping data sets, so the interaction was removed and model simplification was resumed as aforementioned.

The lack of overlap in fish SL data among periods of gnathiid captivity time suggested that there may have been a relationship between the length of time gnathiids spent in captivity and SL. Indeed there was a significant negative relationship (Spearman's rho = −0.38, $p < 0.001$) between captivity time and SL, indicating that larger *Acanthochromis polyacanthus* were exposed to gnathiids held in captivity for less time than smaller ones.

A 2-tailed Fisher's exact test was used to test if small *Acanthochromis polyacanthus* (<10 mm SL) that had been exposed to a gnathiid experienced differential mortality compared to unexposed fish of the same size. We used the statistical programmes JMP In (version 4.0.4 Academic) for Fisher's exact tests, and R (www.r-project.org) to conduct logistic regression and correlation analyses.

RESULTS

Gnathiid and ectoparasite intensity on wild juvenile *Acanthochromis polyacanthus*

Five gnathiids were found in the collection bag water that 3 broods of fish were transported in; 2 were fed and 3 were unfed (Table 1). Eight ectoparasites (2 turbellarians, 3 copepods, 3 monogeneans) and another 5 gnathiids (3.0% prevalence) were found on individuals of the 150 fish that were dissected (Table 1, Fig. 1). No fish had more than 1 parasite. Four of the

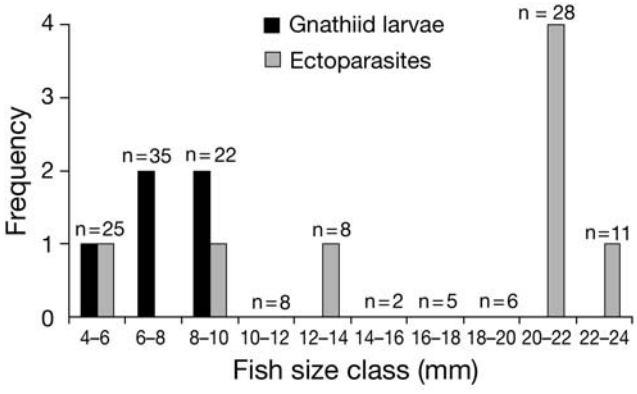

Fig. 1. *Acanthochromis polyacanthus*. Variation in gnathiid and ectoparasite intensity among size classes of wild-caught damselfish. Sample sizes are indicated above bars

Table 1. *Acanthochromis polyacanthus*. Ectoparasites and micropredators recovered from 150 dissected juveniles (autopsies) and from bags used to collect broods (collection bags)

Parasite taxa	Gnathiid length	Feeding state	Host locality	Host SL	Mean brood SL	Brood ID
Autopsies						
Copepoda	–	–	Horseshoe Reef	5.4	5.31	H4
"	–	–	Horseshoe Reef	13.3	9.47	H2
"	–	–	Casuarina Beach	20.7	20.60	O13
Monogenea	–	–	Mermaid Beach	8.3	20.60	M3
"	–	–	Casuarina Beach	21.0	21.11	O9
"	–	–	Casuarina Beach	21.2	21.11	O9
Turbellaria	–	–	Casuarina Beach	22.3	21.63	O15
"	–	–	Casuarina Beach	20.4	21.63	O15
Gnathia sp.	1.42	Fed	Coconut Beach	4.2	4.28	C2
"	1.02	Unfed	Lagoon	6.5	7.60	LA2
"	0.92	Fed	Lagoon	8.1	7.60	LA2
"	0.82	Fed	Lagoon	7.5	7.60	LA2
G. falcipenis	1.02	Unfed	Lagoon	8.0	7.60	LA2
Collection bags						
Gnathia sp.	1.20	Fed	Coconut Beach	–	4.28	C2
"	1.10	Unfed	Coconut Beach	–	4.28	C2
"	0.82	Unfed	Casuarina Beach	–	20.60	O13
"	1.04	Fed	Casuarina Beach	–	20.60	O13
G. falcipenis	2.10	Unfed	Mermaid Beach	–	8.57	M1

fish directly infected with gnathiids were collected from a single brood in The Lagoon, and another infected fish was collected from Coconut Beach. The lengths of each infected fish (SL) and its respective gnathiid are provided in Table 1. The mean length (± SE) of these gnathiids was 1.04 (± 0.09) mm, and the mean SL of infected *Acanthochromis polyacanthus* was 6.86 (± 0.72) mm. The largest gnathiid (1.42 mm) was probably a second stage larva. The 4 smaller gnathiids fall within the size range expected for first stage *Gnathia falcipenis,* to which one gnathiid bore strong morphological resemblance. However, the size ranges for other species, for example *Gnathiia* sp. Type 1 (Grutter et al. 2000a), are considerably smaller: fed first, second, and third stages measure 0.72 to 0.94, 1.0 to 1.34, and 1.56 to 2.06 mm; unfed stages measure 0.51 to 0.69, 0.72 to 1.02, 1.11 to 1.17 mm, respectively, excluding uropods (Grutter 2003). Thus, it is possible that some of these gnathiids were second stage larvae of smaller species.

Whether a gnathiid was found in association with a brood was not related to the mean SL of fish in the brood (df = 1, χ^2 = 0.20, p = 0.65). No gnathiids were found on individual fish >10 mm SL. Of the 150 fish sampled, 82 were <10 mm SL; thus, infection prevalence of fish <10 mm SL was 6.09%.

Host–micropredator interactions in the laboratory

Only 63 of 214 gnathiids that were introduced to *Acanthochromis polyacanthus* fed successfully (see Table 2). Of these 63 engorged gnathiids, 32 attached within the first 2 h and all except 1 remained attached for a further 2 h. At the final survey (i.e. after 6 h), 9 of the original 32 gnathiids were still attached. Ten gnathiids that did not attach in the first 2 h were found attached 4 h after the experiment started and then again at the final survey. Twenty gnathiids that did not attach in the first 2 surveys were found attached to fish at the final observation (6 h). Over the entire experiment, only one gnathiid was observed unattached and engorged on the bottom of the container, i.e. it had fed and detached within 2 h.

Neither fish SL nor experiment date was a significant predictor of whether gnathiids engorged in this experiment (Table 3). However, the effect of gnathiid captivity time was highly significant (p = 0.003) and resulted in a decline in feeding success (Fig. 2).

All fish that were not exposed to gnathiids survived. Six of the 214 (2.8%) fish exposed to a gnathiid died, and 4 of these fish had been fed on by a gnathiid. The mortality rate of infected fish was 4 of 63 (6.3%) compared to 0% for unexposed fish. Fish SL was a signifi-

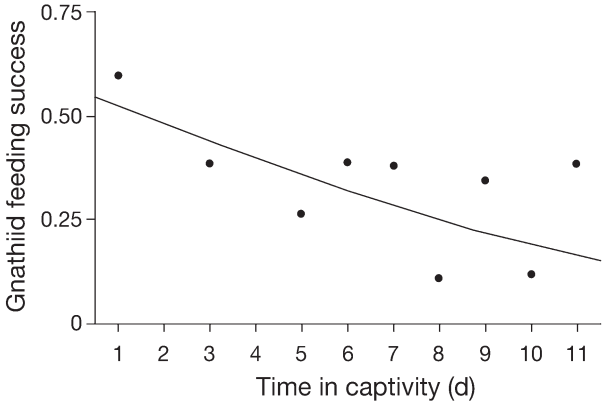

Fig. 2. *Gnathia falcipenis.* Effect of captivity time on the proportion of gnathids that fed. Means (●); logistic fit of feeding success with respect to time in captivity (—)

Table 2. *Acanthochromis polyacanthus* and *Gnathia falcipenis*. Occurrence probabilities for interactions and outcomes based on 214 replicates

Interaction	n	Probability	Outcome	n	Probability
Gnathiid engorges	63	0.29	Fish survives, gnathiid is fed	59	0.27
			Fish dies, gnathiid is fed	4	0.01
Gnathiid does not engorge	151	0.71	Fish dies, gnathiid survives	1	0.007
			Fish and gnathiid survive	65	0.31
			Fish survives, gnathiid is eaten	84	0.39
			Fish dies, gnathiid is eaten	1	0.007
Total	**214**	**1**		**214**	**1**

Table 3. *Acanthochromis polyacanthus* and *Gnathia falcipenis.* Logistic regression of gnathiid engorgement, fish survival, and gnathiid survival with respect to standard length (SL), time gnathiids spent in captivity (captivity), and experiment date (not significant). Significant probabilities (p ≤ 0.05) shown in **bold**; Akaike information criterion (AIC) is listed for each model. *Z*: critical values for coefficients

Model	Parameter	Estimate	SE	*Z*	p
Gnathiid engorgement = captivity AIC = 254.27	Intercept	0.290	0.410	0.71	0.480
	Captivity	−0.171	0.058	−2.97	**0.003**
Fish survival = SL AIC = 39.59	Intercept	−6.224	3.974	−1.57	0.117
	SL	0.959	0.464	2.07	**0.039**
Gnathiid survival = SL + captivity AIC = 270.93	Intercept	−3.797	0.891	−4.26	<0.001
	SL	0.176	0.040	4.44	**<0.001**
	Captivity	0.098	0.060	1.64	0.100

cant predictor of survival for fish exposed to a gnathiid ($p = 0.039$; Table 3, Fig. 3a). The probability of fish survival levelled off at nearly 100% after ~12 mm SL. Using only fish <10 mm SL, the probability of mortality was significantly higher for infected fish (14.3%, n = 42) than for unexposed fish (0%, n = 38) of the same size (df = 1, $\chi^2 = 8.172$, $p = 0.027$).

Of the 214 gnathiids that were exposed to a fish, 151 did not engorge, and of these, the fish consumed 85 (56%). The remaining 66 gnathiids were not eaten and did not parasitise the fish (i.e. both gnathiids and fish were alive at the end of the trials). The probability of a gnathiid surviving the experiment declined significantly with increasing fish SL ($p < 0.001$, Fig. 3b).

DISCUSSION

Gnathiid isopods fed on *Acanthochromis polyacanthus* juveniles in nature and under laboratory conditions. Gnathiids were found on one of the smallest wild fish we examined (4.2 mm SL). The gnathiids recovered directly from fish appeared to be first and second stage larvae; however, one of the gnathiids from the collection bags was an unfed third stage *Gnathia falcipenis,* the same stage and species used in the laboratory experiment. The presence of fed and unfed gnathiids in collection bags suggests that gnathiids could detach during collection and that prevalence based on autopsies (3%) was underestimated. It is not possible to quantitatively adjust this estimate because broods were sub-sampled and the number of gnathiids that detached (if any) before fish were placed in bags is unknown. Fish collections were also made during the daylight hours when, compared to nocturnal or crepuscular periods, gnathiids are often less abundant (Sikkel et al. 2006, Jones & Grutter 2007, but see Grutter et al. 2000b). This evidence suggests gnathiid infection prevalence on wild *A. polyacanthus* may be higher than estimated here, particularly at other times of day.

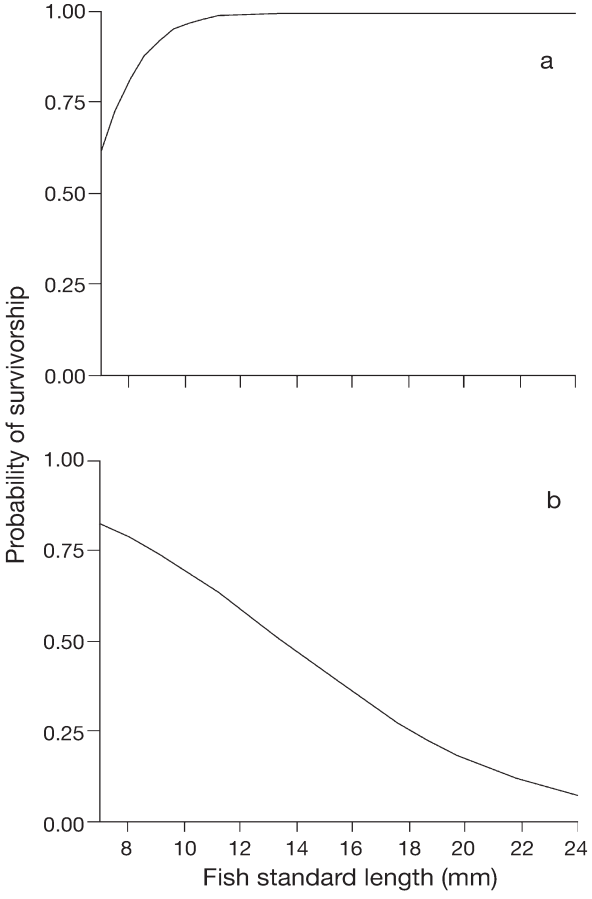

Fig. 3. *Acanthochromis polyacanthus* and *Gnathia falcipenis*. Probability of survival (logistic fit) for (a) fish and (b) gnathiids with respect to fish SL

Laboratory interaction trials produced several novel findings: (1) small juvenile fish were capable of eating gnathiids but larger fish ate more; (2) gnathiids had a 'shelf life'; and (3) gnathiids affected smaller fish more severely. In 39.9% of trials the fish consumed the gnathiid, compared to 29% of trials where the gnathiid fed on the fish. Interestingly, no engorged gnathiids were observed being eaten, or went missing over the entire experiment. Considering that 31 of 32 attachments observed in the first period lasted at least 2 h, it is very unlikely that gnathiids engorged, detached, and were eaten before they could be detected by surveys conducted every 2 h. Thus, micropredation and predation were mutually exclusive in our laboratory experiment and predation occurred more frequently than micropredation. However, rates of micropredation and predation would almost certainly be different in the natural environment where more complex shelter would be available for both fish and micropredators. Despite this, our laboratory experiments explore the effect of relative host size on the qualitative outcome of interactions.

Larger *Acanthochromis polyacanthus* ate more gnathiids than smaller *A. polyacanthus*, indicating that the propensity to eat micropredators increased with ontogeny. Gape width was not limiting because *A. polyacanthus* as small as 8 mm SL, the fourth smallest fish tested, were able to eat third stage *Gnathia falcipenis*. *A. polyacanthus* do not start benthic feeding until they are larger than 11 mm SL (Kavanagh 1998). This trophic shift from solely planktonic to benthic and planktonic feeding may explain why larger juveniles ate more gnathiids. Larger, older juveniles have better visual acuity (Pankhurst et al. 2002) and it is reasonable to assume that they have more experience eating benthic invertebrates and may have previously encountered emerging gnathiids.

By eating gnathiids, *Acanthochromis polyacanthus* was protected from infection. A behaviour is deemed to have a defensive function against parasites if the parasite has a detrimental effect on host fitness and if the behaviour controls the parasite (Hart 1997). The predator–prey interaction between *A. polyacanthus* and *Gnathia falcipenis* fits these criteria, regardless of whether it is an adaptation to micropredator attack or simply foraging behaviour. This report of parasite consumption by potential prey is one of the first in a marine environment. Recent food web analyses indicate that consumption of infective stages of parasites and micropredators can play a substantial role in ecosystem trophic dynamics (Lafferty et al. 2006a,b).

Animals use a range of behavioural defences against micropredators including grouping (Hart 1997), which may also be important for broods of juvenile *Acanthochromis polyacanthus.* The intensity of mobile parasites and micropredators decreases with group size in a range of species including birds, fish and mammals (Schmidtmann & Valla 1982, Poulin 1991, Côté & Poulin 1995, Barber et al. 2000) and Mooring & Hart (1992) suggest that the selfish herd theory may apply to parasitism and micropredation as well as predation. Group vigilance was not examined in our experiments, nor would it be easily tested considering how difficult it is to observe gnathiids interacting with a single host.

The negative relationship between gnathiid viability and time in captivity suggests that gnathiids have a limited time to locate and feed on hosts. This may create a trade-off with regard to host choice, if the time that gnathiids spend searching for an ideal host decreases their probability of feeding. Recent studies show that gnathiids are generalists with distinct host preferences (Jones et al. 2007), and feeding on preferred hosts can increase fitness (Nagel & Grutter 2007). Based on these data we would expect host specificity to lessen as time after moulting increases. Because micropredator viability and host size were confounded, we cannot yet interpret the lack of relationship between host size and feeding success.

Exposure to a single gnathiid caused host mortality in 6 of 214 trials. In 2 of these instances hosts died without being infected. Juvenile damselfish often move erratically as a gnathiid attempts to attach, and in some instances they can repel the gnathiid (C. M. Jones pers. obs.). Mortality without engorgement could have been caused by stress from continual avoidance of the gnathiid in the confined experimental system. It is also possible that unsuccessful attempts to feed on *Acanthochromis polyacanthus* may have injured the fish — gnathiids can leave bleeding wounds at abandoned feeding sites on the damselfish *Dascyllus aruanus* (A. S. Grutter pers. obs.) — although this was not observed in our brief nocturnal surveys.

In the laboratory, gnathiids only caused mortality in the smallest juvenile *Acanthochromis polyacanthus*. Adlard & Lester (1994) also found that cymothoid isopods *Anilocra pomacentri* caused greater mortality in small *Chromis nitida* damselfish than larger ones. Third stage gnathiids (the largest stage) were used in the laboratory for ease of handling and identification, but this probably overestimated the pathogenicity of a typical wild infection, considering wild *A. polyacanthus* were parasitised by first and second stage gnathiids (although one unfed third stage *Gnathia falcipenis* was found in association with broods). Third stage *G. falcipenis* were used because we considered accuracy of the species used more important than using a more representative life-history stage of unknown identity. While this scenario may have overestimated pathogenicity, conducting experiments with gnathiid species that are not natural micropredators of damselfishes could have produced entirely artificial results.

Larger gnathiid stages may appear scarce on wild juvenile *Acanthochromis polyacanthus* because: (1) larger gnathiids are less abundant in the environment; (2) they refrain from feeding on juvenile fish; (3) they are preyed upon directly by *A. polyacanthus*; or (4) they may be preyed upon indirectly. In long lasting or highly deleterious infections, gnathiid survival may be compromised if the juvenile hosts and the gnathiids they are infected with are eaten together by larger fish predators. Since juvenile coral reef fish experience high mortality due to fish predators (Connell 1998, Holbrook & Schmitt 2003, Almany & Webster 2006) selection may favour gnathiids with short attachment times and the ability to detach quickly. Indeed, the presence of unfed and fed gnathiids in collection bags suggests they can quickly detach before or after feeding. Furthermore, the fact that third stage *Gnathia falcipenis* made lengthy attachments to *A. polyacanthus* in the laboratory and that fed third stages were not collected from wild fish suggest that larger gnathiids may not infect small wild fish or, alternatively, if they do, those fish may have been preyed upon and thus not sampled. However, because we only recovered a total of 10 gnathiids from wild fish, conclusions about the nature of typical gnathiid infections should be made with caution.

This study has shown that micropredatory gnathiid isopods feed on juvenile *Acanthochromis polyacanthus,* which in turn, are capable of eating gnathiids, thereby preventing micropredation. However, the applicability of some aspects of this study to the field situation are unclear, and may remain so, due to difficulties observing these extremely small-scale interactions *in situ*. Future laboratory studies could investigate the effect of group vigilance, infections by smaller gnathiids, or repeated infections, all of which are likely

features of natural infections. Although gnathiid micropredators only caused direct mortality in some small juvenile fish, if micropredation events reduce fish growth or performance this may exacerbate the existing high levels of mortality that juvenile fish experience, over and above the direct effect of mortality through micropredation.

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