

Reef-based micropredators reduce the growth of post-settlement damselfish in captivity

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Abstract Despite the ubiquity of micropredators and parasites on coral reefs, their effects on the survival and growth of juvenile fishes are virtually unstudied. Caging and laboratory experiments were used to investigate whether reef based micropredators fed on recently metamorphosed damselfish, the time of day that micropredation occurred, and whether micropredation affected fish growth and survival. Caged juveniles of the damselfish, *Pomacentrus moluccensis*, were held on the reef over four consecutive time periods. Micropredators (gnathiid and cirrolanid isopods) were found associated with caged fish at night only, and cirrolanids were observed attacking and killing some caged fish. In order to test the effect of micropredation on growth and survival without the influence of predatory fishes, groups of five *P. moluccensis* were caged for 2 weeks in one of three treatments: micropredators excluded, mesh control, or micropredators present. There were no significant differences in survival among the treatments, but fish were larger in cages with fewer survivors suggesting that competition for food was intense. Fish exposed to micropredators were larger than fish in the other two treatments, however, micropredator exclusion also excluded plankton; thus, differences in food availability among treatments during crepuscular periods likely confounded the treatment effect on fish growth. A laboratory growth experiment was performed to better control food availability and minimise handling stress, using a validated host-micropredator model. Individual juvenile damselfish,

Dischistodus perspicillatus, were exposed to 0, 1 or 2 micropredators (*Gnathia falcipenis*) each evening and fed equally for 8 days. Mortalities only occurred in fish exposed to micropredators on the first evening of the experiment, and fish exposed to two micropredators each evening were significantly smaller than unexposed fish. These results suggest that repeated gnathiid infections can reduce fish growth in the first week after settlement. Consequently, micropredation may affect the ecology of damselfish after settling on coral reefs.

Keywords Cirrolanidae · Larval fish · Recruitment · Settlement · Growth · Survival

Introduction

Most coral reef fishes have pelagic larvae (Leis 1991) which experience extremely high mortality during and after settlement (Shulman and Ogden 1987; Sale and Ferrell 1988; Letourneur et al. 1998; Planes and Lecaillon 2001; Doherty et al. 2004). In some cases, predation can cause near absolute mortality within 2 days of settlement (Steele and Forrester 2002; Webster 2002) making this a critical transition period. Small-bodied predatory fishes are the proximate source of this mortality (Holbrook and Schmitt 1997, 2002), but ultimately, survival depends on the ability to grow quickly, as demonstrated by intra-cohort otolith comparisons between settlers and survivors at a later date (Searcy and Sponaugle 2001; Bergenius et al. 2002; Vigliola and Meekan 2002; Hoey and McCormick 2004; Hawn et al. 2005; Meekan et al. 2006; Gagliano and McCormick 2007). Thus, determining the factors that affect fish growth and the magnitude of these effects is necessary to understand fish survival.

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While much attention has been paid to the effects of vertebrate predators on growth and survival, few studies have investigated or even considered the effects that invertebrate predators, parasites and micropredators may have on recruiting fish. With regard to parasitic and carnivorous isopods, this is potentially a significant oversight, considering their relatively large size (Fig. 1), abundance and ubiquity in the benthos (Keable 1995; Grutter et al. 2000a; Jones and Grutter 2007) and on adult fishes (Grutter and Poulin 1998; Sikkil et al. 2006) of coral reefs. Whether or not isopods interact with coral reef fish settling from the plankton at the end of the larval phase and the results of any interactions are largely unknown, due to the nocturnal habits of these isopods (Stepien and Brusca 1985; Grutter and Hendrikz 1999; Sikkil et al. 2006; Jones and Grutter 2007) and often brief duration of associations with adult fishes (Grutter 1995, 2003).

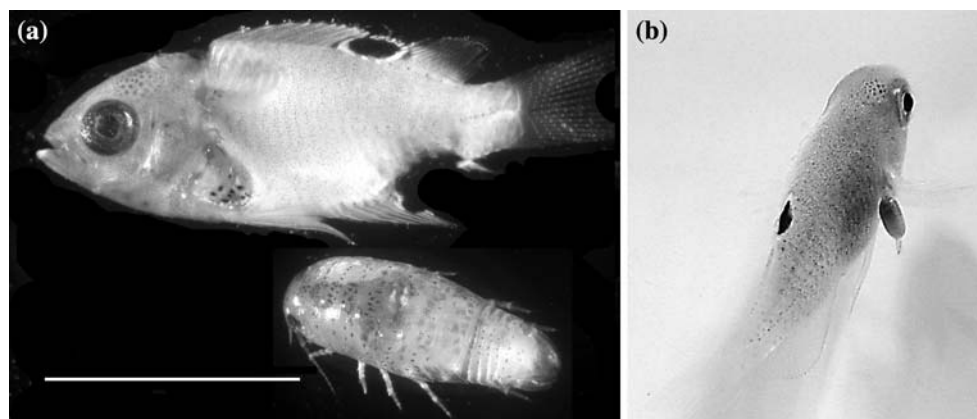
Previous work on permanently attached (cymothoid) isopods has shown that they can significantly reduce the growth and survival of recruits and fecundity of adult pomacentrids (Adlard and Lester 1994). Similar results have been found for permanently attached copepods on gobies (Finley and Forrester 2003). Thus, it appears that large ectoparasitic crustaceans that associate with small coral reef fishes for lengthy periods have a pervasive influence on host mortality. However, permanently attached parasites such as these are often relatively host-specific and their effects are confined to one or few species on coral reefs. Gnathiid isopods on the other hand, appear to have much lower host specificity (Smit and Davies 2004; Jones et al. 2007), and the family has been recorded from 70% of 56 species of adult fishes examined at Heron and Lizard Islands (Grutter and Poulin 1998).

The first surveys of recently settled coral reef fishes found they were parasitised by monogeneans, cestodes and trematodes, but lacked other common parasites, such as nematodes and ectoparasitic crustaceans (Rigby and Dufour 1996; Cribb et al. 2000). However, Cribb et al.

(2000) suggested that most ectoparasites would have been under-reported because fish were dead long before the time of dissection and ectoparasites may have dissociated from the host. Indeed, a recent study has shown that >3% of 150 brooded *Acanthochromis polyacanthus* were infected with gnathiid isopods when they were collected without anaesthetics and placed in sealed plastic bags (Penfold et al. 2008). In the laboratory, this study also showed that: gnathiids occasionally caused direct mortality, damselfish often ate gnathiids, and that smaller fish were less able to eat gnathiids and more likely to die as a direct result of parasitism. Thus, dynamic interactions involving juvenile damselfish and gnathiids do occur, but often go unnoticed.

These discoveries prompted consideration of which other groups of isopods may interact with recruiting coral reef fishes, when this might occur over a 24 h time scale, and whether there are any long-term consequences of these interactions. It was hypothesised that most micropredation on juvenile damselfish would occur at night, because many isopods are nocturnally active (Stepien and Brusca 1985; Bruce 1986; Jones and Grutter 2007) and at this time there would be less predation pressure on micropredators from the host, as most damselfishes are diurnal planktivores (Hobson 1991). Diel changes in infection prevalence were investigated by caging recently metamorphosed damselfishes for 3 h at a time, every 4 h, over a period of 24 h (experiment 1). Based on this experiment, a long-term caging experiment was performed in an attempt to observe the effects of small invertebrate micropredators, in the absence of fish predators, on damselfish for 2 weeks after settlement (experiment 2). Despite these attempts, the affects of micropredators on recruit growth in experiment 2 were confounded by food availability. In order to address this problem, a laboratory experiment was conducted where micropredator exposure and food availability was precisely controlled (experiment 3), using a gnathiid species that had recently been shown to prey on the target damselfish host (Jones et al. 2007).

Fig. 1 (a) *Pomacentrus amboinensis* attacked by the cirrolanid isopod *Cirolana improceros* (scale bar = 5 mm) and (b) an engorged gnathiid attached behind the right pectoral fin of a recently settled *P. amboinensis*



Materials and methods

Study area

The study was conducted on natural patch reefs off Casuarina Beach, Lizard Island Research Station, (14°40' S, 145°28' E) Great Barrier Reef (GBR). This area was chosen for a number of logistic and safety reasons. It is sheltered from prevailing southeast winds, accessible at most tides, relatively shallow (0–6 m) and very close to the research station, making it an ideal location for boating at night. The reefs in this area are interspersed with patches of sand and rubble that are visible from a boat, upon which, cages and weighted traps could be placed without damaging living coral.

Study species

Pomacentrus moluccensis were used in caging experiments 1 and 2 because they are abundant in light traps at Lizard Island (Milicich and Doherty 1994) and they settle gregariously in conspecific groups (Öhman et al. 1998). It was decided that caging groups of fish instead of individuals would increase the chances of recovering parasites for a given caging effort.

In experiment 3, *Gnathia falcipenis* was used as a focal parasite for a number of reasons. It is relatively abundant at the study site (Jones and Grutter 2005), and it is one of the few gnathiid species at Lizard Island that can be reliably identified as a second or third stage larva under low-power magnification. Also, 28 host identifications have been made for *G. falcipenis* from the study site using molecular techniques (Jones et al. 2007). Based on these data, *Dischistodus perspicillatus* was chosen as a model host because it has been shown to be a natural host of *G. falcipenis* and it is readily available and identifiable in light traps.

Diel caging experiment (1)

Recently metamorphosed *P. moluccensis* were collected from light traps (for design see Meekan et al. 2001) moored in 8–12 m of water west of Casuarina Beach, in October 2005. Fish were kept in 120 l flow-through aquaria and fed cultured *Artemia* nauplii from the time of collection (07:00 h) until used in experiments (11–23 h later). Fish were placed in plastic 'sub-cages' inside larger weighted wire cages (for design see Grutter 1996) as in Fig. 2, but with only one sub-cage per wire cage. This was done to protect plastic sub-cages from the reef environment and caged recruits from the possible influence of larger fishes. Sub-cages were constructed out of 2 l plastic containers with windows (12 × 5 cm) cut into each side and



Fig. 2 Wire cage holding three feeding sub-cages, each with 1 mm mesh

the lid (12 × 12 cm). Side windows were situated 2.5 cm from the bottom of each sub-cage so that it could hold water when lifted out of the sea. Fly-screen mesh (1 mm) was glued to each window with a hot-melt glue gun. Sub-cages were attached to wire cages with rubber bands and metal clips to prevent them from floating.

Groups of three *P. moluccensis* were caged for 3 h periods (18:30–21:30; 00:30–03:30; 06:30–09:30; 12:30–15:30) consecutively over 24 h. This was done on October 29–30 (3 cages), November 6–7 (8 cages), 8–9 (8 cages) and 10–11 (8 cages), 2005. No fish were used more than once, thus, 324 fish were caged over 4 × 24-h periods. Wire cages were tethered to a surface float made with an empty 2 l bottle. Cyalume light sticks were placed inside each float so that it was visible at night. At the end of the caging period, wire cages were retrieved by the surface float, and sub-cages were carefully placed into individual 10 l buckets with lids. Buckets containing sub-cages were transported back to the laboratory and left in a darkened room for 4 h. The purpose of this was to allow isopods sufficient time to detach in an environment where they were less likely to be eaten (i.e. in darkness). Fish were then returned and the water in each bucket was filtered through 62 µm mesh to collect isopods.

Two-week caging experiment (2)

Groups of five *P. moluccensis* were caged for 2 weeks at Casuarina Beach from 3 to 17 December 2005. Three treatments were used in an attempt to investigate the effects of parasites/micropredators on newly recruited damselfish: micropredators excluded; fine mesh control; micropredators present. Each treatment was replicated 15 times. In this experiment, three sub-cages (one of each treatment) were housed within each wire cage (Fig. 2). In

order to exclude micropredators, sub-cages were constructed as above, but with 100 µm mesh instead of 1 mm mesh. The ‘mesh control’ treatment was designed to control for the effects of reduced water flow from the smaller mesh, but still allow micropredators to enter; these sub-cages had 100 µm mesh on the four vertical walls of the cage, but the lids had 1 mm mesh. In the ‘micropredators present’ treatment, all sides of the sub-cages were covered with 1 mm mesh, exactly the same as the sub-cages in experiment 1.

One of the problems with using 100 µm mesh to exclude micropredators from sub-cages was that it also excluded planktonic food items. In an attempt to avert this problem, fish were placed in treatment cages at night only. This procedure was used because the results of experiment 1 suggested that most isopods were interacting with *P. moluccensis* at night and also because *P. moluccensis*, like most damselfishes (Randall et al. 1997), are diurnal planktivores. Thus, all fish were kept in identical feeding sub-cages during the day and in their treatment sub-cages at night. Cage changeover took up to 2 h to complete and occurred between 06:20 and 08:20 each morning and between 16:27 and 18:48 each evening. During the experiment, the sun rose between 05:40 and 05:44 and set between 18:36 and 18:44, Australian Eastern Standard Time. After each changeover, the sub-cages that were not in use were washed with fresh water to prevent fouling. At approximately 11:00 and 15:00 each day, fish were fed by snorkellers. Cultured *Artemia* nauplii and macerated fish flake were loaded into two 100 ml syringes (without needles), which were used to inject 5 ml of this mixture into each sub-cage through holes in the mesh screen. Fish were measured at the start of the experiment and measured and weighed at its conclusion.

Multiple infection experiment (3)

Sixty-four recently metamorphosed *D. perspicillatus* from light traps were fed equally and exposed to three densities of gnathiids for seven nights (8 days) to examine the effects of repeated infections on growth and survival on 4–13 November 2006. The three treatments were exposure to 0, 1 and 2 unfed gnathiids each evening. Two fish that died on the first night of the experiment were replaced and underwent experimentation for one extra night. Fish were acclimated in a 120 l aquarium for 2 days before use in the experiment where they were fed cultured *Artemia* twice daily. In the morning of the first day of the experiment, fish were measured and placed in separate 25 l plastic aquaria (43.2 × 27.8 × 31.9 cm) that had a 2 cm layer of sand and a pipe shelter. Each fish was kept in a separate tank. Sand was collected from above the high tide mark and soaked then rinsed with fresh water to ensure that it was clean and

free of invertebrates, pathogens, or food for the fish. Filtered seawater flowed continuously into tanks and the outlet valve was filtered through 100 µm mesh to prevent gnathiids from escaping. Half-way through the experiment (day 4) the water was turned off and outlet filters were washed with fresh water to remove detritus and algae. The tank outlet was blocked so that the filter could be cleaned without losing any water (and gnathiids). Each fish was fed at 09:00 and 15:00 each day and was given one macerated high protein food pellet weighing ~10 mg (Orca, Taiwan) and 10 ml of concentrated *Artemia* nauplii.

G. falcipenis were collected from reefs off Casuarina Beach using small illuminated traps (Jones and Grutter 2007) and stored in 5 ml vials for 1–3 days before use in experiments. In the first four nights of the experiment, only third-stage *G. falcipenis* were used and in the latter three nights, second stages were used because too few third-stages were available from the bottle traps. Gnathiids were added to tanks between 20:00 and 21:00 each night, because *G. falcipenis* are probably more active nocturnally (although they have also been found in association with diurnally collected damselfishes (Penfold et al. 2008)).

Statistics

Experiments 2 and 3 were carried out using a randomised block design. In the caging experiment, one sub-cage of each treatment was randomly assigned to a position within the wire cage. In the tank experiment, wet benches holding aquaria were wide enough to accommodate three tanks and each treatment was randomly assigned to a position within the block of tanks. All data were checked for normality and equal variances with Shapiro–Wilk tests and Bartlett’s tests, respectively, before using parametric statistics. In the diel caging experiment (1), differences in the number of isopods recovered per cage among caging periods and between day and night were analysed with Kruskal–Wallis and Wilcoxon tests, respectively. Differences in the number of fish surviving among treatments in the 2-week caging experiment (2) were examined with a Kruskal–Wallis test. In the two-week caging experiment, means of fish length and fish weight per cage were used as replicates to avoid non-independence issues. Mean weights of fish from cages with three survivors ($n = 3$) were much larger than cages with four or five survivors (see ‘Results’). Therefore, to examine the treatment effect without the influence of survivorship on end weight and growth, the cages with three survivors were excluded from further analysis. Differences in length and weight among treatments in experiments 2 and 3 were analysed with one-way Analysis of Variance (ANOVA) and means were compared using Tukey’s honestly significant difference (HSD) tests. All statistical analyses were performed using JMPIN v4 (SAS Institute).

Results

Diel caging experiment (1)

Twelve isopods were collected in total, four of these were engorged gnathiids and eight were cirolanids. All of the cirolanid isopods that were collected between 00:30 and 03:30 were identified as *Cirolana improceros*, except one, which was a species of *Eurydice* collected at 21:30. One gnathiid that had fed (1.06 mm long) was collected at 00:30–3:30 and the remaining three were collected at 18:30–21:20. These were 1.04, 1.02 and 1.20 mm long; the latter was identified as a first stage *G. falcipenis*, which had not fed. There were no significant differences in counts of isopods among caging periods. No isopods were collected during the day and the difference in counts between day and night was significant ($\chi^2 = 7.4$, $df = 1$, $P = 0.007$).

On two occasions multiple cirolanids were found in cages; one cage had five and the other had two. Fish mortality was observed in these cages. In the cage with five cirolanids, one fish had been completely consumed and only a small skeleton remained. The other mortality was witnessed as the contents of one of the sub-cages were transferred into a bucket. The isopod attached to the head of the fish, ate one of the eyes, then the entire digestive tract and some of the dorsal musculature. This occurred within seconds of attachment and resulted in immediate mortality.

Two-week caging experiment (2)

There were no significant differences in mortality among the three treatments. Survivorship in the micropredators present, mesh control and micropredator exclusion treatments was 96%, 94.7% and 90.7%, respectively. However, mean fish weights in cages that had three fish survivors (58.25 mg) were greater than mean fish weights in cages with four (51.16 mg) and five (51.10 mg) survivors ($F_{2,42} = 4.86$, $P = 0.013$; Fig. 3). Thus, subsequent investigations of treatment effects did not include cages with three survivors. Fish in ‘micropredators present’ cages were significantly heavier than fish in fine mesh cages (micropredators excluded) ($F_{2,39} = 4.26$, $P = 0.021$; Fig. 4). The mean weights of fish in the mesh control treatment were not significantly different from either of the other treatments. There were no significant differences in fish length among all treatments.

Multiple infection experiment (3)

Two *D. perspicillatus* exposed to two gnathiids died on the first night of the experiment. A gnathiid was observed attached to one of these fish before it died. One other attachment was witnessed over the duration of the

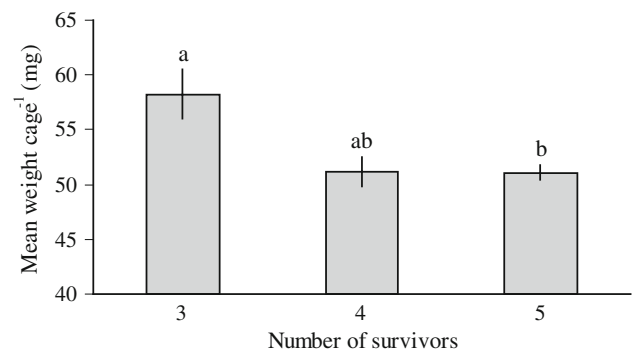


Fig. 3 Mean weight per cage (\pm SE) of *Pomacentrus moluccensis* in cages with three ($n = 3$), four ($n = 8$) and five ($n = 34$) fish survivors (out of an initial five fish) after 2 weeks on the reef. Means that are significantly different are labelled with different letters (a and b)

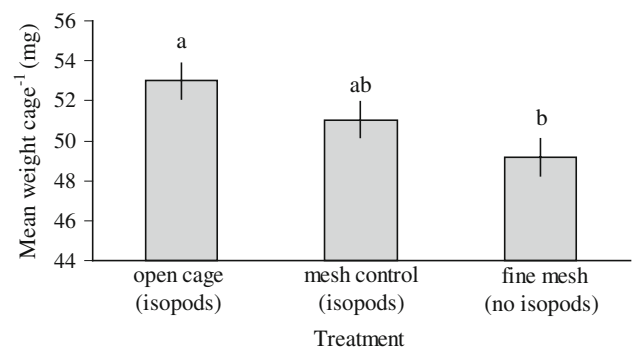


Fig. 4 Mean weight per cage (\pm SE) of *Pomacentrus moluccensis* exposed to; micropredators, fine mesh control, and micropredator exclusion (fine mesh) after 2 weeks on the reef. Means that are significantly different are labelled with different letters (a and b)

experiment, however, it should be noted that fish were not constantly monitored for such occurrences. Fish were not significantly different in length (standard length [SL]) at the start of the experiment. At the end of the week, the percentage growth in SL ($F_{2,59} = 7.08$, $P = 0.002$; Fig. 5a) and fish weight ($F_{2,59} = 4.16$, $P = 0.020$; Fig. 5b) were significantly different among treatments. Fish that were exposed to no gnathiids were found to differ in length and weight from those that had been exposed to two gnathiids (Tukey's HSD tests, $P < 0.05$). Fish exposed to 0, 1 and 2 gnathiids each night weighed an average of 43.66, 41.83 and 38.46 mg, were 10.39, 10.30 and 9.93 mm SL and increased in standard length by an average of 9.91%, 7.28% and 4.39%, respectively. There were no significant differences among treatments in Fulton's K condition index.

Discussion

Exposure to two gnathiids each evening halved the growth in SL for *D. perspicillatus* over the week-long experimental

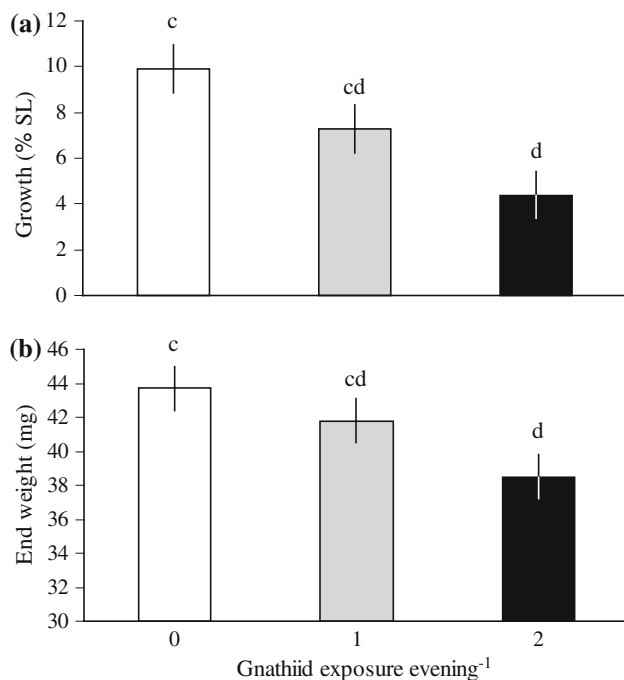


Fig. 5 Mean (\pm SE) (a) growth (standard length), and (b) weight of *Dischistodus perspicillatus* exposed to 0, 1, or 2 *Gnathia falcipenis*, nightly for seven nights. Means that are significantly different are labelled with different letters (c and d)

period. Fish exposed to gnathiids were shorter and weighed less; hence, Fulton's K was unaffected. This is the first demonstration that gnathiids can significantly affect the growth of recruiting coral reef fish in the laboratory, and it highlights the potential for gnathiids to indirectly affect wild fish survivorship tremendously via size selective mortality. However, quantifying the extent to which gnathiids affect the growth of recently settled juveniles in the wild will require more data involving the more commonly found smaller-staged gnathiids, better and more estimates of wild gnathiid prevalence, and perhaps most importantly, turnover rate on fish. Presently, autopsy data from *Pomacentrus amboinensis* and *A. polyacanthus* suggest that gnathiids parasitise >3% of these fishes when sampled during the day, but the proportion of these fishes parasitised each day may be much higher if feeding bouts are brief. Gnathiids parasitising teleosts outside the GBR, such as *Gnathia maxillaris*, *Gnathia africana*, *Gnathia piscivora* and *Paragnathia formica*, have been reported attaching to hosts for 2 h–2 days (Stoll 1962; Paperna and Por 1977; Upton 1987; Smit et al. 2003). On the GBR however, 23% of first and second stage *Gnathia* Type 1 (Grutter et al. 2000b) had fed and detached within 30 min of exposure to adult *Hemigymnus melapterus* (see Grutter 2003) and 81% had detached within 1 h. If gnathiids parasitising juvenile damselfish turn over on fish every 1–2 h, and nocturnal and diurnal prevalence are similar, then daily rates of parasitism could be 12–24 times greater than current 'snapshot' estimates.

Experiment 3 used second and third stage gnathiids, but it could have better approximated typical wild infections by using first and second stages that appear to be more abundant than third stages on juvenile damselfishes (Penfold et al. 2008). Also, the exact number of events of parasitism that took place during the study is unknown. By capturing fish and exposing them to gnathiids in smaller observable containers each night, the number of attachments could have been controlled more precisely, but this would have greatly increased handling stress, possibly obscuring the changes in growth that resulted from parasitism. Using the same focal parasite, Penfold et al. (2008) found that juvenile *A. polyacanthus* ate 39% of gnathiids in interaction trials. Therefore, even though fish exposed to 1 and 2 gnathiids each evening could have each been parasitised up to 7 and 14 times, respectively, it is also possible that fewer events of parasitism may have occurred if fish ate some of the gnathiids, or if some gnathiids did not attach to the fish.

The results of the multiple infection experiment (3) demonstrate that when food availability is controlled precisely, gnathiid micropredation reduces rather than increases fish growth. Therefore, in the two-week caging experiment, the most likely explanation for relatively low growth of fish in the micropredator exclusion treatment was that the fine mesh also excluded food items. Cage changeover took place at dawn and dusk when many zooplankters (food) emerge from the reef (Jacoby and Greenwood 1988), hence, fish in open cages probably had more access to food in the time between cage changeover and nightfall and similarly at sunrise.

The diel caging experiment retrieved very few gnathiids, but it also collected cirrolanid isopods which have not been found on damselfish previously. Without autopsy data for *P. moluccensis* it cannot be determined whether the four gnathiids recovered are an over- or underestimate of wild prevalence. However, it was apparent that micropredation and parasitism were more likely to occur at night in cages. Although caging studies are prone to caging artefacts, in this instance, cages are one of the few tools available for studying nocturnal micropredation and parasitism in the wild, as it is difficult to collect hosts or observe these processes at night. Discovering cirrolanid isopods in cages and witnessing predation on a damselfish was interesting because these isopods are abundant at Lizard Island, but are usually regarded as scavengers (Keable 1995). However, cirrolanids have also been referred to as opportunists or micropredators (Bruce 1981) and they have been known to infest and harm caged adult fishes (Stepien and Brusca 1985). Cirrolanids were observed preying on juvenile *P. moluccensis* in cages, but the extent to which this occurs in the wild is unknown, however, direct mortality due to micropredators is probably rare considering the results of the two-week caging experiment (2).

Although the effect of micropredators on fish growth in experiment 2 was confounded by food availability, the results of this study provided some insight regarding the maximum amount of direct mortality that could be attributed to micropredators. Survivorship in open cages (micropredators present) was not significantly different from that in the other two treatments, and thus, the death of three of the 75 fish cannot be attributed specifically to micropredators. However, it is possible that micropredators were involved. If micropredators were the source of this mortality, it was only 4–4.6% over the two-week caging period. Therefore, it is likely that gnathiids and other isopods carry more influence on survival via indirect effects; by reducing competitive ability, swimming performance and growth, than by direct mortality.

Factors affecting the growth of juvenile coral reef fish include temperature (McCormick and Molony 1995; Spoungue et al. 2006), food availability (McCormick and Molony 1992; Kerrigan 1994), maternal effects (Kerrigan 1997), competition (Jones 1987) and predation (Connell 1998). With the exception of Adlard and Lester (1994), the effects of micropredators on the growth of juvenile coral reef fish have not been examined. This study demonstrates considerable capacity for gnathiids to reduce the growth of juvenile coral reef fish, given the dynamic nature of their infections, but more work is required to determine the magnitude of their effects.

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