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REPORT

Impact of micropredatory gnathiid isopods on young coral reef fishes

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Abstract The ecological role of parasites in the early life-history stages of coral reef fish, and whether this varies between fish with and without a pelagic phase, was investigated. The susceptibility to, and effect of reef-based micropredatory gnathiid isopods on larval, recently settled, and juvenile fishes was tested using two damselfishes (Pomacentridae): *Neopomacentrus azysron*, which has pelagic larvae, and *Acanthochromis polyacanthus*, which does not. When larval and recently settled stages of *N. azysron* and very young *A. polyacanthus* juveniles (smaller than larval *N. azysron*) were exposed to one or three gnathiids, the proportion of infections did not vary significantly among the three host types or between the number of gnathiids to which the fish were exposed. The overall infection was 35%. Mortality, however, differed among the three gnathiid-exposed host types with most deaths occurring in larval *N. azysron*; no mortalities occurred for recently settled *N. azysron* exposed to one or three gnathiids, and *A. polyacanthus* exposed to one gnathiid. Mortality did not differ significantly between larval *N. azysron* and *A. polyacanthus* juveniles, failing to provide support for the hypothesis that reef-based *A. polyacanthus* juveniles are better adapted to gnathiid attack than fish with a pelagic phase. The study suggests that settling on the reef exposes young fish to potentially deadly micropredators. This supports the idea that the pelagic phase may allow young fish to avoid reef-based parasites.

Keywords Coral reef fish larvae · Dispersal · Gnathiidae · Migration · Survival

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Introduction

Mortality during the larval stage of marine fishes is almost absolute. Little is known of the agents of this mortality, but it is suggested that most are eaten by predators (Bailey and Houde 1989; Leis and McCormick 2002). Particular individuals are likely to be more susceptible to predation than others as a result of factors that lower larval body condition, growth, or performance (Searcy and Sponaugle 2000; Bergenius et al. 2002; McCormick and Hoey 2004). These factors potentially include starvation, disease, and parasitism. At present, little is known of the prevalence or importance of these agents on the condition of larval marine fishes, or how the prior history of incidence may influence performance and survival in later life stages (Leis and McCormick 2002).

Parasites are well known to affect the behavior and ecology of adult fishes (see review by Barber et al. 2000). However, it has been predicted that the effect of parasites on fish larvae and juveniles will be magnified due to low body reserves and high metabolism (Strathmann et al. 2002). Surprisingly, almost no research has been done on how parasites affect the survival of the larval and recently

settled stages of coral reef fish. To our knowledge, only two studies have quantified the parasites of larval fish at time of settlement. In French Polynesia, using crest nets to collect recruiting fish, Rigby and Dufour (1996) examined larval groupers, *Epinephelus merra*, for internal parasites. They found that 4% were infected with trypanorynch blastocysts and phyllobothriid metacestodes, encysted on the outside of the gastrointestinal tract. In New Caledonia, using similar collecting techniques, Cribb et al. (2000) found 13 parasite platyhelminth species with 23% of fish from 38 species being infected. There appears to be only one study that experimentally investigated the effect of parasitism on juvenile coral reef fish, which found that infection by the parasitic isopod, *Anilocra pomacentri*, on juveniles of the fish species, *Chromis nitida*, significantly reduced their survivorship and growth in the field (Adlard and Lester 1994). Their results highlight the effects that parasite infection may have on young coral reef fish. However, the role of parasitism in the larval and recently settled stages of coral reef fish is far from clear.

The bipartite nature of the life cycle of demersal fishes means that individuals are likely to be exposed to different threats in the larval and juvenile phase. Indeed, it has been hypothesized that the evolution of dispersal enables terrestrial hosts to avoid debilitating parasites (Clobert et al. 2001). A recent hypothesis proposed that parasitism of fish at the vulnerable larval stage may be a selective force in the evolution of the pelagic phase (Combes 2001; Strathmann et al. 2002). Migration of fish larvae into the water column could break some cycles of parasite transmission through separation of the parents and offspring. It may also lower transmission rates, as larval fish may be less suitable hosts due to their small size and sparse distribution (Strathmann et al. 2002).

Despite the potential importance of parasites to the population dynamics of coral reef fishes, little is known of how parasites affect young fish. The few studies on this subject have focused on the prevalence of parasite infections and found that parasite prevalence and diversity generally increases with age, possibly due to changes in habitat, behavior, diet or increased host size (Rigby and Dufour 1996; Cribb et al. 2000; Sasal 2003). In comparison to the large body of knowledge about parasites of adult reef fish, the understanding of how parasites affect young fish is almost non-existent.

The larvae of gnathiid isopods are some of the most common parasites of adult reef fish (Grutter and Poulin 1998). Gnathiids are reef-based parasites, feeding on host fluid for several hours or days until becoming engorged and returning to the benthos to moult (Monod 1926; Paperna and Por 1977). Gnathiids are mobile temporary parasites classified as micropredators since they do not ingest the whole animal and kill it, but rather take small meals and then leave their prey (host) (Lafferty and Kuris 2002). Micropredators attack multiple prey in the same way as predators, but the impact of a single micropredator on the victim is usually small, like that of a typical parasite. High densities of gnathiids, however, can reduce hematocrit and cause direct mortality, and lengthy attachments can result in tissue damage (reviewed in Jones and Grutter 2005). On coral reefs, larval fishes are relatively small (Leis and Carson-Ewart 1997) compared with gnathiids (Grutter 1994), making it likely that the larvae are more vulnerable to gnathiid attack than the adults. Furthermore, there is evidence that at least one hemogregarine (Apicomplexa) blood parasite appears to be vectored by gnathiids (Davies et al. 2004). Whether gnathiids impact larval or juvenile stage coral reef fishes, however, is unknown.

If the pelagic phase allows fish to avoid reef-based parasites then fish without a pelagic phase should have evolved adaptations to such parasites. Only a few species of coral reef fish have no pelagic larval period and show parental care of juveniles. The damselfish *Acanthochromis polyacanthus* is the only such example on the Great Barrier Reef (GBR) (Leis and McCormick 2002). Parents guard benthic nests and eggs hatch, after 16 days, releasing juveniles. Parents care for these juveniles until they are almost half the size of the adult. If fishes use the pelagic phase to escape micropredatory parasites at a particularly vulnerable time, then *A. polyacanthus* must have some special adaptations to avoid this fate.

This study investigated the effect of gnathiids on the young stages of two coral reef damselfishes (Pomacentridae). The main focus was on the parasite–host interaction at the important transition stage between the pelagic larva and the demersal recently settled fish. Specifically, the aim was to compare the susceptibility of larval and recently settled stages of a damselfish species with a pelagic life cycle (*Neopomacentrus azysron*) with a species that has no pelagic larval stage (*A. polyacanthus*) to reef-based micropredatory gnathiid isopods (*Gnathia* sp.). *N. azysron* was used due to its abundance in light trap catches and on the reef and because, like most coral reef fish, it has a pelagic larval stage. *A. polyacanthus* (Pomacentridae) was used for comparison to *N. azysron* because it is the only fish species at the study site that does not have a pelagic phase (Randall et al. 1997).

Materials and methods

Host collection

Fish were collected at Lizard Island, GBR, Australia (14°40′S, 145°28′E) in January 2004. Late-stage larval *N. azysron* fish were collected with light traps (Meekan

et al. 2001), which were moored away from the reef, over sand. Traps were set out overnight and emptied each morning (0700 h). Reef stages of *N. azysron* and *A. polyacanthus* were collected using hand nets.

Fish were kept in covered holding tanks with constant aeration and water flow. Three fish were randomly selected from holding tanks and transferred to individual 280 ml clear plastic holding containers (115 mm diameter; 50 mm depth), which were filled with filtered (62 μm) seawater and kept at a constant temperature (28–29°C). To provide shelter for the gnathiids that would be released into the containers, a 1 cm^2 piece of mesh (2 mm mesh size) was placed in the center of the container.

Infection

To test the susceptibility of larval *N. azysron*, recently settled *N. azysron*, and very young (about 10 days old, Kavanagh 2000) *A. polyacanthus* to infection by parasites (*Gnathia* sp.), fish were subjected to one of three densities of unfed third stage gnathiids which were collected from a culture (Grutter 2001) of an undescribed species of *Gnathia* sp. (Type 1 in Grutter et al. 2000). Gnathiids were used, as they are common on reef fish (Grutter and Poulin 1998) and the third stages are easy to recognize and handle (Grutter and Heindrikz 1999). The three treatments were: (1) a control with a fish exposed to no gnathiids, (2) a fish exposed to one gnathiid, and (3) a fish exposed to three gnathiids. Filtered seawater was added to the control to simulate adding gnathiids and thus control for any disturbance to the fish. *Gnathia* sp. were added to holding containers one at a time using a 5 ml pipette. Different gnathiids and fish were used in all the trials.

Observations

Fish were observed at 15 min intervals for 240 min or until any *Gnathia* sp. that had attached to fish had dropped off the fish. Records were made of whether the gnathiid was present or absent in the container, was feeding or not feeding on the fish, and of the infection site (head, pectoral/caudal/dorsal fin, body, mouth, gills), and status of fish (dead or alive). After fixing in 80% ethanol, fish were weighed (g) and their standard length (SL) measured (mm). Binary logistic regressions were performed using the software R 1.9.0. (R Development Core Team 2006) to compare the proportion of fish infected and uninfected, dead and alive after exposure to either one or three gnathiids among the three host types (recently settled *N. azysron*, juvenile *N. azysron*, very young *A. polyacanthus*); and level of gnathiid exposure (0, 1, 3 gnathiids) within groups. Results of these analyses are reported as the change in deviance (Δdev) as each term is added. As a measure of susceptibility, the time taken for *Gnathia* sp. to attach to and feed on fish among the three host types was compared using Kaplan–Meier survival analysis with the software JMP IN 4.

Results

Gnathia sp. attached to and fed on both of the host species tested, *N. azysron* and *A. polyacanthus* (Table 1). Not all

Table 1 Percentage of fish infected with one to three gnathiids and percent mortality when exposed to three different levels of parasitic *Gnathia* sp. for juvenile *Acanthochromis polyacanthus* and *Neopomacentrus azysron*

Species	*n*	Total % of fish infected	Total % fish mortality	Mean weight (g) ± SE	Mean SL (mm) ± SE
Acanthochromis polyacanthus	51			0.038 ± 0.001	10.7 ± 0.07
Very young (Demersal)					
Exposed 0	17	–	0	0.038 ± 0.001	10.7 ± 0.11
Exposed 1	17	23.5	0	0.038 ± 0.001	10.7 ± 0.11
Exposed 3	17	41.2	11.8	0.038 ± 0.001	10.7 ± 0.14
Neopomacentrus azysron	75			0.055 ± 0.001	12.4 ± 0.08
Larval (Pelagic)					
Exposed 0	25 (24)	–	0	0.053 ± 0.002	12.3 ± 0.16
Exposed 1	25 (22)	32.0	12.0	0.055 ± 0.002	12.4 ± 0.13
Exposed 3	25 (24)	56.0	16.0	0.056 ± 0.002	12.7 ± 0.14
Recently settled (Demersal)	75			0.070 ± 0.002	13.1 ± 0.14
Exposed 0	25	–	0	0.067 ± 0.003	13.0 ± 0.25
Exposed 1	25	28.0	0	0.072 ± 0.003	13.3 ± 0.20
Exposed 3	25	28.0	0	0.070 ± 0.004	13.1 ± 0.26

Note: Mean weight and standard length (SL) ± SE (standard error) are given. *n* = number of trials. Note that five larval *N. aysron* were lost after the experiment and so could not be weighed nor measured; actual samples sizes of fish used to calculate mean weight and SL are in parentheses

fish exposed to gnathiids became infected with a gnathiid. When exposed to one or three gnathiids, the overall proportion of infections that occurred was 0.35 and the proportion did not vary significantly between the three host types (larval *N. azysron*, recently settled *N. azysron*, and very young *A. polyacanthus*) or the number of gnathiids to which the fish were exposed. Further, there was no evidence that the effect of the exposure level varied between the species. Table 2 shows the number of infections that occurred when fish were exposed to three gnathiids. Whether infection by one gnathiid influenced the probability of subsequent infections was tested. For each host type, the proportions of fish infected by 0, 1, 2, or 3 gnathiids did not differ from the proportions expected if each infection event was independent (see Table 2).

Weight and standard length differed significantly among species (Table 1) (ANOVA, Weight: $F_{2,193} = 108$, $P < 0.0001$ and SL: $F_{2,193} = 112.36$, $P < 0.0001$) and all pairs differed significantly for both variables (Tukey–Kramer $P < 0.05$). Recently settled *N. azysron* were significantly heavier and longer than larval *N. azysron* and very young *A. polyacanthus.* Larval *N. azysron* were also larger than very young *A. polyacanthus*.

Gnathiids attached to various sites on the fish including the gills, behind the eyes, mouth, body, and on the dorsal, caudal and pectoral fins. On first contact with a gnathiid, fish would often become agitated and try to shake off the parasite. Often, swimming ability was impaired when *Gnathia* sp. attached to individuals, particularly on the fins or gills. This occurred in all the stages tested. However, once gnathiids had begun feeding, fish would remain stationary and rest against the bottom or the side of the experimental container. If the site of attachment was either the caudal or pectoral fin, fish would show difficulty in balancing, and consequently in swimming.

Mortalities occurred for larval *N. azysron* exposed to both one (12.0%) or three (16.0%) gnathiids and very young *A. polyacanthus* exposed to three gnathiids (11.8%) (Table 1). No mortalities occurred for recently settled *N. azysron* exposed to gnathiids. Among fish exposed to gnathiids, the proportion of mortalities was significantly different among the three host types (Δdev = 9.29, df = 2, $P = 0.0096$), with most deaths occurring in larval *N. azysron*. There was no significant difference in mortality between larval *N. azysron* and very young *A. polyacanthus* exposed to gnathiids (Fisher's Exact test). Mortality did not differ significantly between fish exposed to 1 or 3 gnathiids and there was no evidence that the effect of exposure level on mortality differed among the host types. Gnathiid infection was associated with all but one of the fish mortalities; this latter mortality involved a recently settled *N. azysron* exposed to one gnathiid but which did not become infected. No mortalities occurred in control fish not exposed to gnathiids. For those fish exposed to three *Gnathia* sp. that became infected, the mortality rate did not vary significantly according to the number of gnathiids infecting fish (Table 2); similarly, there was no difference in the mortality between the three host types (Table 2).

Individual third stage *Gnathia* sp. either remained stationary against the surface of the container or swam around before attaching to the fish between 15 and 180 min after the start of the experiment. Once attached, their feeding time ranged between 15 and 420 min. The time taken for gnathiids to attach to fish exposed to one gnathiid (Fig. 1) did not differ significantly among larval *N. azysron*, recently settled *N. azysron*, or very young *A. polyacanthus*,

Table 2 Total number of *Gnathia* sp. infections and mortalities when exposed to three *Gnathia* sp. under laboratory conditions for juvenile *Neopomacentrus azysron* and *Acanthochromis polyacanthus*

No. *Gnathia* sp. infections	*N. azysron*				*A. polyacanthus*	
	Larval		Recently settled		Very young	
	Number	Total fish mortality	Number	Total fish mortality	Number	Total fish mortality
0	11	0	18	0	10	0
1	8	1	5	0	6	1
2	4	2	2	0	0	0
3	2	1	0	0	1	1
Probability of infection per gnathiid	0.293		0.12		0.176	
Deviance for H_0 of independent infection	3.34 ($P = 0.19$)		1.63 ($P = 0.44$)		5.57 ($P = 0.06$)	

Note: If each infection event is independent with probability P, the expected proportions of fish with 0, 1, 2, and 3 infections should follow a binomial expansion with terms $(1 - P)^3$, $3P(1 - P)^2$, $3(1 - P)P^2$, P^3 . This P, shown in table, was estimated for each host type by minimizing the deviance (also shown, 2 df) from the independence model

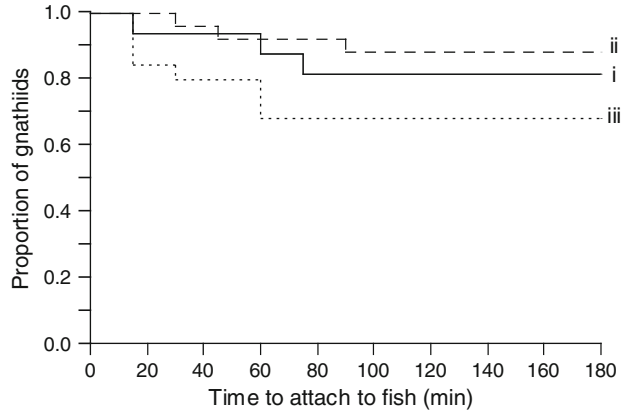

Fig. 1 *Neopomacentrus azysron* and *Acanthochromis polyacanthus*. Time taken (min) for third stage *Gnathia* sp. to attach to (i) larval *N. azysron* ($n = 25$), (ii) recently settled *N. azysron* ($n = 25$), and (iii) very young *A. polyacanthus* ($n = 25$)

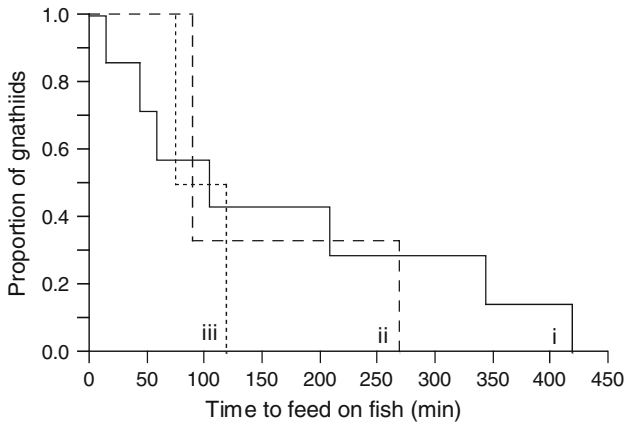

Fig. 2 *Neopomacentrus azysron* and *Acanthochromis polyacanthus*. Time taken for third stage *Gnathia* sp. to feed on (i) larval *N. azysron* ($n = 7$), (ii) recently settled *N. azysron* ($n = 3$), and (iii) very young *A. polyacanthus* ($n = 2$)

ranging between 15 and 180 min. Similarly, there were no significant differences in the time it took gnathiids to feed on fish (Fig. 2) among larval *N. azysron*, recently settled *N. azysron*, or very young *A. polyacanthus*, ranging from 15 to 420 min.

Discussion

This study demonstrates that larval fish are susceptible to infection by isopod micropredators (*Gnathia* sp.) and that a single infection by a *Gnathia* sp. can kill a larval fish in the laboratory. In contrast, no mortalities were observed for recently settled fish infected with *Gnathia* sp. Most likely a greater host size increased the ability of recently settled fish to survive an attack by *Gnathia* sp. Thus, *N. azysron* settle at a stage which coincides with a size when they are physically capable of withstanding an attack by a micropredator.

The much greater parasite-to-host size ratio in recently settled fish compared to adult fish, however, may still pose a problem for recently settled fish; even though parasitism may not cause mortality it may increase stress, increasing their susceptibility to predation or causing a reduction in competitive fitness (Rigby and Dufour 1996). For example, the behavior of fish was often altered and their swimming ability impaired when *Gnathia* sp. attached to individuals, particularly on the fins or gills. Such abnormal behavior in fish is likely to be a signal used by predators that the fish are not fit, increasing the likelihood that such individuals will be preyed upon.

Whether gnathiids infect young fish in the wild has not yet been determined for *N. azysron* but infection has been found for some *A. polyacanthus* juveniles (Penfold et al. in press). The likelihood of detecting such events is rare, as gnathiids are found in low numbers on small fish (Grutter and Poulin 1998) and they remain on fish only while feeding, which for the fish types tested here ranged from 15 to 420 min while in adult *Hemigymnus melapturus* it is about 60 min (Grutter 2003).

Juvenile *A. polyacanthus*, which lacks a pelagic larval phase, was also infected by *Gnathia* sp. under experimental conditions. However, whereas 11.8% of *A. polyacanthus* exposed to three gnathiids and infected by one or three parasites died, no mortalities resulted from exposure to, and infection by, a single *Gnathia* sp. This suggests that more than one *Gnathia* sp. is needed to kill very young *A. polyacanthus*. However, these results should be interpreted cautiously as mortality was not significantly affected by level of exposure. Furthermore, juveniles under experimental conditions were not cared for by parents, a behavior which occurs naturally on the reef (Robertson 1973). In the wild, parents defend juveniles from small predators for several months until they are 30–40 mm SL (Allen 1975; Nakazono 1993), which includes the size range of fish sampled here (10.0–11.5 mm SL). More information is needed on whether parental care plays a role in preventing or reducing gnathiid attacks on offspring.

It is interesting that despite the significantly smaller body size of *A. polyacanthus* compared with larval *N. azysron* (10.0–14.0 mm SL), the rate of mortality of *A. polyacanthus* from exposure to *Gnathia* sp. attacks did not differ significantly to that of larval *N. azysron*, although the 95% confidence interval for the odds ratio is broad and thus consistent with substantial differences in mortality between the species in either direction. Based on their size, *A. polyacanthus* used in the experiment were approximately 10 days old (Kavanagh 2000) while larval *N. azysron* were approximately 23 days old (based on *Neopomacentrus cyanamos* larval duration; Wilson and McCormick 1999).

Thus, despite their greater size and age, there was no evidence that larval *N. azysron* were less vulnerable to gnathiids than smaller and younger *A. polyacanthus.* The converse pattern of a significantly lower rate of mortality in *A. polyacanthus* smaller than larval *N. azysron* would have provided support for the idea that *A. polyacanthus* juveniles, all of which remain on the reef when young, are physically better adapted to surviving an attack by a gnathiid than fish that have a pelagic phase. Possibly, rather than being physically superior, young *A. polyacanthus* may instead rely on parental care behavior (Allen 1975; Nakazono 1993) to reduce the effects of such parasites. For example, parents are planktivorous (Thresher 1985) and may eat gnathiids in the water column while they seek for hosts. Or, possibly, parents may modify the substratum making it unfavorable for gnathiids which spend most of their life in the benthos (Smit and Davies 2004).

The feeding time of *Gnathia* sp. on fish was variable and in most cases was longer (up to 420 min) than the 60 min it takes for gnathiids to become engorged and drop off when feeding on adult wrasse *H. melapterus* (Grutter 2003). Some fish appeared highly stressed while gnathiids fed on them. Fish that behave abnormally as a result of parasitic infection are at a greater risk of predation (Lafferty 1999), and thus young fish being attacked by gnathiids may have a greater risk of being eaten. Since gnathiids on such fish would likely also be eaten, it may be costly for gnathiids to feed on small fish. Further studies are needed to investigate the prevalence of gnathiids and other micropredators on young fish, whether micropredators have a preference for larger hosts, and whether fish (and their gnathiids) are more likely to be eaten when being attacked by gnathiids.

Whether larval fish settlement behavior is influenced by gnathiid abundance patterns is unclear. There is much seasonal, lunar, diel, and spatial variation in the abundance patterns of larval gnathiids (reviewed in Jones and Grutter 2007). Although initially thought to mainly emerge or attack fish at night, fine-scale temporal studies are increasingly suggesting that gnathiids in the Caribbean (Chambers and Sikkel 2002; Sikkel et al. 2004, 2006) and the GBR (Grutter 1999) tend to be more abundant during the crepuscular periods. Thus, the risk of attack by a gnathiid seems highest around dawn and/or sunset. Although many fish settle at night, mostly based on studies of pomacentrids, a large proportion also settle during the day (Leis and McCormick 2002). Information on the fine-scale diel patterns of settlement for the majority of fishes, however, is lacking (Leis and McCormick 2002). Diel patterns of settlement in fish are assumed to be shaped by predation, generally thought to be highest during crepuscular periods, intermediate during the day, and lowest at night (Leis and McCormick 2002). However, the only empirical test of this hypothesis found that predation rates were highest at dusk and night and lowest during the day, raising the question of whether temporal patterns in larval settlement are indeed driven by temporal patterns of predation (Danilowicz and Sale 1999). Holbrook and Schmitt (1997) found that most settlement occurred between midnight and dawn when predation risk was low, with predation risk highest during the first half of the night and high at dawn. Booth (1991) found higher settlement at night compared with crepuscular periods. Dufour and Galzin (1993) found more fish arriving on the reef at dusk and at night, mainly on moonless nights. Clearly, more studies are needed on the link between gnathiid abundance and larval fish settlement patterns to determine the role of parasites in influencing the timing of fish settlement.

In conclusion, larval and very young reef-based juveniles were susceptible to potentially fatal attack by gnathiids. These findings highlight the ecological importance of parasitism on very young coral reef fish. Since gnathiids need to leave their host for the benthos after each meal in order to moult to the next stage (Monod 1926), their transmission from host to host is unlikely in the pelagic environment. Such parasites are unlikely to be as easily evaded on the reef compared to larger predators, due to their small size (Grutter 1994), which allows them to invade microhabitats inaccessible to larger predators. Living on the reef therefore likely exposes young fish to potentially deadly micropredators. By avoiding the reef, fish can avoid such micropredators. This study supports the idea that the pelagic phase may allow young fish to avoid reef-based parasites (Combes 2001; Strathmann et al. 2002).

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