



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 trypanorhynch blastocysts and phyllobothriid metacestodes, encysted on the outside of the gastrointestinal tract. In New Caledonia coral reefs, larval fishes are relatively small (Leis and Carson-Ewart 1997) compared with gnathiids (Grutter 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 (Combès 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 (Strathman et al. 2002). 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 (Combès 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 (Strathman 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; Sasa 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 (Mondak 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 fish were collected at Lizard Island, GBR, Australia (14°44'00"S, 145°28'E) in January 2004. Late-stage larval fish were collected with light traps (Meekan

et al. 2001), which were moored away from the reef, over containers one at a time using a 5 ml pipette. Different sand. Traps were set out overnight and emptied each morning (0700 h). Reef stages *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 (0.2 µm) seawater and kept at a constant temperature (28.0°C). To provide shelter for the gnathiids that would be released into the containers, a 1 cm<sup>2</sup> 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 (*Gnathiasp.*), fish were subjected to one of three densities of unfed third stage gnathiids which were collected from culture (Grutter 2001) of an undescribed species (*Gnathia sp.* (Type 1 in Grutter et al. 2000). Gnathiids were used, as they are common on reef fish (Grutter and Pod1998) 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 tanks

**Observations**

Fish were observed at 15 min intervals for 240 min or until any *Gnathiasp.* 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 *N. azysron*) and level of gnathiid exposure (0, 1, 3 gnathiids) within groups. Results of these analyses are reported as the change in deviance (Δ<sub>dev</sub>) as each term is added. As a measure of susceptibility, the time taken for *Gnathiasp.* 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**

*Gnathiasp.* attached to and fed on both of the host species (*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 gnathiid 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
<i>Acanthochromis polyacanthus</i>	51			0.038 ± 0.001	10.7 ± 0.07
Very young (Demersal)					
Exposed 0	17	0	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
<i>Neopomacentrus azysron</i>	75			0.055 ± 0.001	12.4 ± 0.08
Larval (Pelagic)					
Exposed 0	25 (24)	0	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	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. azysron* 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 on the caudal or pectoral fin, fish would show difficulty in swimming. 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) and there was no evidence that the effect of exposure level

Weight and standard length differed significantly among species (ANOVA, Weight:  $F_{2,193} = 108$ ,  $P < 0.0001$  and SLF:  $F_{2,193} = 112.36$ ,  $P < 0.0001$ ) 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 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 recently settled N. azysron or very young A. polyacanthus

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

No. Gnathia sp. infections	N. azysron		Recently settled		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

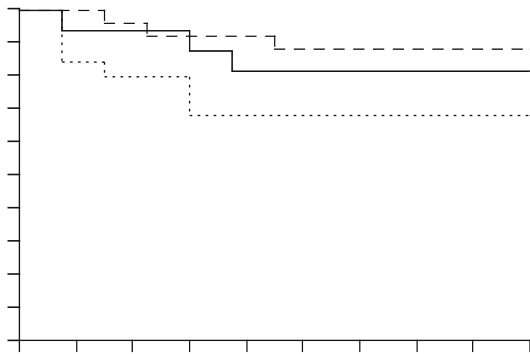


Fig. 1 *Neopomacentrus azysron* and *Acanthochromis polyacanthus*. Time taken for third stage *Gnathiasp.* to attach to (i) larval *N. azysron* (n = 25), (ii) recently settled *N. azysron* (n = 25), and (iii) very young *A. polyacanthus* (n = 25)

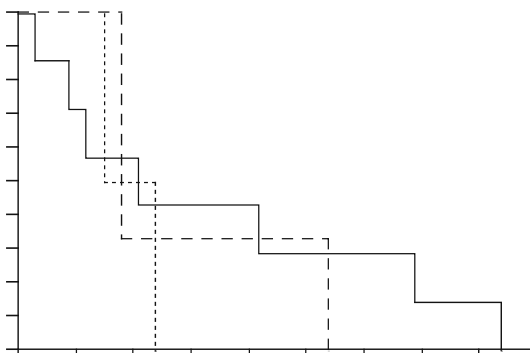


Fig. 2 *Neopomacentrus azysron* and *Acanthochromis polyacanthus*. Time taken for third stage *Gnathiasp.* to feed on (i) larval *N. azysron* (n = 7), (ii) recently settled *N. azysron* (n = 3), and (iii) very young *A. polyacanthus* (n = 2)

ranging between 15 and 180 min. Similarly, there were no significant differences in the time it took gnathiaids to feed on *Psh* (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 *Psh* are susceptible to infection by isopod micropredators (*Gnathiasp.*) and that a single infection by a *Gnathiasp.* can kill a larval *Psh* in the laboratory. In contrast, no mortalities were observed for recently settled *Psh* infected with *Gnathiasp.* Most likely a greater host size increased the ability of recently settled *Psh* to survive an attack by *Gnathiasp.* 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 *Psh* compared to adult *Psh*, however, may still pose a problem for recently settled *Psh*; 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 *Psh* was often altered and their swimming ability impaired when *Gnathiasp.* attached to individuals, particularly on the fins or gills. Such abnormal behavior in *Psh* is likely to be a signal used by predators that the *Psh* are not fit, increasing the likelihood that such individuals will be preyed upon.

Whether gnathiaids infect young *Psh* 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 gnathiaids are found in low numbers on small *Psh* (Grutter and Poulin 1998) and they remain on *Psh* only while feeding, which for the *Psh* types tested here ranged from 15 to 420 min while in adult *Hemigymnus melapturus* is about 60 min (Grutte 2003).

Juvenile *A. polyacanthus* which lacks a pelagic larval phase, was also infected by *Gnathiasp.* under experimental conditions. However, whereas 11.8% of polyacanthus exposed to three gnathiaids and infected by one or three parasites died, no mortalities resulted from exposure to, and infection by, a single *Gnathiasp.* This suggests that more than one *Gnathiasp.* 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 (Roberts 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 *Psh* 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 *Gnathiasp.* 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 cyanomos* 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 *N. azysron* 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 Davie 2004).

The feeding time of gnathiids on *N. azysron* 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 *Thalassoma melapterus* (Grutter 2003). Some *N. azysron* appeared highly stressed while gnathiids fed on them. Fish that behave abnormally as a result of parasitoinfection are at a greater risk of predation (Lafferty 1999), and thus young *N. azysron* being attacked by gnathiids may have a greater risk of being eaten. Since gnathiids on such *N. azysron* would likely also be eaten, it may be costly for gnathiids to feed on small *N. azysron*. Further studies are needed to investigate the prevalence of gnathiids and other micropredators on young *N. azysron*, whether micropredators have a preference for larger hosts, and whether *N. azysron* (and their gnathiids) are more likely to be eaten when being attacked by gnathiids.

Whether larval *N. azysron* 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 *N. azysron* 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 *N. azysron* 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 *N. azysron* species, however, is lacking (Leis and McCormick 2002). Diel patterns of settlement in *N. azysron* 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 Stoen 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 *N. azysron* 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 *N. azysron* settlement patterns to determine the role of parasites in influencing the timing of *N. azysron* 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 *N. azysron*. 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 *N. azysron* to potentially deadly micropredators. By avoiding the reef, *N. azysron* can avoid such micropredators. This study supports the idea that the pelagic phase may allow young *N. azysron* to avoid reef-based parasites (Combs 2003; Strathmann et al. 2002).

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